RESPONSE OF UNGRAFTED AND GRAFTED GRAPEVINE CULTIVARS AND ROOTSTOCKS (*VITIS* SP.) TO WATER STRESS

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Abstract

Aims: The responses of two *Vitis vinifera* cultivars (Cardinal and Superior Seedless) and two rootstocks (110R and SO4) to drought, the effect of grafting and the interactions of scion/rootstock were investigated.

Methods and results: The vines were subjected to a progressive water stress in greenhouse controlled conditions. At the end of the water stress treatments, physiological analyses were carried out (stem water potential, dry matter production, soluble sugars, proline as well as ions Na^+ and K^+). Drought was expressed by the drop of the stem water potential in the stressed vines as compared to their controls. Furthermore, tolerance and sensitivity were linked to the accumulation of soluble sugars and proline as well as the equilibrium of K^+ and Na^+ in the leaves.

Conclusion: When ungrafted, Cardinal was more tolerant to water stress than Superior Seedless. The grafted vines exhibited more vigour, moreover, the combination of Cardinal with SO4 and Superior Seedless with 110R revealed to be the advantageous associations under water stress.

Significance and impact of study: This work has been carried out to investigate the differential responses of grapevine cultivars to drought stress and the impact of grafting under water shortage conditions.

Key words: *Vitis*, water stress, water potential, osmolytes

Résumé

Objectif : Dans ce travail, nous avons étudié la réponse de deux variétés de vigne (Cardinal et Superior Seedless) et deux porte-greffes (110R et SO4) à la sécheresse, ainsi que l'effet du greffage et les interactions greffon/porte-greffes sous cette contrainte.

Méthodes and résultats : Les vignes, conduites sous serre contrôlée, ont été soumises à un stress hydrique progressif par cycles de déshydratation suivis par un arrêt total d'irrigation. À la fin des traitements hydriques, des analyses physiologiques ont été réalisées (potentiel hydrique caulinaire, production de matière sèche et dosage des sucres solubles, de la proline, ainsi que des éléments minéraux Na^+ et K^+). Le stress hydrique s'exprime chez les vignes par la baisse du potentiel hydrique. La tolérance et la sensibilité se sont associées chez les vignes stressées à la variation des teneurs des feuilles en sucres solubles et en proline comparée aux feuilles bien hydratées, ainsi qu'à l'équilibre entre les teneurs foliaires en K^+ et Na^+.

Conclusion : La variété Cardinal non greffée s'est montrée plus tolérante au stress hydrique que la variété Superior Seedless. Les résultats obtenus montrent une vigueur plus élevée chez les vignes greffées soumises à la contrainte hydrique. Les associations de Cardinal à SO4 et de Superior Seedless à 110R se sont révélées plus avantageuses en conditions stressantes que les deux autres combinaisons.

Signification et impact de l'étude : Ce travail a été établi afin d'explorer les réponses différentielles des variétés de vignes au déficit hydrique ainsi que l'impact du greffage dans les conditions d'alimentation restreinte en eau.

Mots clés: *Vitis*, stress hydrique, potentiel hydrique, osmolytes

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INTRODUCTION

Water availability is becoming more and more limited, especially in the south Mediterranean areas. The lack of adequate moisture, leading to water stress, is a common feature in rainfed areas (Cabuslay, 2002). Prolonged water shortage affects all of the metabolic processes and often results in a severe reduction of plant productivity (Taylor 1996).

Although table grapes are generally irrigated, grapevine is regularly exposed to seasonal water limitations. In vineyards where water supply is not restricted, vegetative growth becomes excessive and can compete for assimilates with berries. On the other hand, severe water shortage decreases the production of assimilates and affects the yield and the quality (Pellegrino *et al.*, 2006). In this context, the responses of grape to drought were largely investigated (Patakas *et al.*, 1997a, b; 1998; 1999; 2002; Düring, 1984; Mériaux *et al.*, 1981; Iacono *et al.*, 1998; Peterlunger and Iacono 2000; Davies *et al.* 2000; Pellegrino *et al.*, 2006…). It was established that the response of grapevine cultivars to water stress depends on several factors such as the genotype, the drought intensity, the soil and climate characteristics as well as the developmental stage (Gómez del Campo *et al.*, 2005).

Vines are often grafted on different hybrid rootstocks and the response to water stress depends considerably on the combination scion-rootstock (Dry *et al.*, 2001, Fisarakis *et al.*, 2001). Rootstock influences the scion behaviour and affects its vigour and yield (Ezzahouani and Williams, 2005; Paranychianakis *et al.*, 2004) as well as its tolerance to drought (Düring, 1994). Indeed, the cultivars Müller Thurgau and Rhine Riesling improved their drought tolerance when they were grafted on hybrid rootstocks (Iacono and Peterlunger, 2000). The rootstocks revealed to play a major role in determining the scion's water status in a dry year. Similarly, 1103 and SO4 rootstocks improved the productivity of Alphonse Lavallée grapevines (Ezzahouani and Williams, 2005).

Among the adaptive responses of plants to water deficit, the accumulation of proline and soluble sugars seems to play osmotic and homeostatic roles (Patakas *et al.*, 1997 a, b; Bray 1997; Flexas *et al.*, 1998; Shultz 1996; Ndung'u *et al.*, 1997). Besides, sugars are involved in stabilising membranes and proteins (Mohamed *et al.*, 2000, Folkert *et al.*, 2001); whereas, proline is involved in scavenging hydroxyl radicals (Wang *et al.*, 2004), signal regulation (Maggio *et al.*, 2002) and membrane protection (Rudolph *et al.*, 1985; Mansour 1998). Ionic accumulation (K^+, Na^+, Cl^-) may control water retention by initiating stomatal closure and acting as major osmoticums (Patakas *et al.*, 2002; Wang *et al.*, 2003; Hosy *et al.*, 2003). Potassium is a macronutrient which plays important cellular roles such as charge equilibrium, activation of enzymatic reactions and vacuolar osmotic pressure. Nevertheless, an excessive accumulation of Na^+ is disadvantageous (Maathius *et al.*, 1999).

In Tunisia, there is very little information on the behaviour of grapevine subjected to drought as well as the effects of grafting on the vine response to stress. Thus, the present work report the response of two ungrafted and grafted vine cultivars as well as two rootstocks to water deficit and try to elucidate the relationship between the accumulation of osmolytes and the tolerance of grapevine to drought.

MATERIALS AND METHODS

1. Plant material and culture conditions

Two *Vitis vinifera* cultivars (Cardinal and Superior Seedless) and two *Vitis* hybrids 110R (*V. berlandieri* X *V. rupestris*) and SO4 (*V. berlandieri* X *V. riparia*) were studied.

Self rooted vines from both cultivars and rootstocks were obtained from dormant cuttings. Several combinations between cultivars and rootstocks (Cardinal/110R, Cardinal/SO4, Superior Seedless/110R, Superior Seedless/SO4) were established. Both grafted and self rooted vines were cultivated in 10 L pots filled with a sandy loam soil in a controlled greenhouse (Temperature regime: 24 °C day/18 °C night, Relative Humidity: 60-70 %, Photoperiod: 16 h, Minimal Light Intensity: 25 $W.m^{-2}$).

Two months prior to stress application, the vines were periodically irrigated to saturation (100 % of soil equivalent humidity calculated from a representative sample of the soil as the saturating amount of water for the soil, administrated on three times per week) until they reached an adult stage (30 nodes approximately, expanded leaves). The vines were randomly divided into two equivalent sets, the first continued to receive a regular irrigation (control), whereas the second (stressed) received a weekly water volume equivalent to 20 % of field capacity, administrated at the same time as the controls. Within four weeks, irrigation frequency of stressed vines was limited to once every two weeks. Finally, it was completely stopped for one month. The control vines continued to receive a regular irrigation.

2. Physiological and biochemical analyses

a- Growth parameters

One month after withholding irrigation, plants were harvested and fresh weight of the different parts from each plant (leaf, stem and root) were determined. Total leaf area was measured using a planimeter (LiCor Li-3000A).

Then, plant material was dried at 60 °C for 48 hs and the dry weight was measured. To elucidate more precisely the modifications on the plant development, ratios of root dry weight (RDW) over shoot dry weight (SDW) were calculated.

b - water potential

Midday stem water potential was measured during the last day of the experiment (12 weeks of drought application) using a pressure chamber equipped with a digital manometer (Scholander *et al.*, 1964). Water potential is expressed as the mean of three measurements on three adjacent vines from stressed and control sets. Stem sections, composed of one node and one fully expanded leaf, were cut in the medium of the principal stem (between the 15th and the 20th node) and water potential was immediately measured.

c- Sugar content

Leaf soluble sugar content was determined according to the method of Morris (1948) using the anthrone reagent. Fully expanded leaves, collected at the end of the experiment and dried at 60 °C for 48 hs, were extracted with ethanol 80 % at 80 °C for 30 mn. After a 10 mn centrifugation at 6000 $tr.mn^{-1}$, the supernatant was used for analysis. Twenty five µL of supernatant was combined with anthrone reagent and heated at 100 °C for 10 mn. Sugar content was determined by measuring the absorbance at 640 nm with a spectrophotometer (Ultrospec 2000, Pharmacia). The absorbance values were regressed as concentrations (mmol sugar. g^{-1}DW) according to a standard curve previously established, based on a set of glucose standard solutions.

d- Proline content

Free proline was extracted and quantified according to Bates method (1973), using 0.5 g of fresh fully expanded leaves collected at the day of the final harvesting. Extraction was made in aqueous sulfosalicylic acid (3 % w/v). After a 20 mn centrifugation at 6000 $tr.mn^{-1}$, soluble proline was mixed with ninhydrin reagent at 100 °C before to be selectively solubilized in 2 ml toluene. The absorbance of the organic phase was monitored at 520 nm with a spectrophotometer (Ultrospec 2000, Pharmacia). Proline concentration, expressed as mmol proline. g^{-1}FW, was determined with reference to a standard concentration curve.

e- Mineral ion content (Na^+, K^+, CL^-)

Dry plant material (leaf, stem, root) was ground to a fine powder and twenty-five mg of each sample were extracted with 50 mL of 0.7 % nitric acid during 48 hrs. K^+ and Na^+ were directly monitored in the extracts using an absorption atomic spectrophotometer (AAS vario 6) and expressed as $mmol.g^{-1}$DW. Chloride ion content was determined on the same nitric extracts using a potentiometer equipped with a chloride-selective electrode.

f- Statistical treatment of data

Data from all of the above measurements, obtained from sets of 12 plants per treatment for each genotype, were subjected to a factorial ANOVA analysis and means were separated by Duncan's significant difference test. Statistical analysis were made for each cultivar, ungrafted and grafted, control versus stressed, and for the two rootstocks (control versus stressed), separately.

RESULTS AND DISCUSSION

1. Growth and interaction scion-rootstock

a- Biomass

In the irrigated vines, the combination of the scion Cardinal with 110R and SO4 root systems resulted in a significant increase of the scion's vigour (vs. ungrafted) as expressed by the increase of the shoot dry matter (leaf and stem, table 1). This impact was slightly but not significantly verified in Superior Seedless. In the same manner, the association of Cardinal to 110R appears more effective in the optimal conditions (Table 1).

However, under drought stress, this situation was significantly modified. The root system of SO4 seems to confer more stability and vigour to the combination with Cardinal. The rootstock 110R is, to some extent, more suitable with Superior Seedless; although no significant differences were recorded for the production of dry matter in stems and roots (Table 1).

In our experiments, stress was applied gradually by cycles of dehydrations followed by a withholding of irrigation. Drought, although imposed for a prolonged time period, did not seem to affect significantly the grafted cultivars, but affected the production of plant dry matter only in the own rooted *Vitis* genotypes. The decline of growth was significantly exhibited in rootstocks as compared to cultivars (Table 1). Moreover, the growth of the 110R rootstock, normally more vigorous than SO4 in standard conditions, was significantly more altered.

The ratio between root and shoot dry weights (RDW/SDW) decreased in Cardinal and 110R (figure 1). Although it did not provide significant differences in all cases, this ratio was slightly more affected when the cultivars were grafted on 110R than on SO4, especially for Cardinal. In addition, when comparing the two rootstocks, total plant dry matter of SO4 was less affected than 110R (96.9 % and 60 % of respective controls, table 1). Besides, the ratio RDW/SDW was significantly

Table 1 - Effect of water stress on dry matter production in two grafted and ungrafted grapevine cultivars and two rootstocks (*Vitis* sp.)

Values represent standard deviation between treatments at P < 0,.05, superscript letters represent statistical differences between controls and stressed analysed for each cultivar (grafted and ungrafted) and the two rootstocks, separately. NS : non significant, *: P < 0,05

			Leaf	Stem	Root	Plant Dry Weight (PDW)
Cardinal	ungrafted	Control	4,40 ±0,6 *bc	8 ,33 ±0,5 *bc	7,87 ±0,8 *a	20,6 ±0,5 NS b
		Stressed	4,70 ±0,4 *bc	5,60 ±0,3 *c	4,60 ±1,6 *b	14,9 ±1,5 NS b
	/110R	Control	7,65 ±1,1 *a	27,60 ±4,7 *a	7,95 ±1,3 *a	43,2 ±5,0 NS a
		Stressed	2,98 ±0,3 *c	14,93 ±1,5 *b	2,85 ±0,4 *b	20,8 ±1,2 NS b
	/SO4	Control	3,98 ±0,6 *bc	13,28 ±3,3 *b	1,85 ±0,7 *b	19,1 ±1,9 NS b
		Stressed	5,70 ±0,9 *ab	12,80 ±1.7 *b	2,30 ±0,6 *b	20,8 ±1.6 NS b
Superior Seedless	ungrafted	Control	4,13 ±1,4 *a	15,37 ±1,2 NS ab	5,33 ±0,9 NS a	24,8 ±1,7 NS ab
		Stressed	2,13 ±0,5 *b	12,17 ±1,2 NS a	3,57 ±0,1 NS a	17,9 ±0,2 NS b
	/110R	Control	3,75 ±1,0 *a	20,33 ±6,1 NS a	4,60 ±0,9 NS a	28,7 ±2,5 NS a
		Stressed	3,20 ±0,4 *ab	18,90 ±4,1 NS ab	4,03 ±0,6 NS a	26,1 ±5,9 NS ab
	/SO4	Control	4,60 ±0,3 *a	19,38 ±3,9 NS ab	4,48 ±0,7 NS a	28,5 ±1,4 NS a
		Stressed	2,26 ±0,3 *b	19,26 ±4,0 NS ab	4,08 ±1,0 NS a	25,6 ±3,5 NS ab
Rootstocks	110R	Control	11,10 ±2,0 *a	26,38 ±4,3 *a	21,64 ±1,8 *a	59,1 ±6,7 *a
		Stressed	8,92 ±1,6 *b	18,44 ±1,7 *b	8,52 ±2,1 *b	35,9 ±2,9 *b
	SO4	Control	5,36 ±0,6 *c	15,68 ±2,8 *b	8,30 ±1,3 *b	29,3 ±3,6 *bc
		Stressed	6,48 ±0,8 *c	14,28 ±3,1 *b	7,64 ±1,3 *b	28,4 ±3,5 *c

steady in SO4 in comparison with 110R in which, a significant decrease was registered (figure 1).

In the majority of the studies concerning plant's growth under drought, the application of water stress affects plants' growth and development (Dry and Loveys, 1999; Bessis *et al.*, 2000). Grapevine did not escape to this rule (Bessis *et al.*, 2000). Indeed, in our study, the prolonged water shortage caused a decline of growth in the majority of the genotypes, as revealed by the decrease of the dry matter production in the stressed vines compared to their respective controls.

Rootstocks are more vigorous than *Vitis vinifera* cultivars in normal conditions and the grafting has been reported not only to increase vine vigour (Paranychianakis *et al.*, 2004), but also the production and the quality of grape (Ezzahouani and Williams, 2005).

Besides, the grafting reduced rather the root dry matter in the combinations. This result can be attributed to the competition for assimilates between the scion and the roots, a limiting factor to determine the most suitable combinations between *Vitis vinifera* scions and rootstocks. Generally, the limitation of the root elongation under drought is commonly observed in many plant species such as maize and tomato (Liptay *et al.*, 1998) as well as in grapevine (Del Campo *et al.*, 2005) and can decrease in turn the distribution of assimilates between roots and canopy (Mapfumo *et al.*, 1994). This ratio is a key element in the appreciation of the efficiency of the root system in supporting canopy water supply (Iacono *et al.*, 2000).

Thus, vigour improvement in the associations would be attributed to the intrinsic potentialities of both scion and rootstock as to their mutual interactions.

b) Leaf area

Under the unrestricted water supply conditions, the cultivar Superior Seedless exhibited a more expanded leaf area compared to the cultivar Cardinal and a better vigour was registered in 110R rootstock as compared to SO4. The grafting of Cardinal on 110R rootstock improved the scion's leaf expansion more than on SO4 rootstock. However, Superior seedless leaf area was slightly reduced on both rootstocks (figure 2).

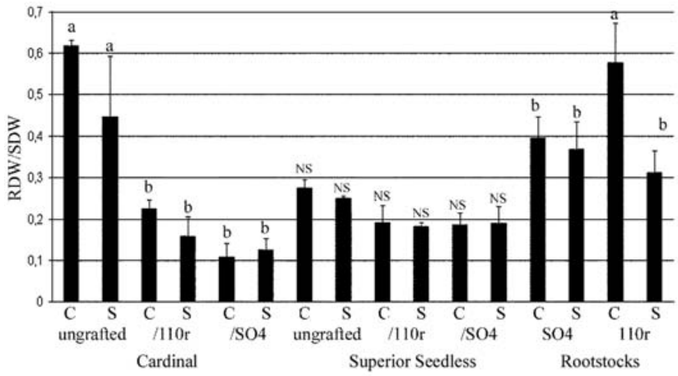

Figure 1 - Modifications of the ratio RDW/SDW in grapevines submitted to prolonged water stress.

Vertical bars present ± standard deviations of the mean and different letters represent significant difference at the 5 % level using Duncan's test between controls and stressed of each cultivar (ungrafted and grafted) and both rootstocks, separately.

Under drought conditions, a reduction of the leaf area was registered for all of the genotypes. Nevertheless, the leaf system of Cardinal self rooted was not significantly affected. Moreover, a significant reduction in the total leaf area was registered for the combination of Cardinal with 110R (18 % of the controls) and for Superior Seedless (33 % of the controls, figure 2). For the rootstocks, the total leaf area of 110R was significantly altered by drought (53 % of the control), as compared to SO4 (81 % of the control, figure 2).

Although all the vines were cultivated under the same conditions and submitted to drought at similar developmental stage, the leaf expansion varied considerably among genotypes. According to data given in figure 2, this variation seems apparent among both cultivars (Cardinal and Superior Seedless) and rootstocks (110R and SO4).

The leaf system, which mediates water losses *via* transpiration and photosynthetic gas exchanges, seemed to be affected by the prolonged drought application. Indeed, water supply limitations induce abscission and reduction of the leaf area (Münns, 2000; Gómez-Del-Campo *et al.*, 2003). Thus, the decline of the leaf area in these genotypes is not only due to the reduction in biomass production but also, and partially, to the leaf abscission mediated by hormonal signalling.

The reduction of the leaf area was widely reported under water deficit conditions (Winkel and Rambal, 1993). This reduction concerns more the leaf area than the leaf dry matter, suggesting a marked impact of water stress on leaf expansion rather than on matter production and photosynthetic assimilation (Yong Mok, 2001).

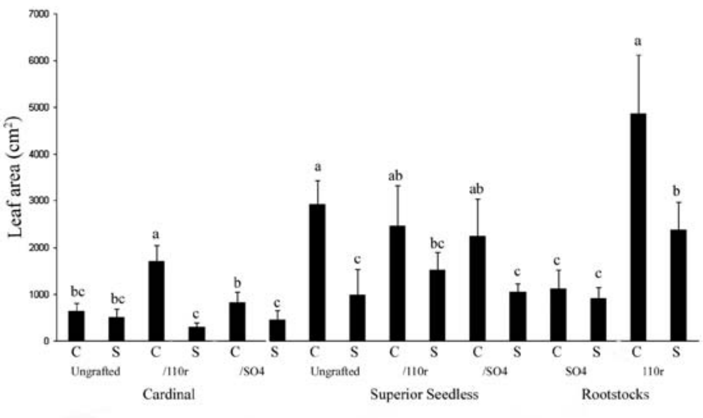

Figure 2 - Total leaf area of *Vitis* genotypes submitted to prolonged water stress.

Vertical bars present ± standard deviations of the mean and different letters represent significant difference at the 5 % level using Duncan's test between controls and stressed of each cultivar (ungrafted and grafted) and both rootstocks, separately.

2. Stem water potential

The stem water potential measured in the vines that received an optimal irrigation ranged between -0.4 and -0.8 MPa (figure 3). Conversely, under stress, the water potential dropped significantly, except in the 110R rootstock (-1.1 MPa, figure 3). Stem water potential of SO4 rootstock decreased significantly under stress (-1.9 MPa, against -0.75 MPa in controls). Besides, in the stressed Cardinal vines, the water potential dropped more when ungrafted (-1.37 MPa), than when grafted on SO4 (-1.15 MPa) or 110R (-1.0 MPa). According to water potential levels, Superior Seedless was more dehydrated than Cardinal, whatever grafted or not (stem water potential levels ranging between -1.5 and -1.8MPa, figure 3).

At midday, transpiration is at its highest level and stem water potential becomes the most convenient for a reliable estimation of water deficit (Choné *et al.*, 2001). Stem water potential was reported to be an indicator of dehydration and water status degradation (Düring, 1984).

Among the stressed vines, Cardinal registered the minimal stem water potential decrease when compared to the sensitive cultivar Superior Seedless. This suggests that Cardinal avoided damaging the water status *via* a minimal decrease of the water potential. The conservation of leaf system expansion is an additional potential that helps plants to limit the transpirational loss. Furthermore, Cardinal was reported to be able to adjust its intrinsic anatomical properties under severe environmental stresses such as high temperatures, through leaf blade thickening (Ben Salem-Fnayou *et al.*, 2005). Among the grafting combinations, Superior Seedless displayed the lowest levels of water potential, especially when associated to the rootsystem of SO4. Cardinal vines lowered less their water potential on both rootstocks (figure 3). The variability of the water potential modifications under drought are in accordance with Grzesiak *et al.* data (2006), who reported that drought stress lowers less the water potential within the resistant plants than within the sensitive ones. On the other hand, water status is highly influenced by the leaf system expansion, a limiting factor for water status homeostasis.

4) Osmolyte accumulation

a) Total Soluble sugars

Accumulation of leaf soluble sugars varied among the different genotypes. The cultivar Cardinal accumulated significantly soluble sugars (150 % of the control), however, superior seedless exhibited alteration of the accumulation of sugars (40 % of the controls, table 2). The increment of the soluble sugars amounts in the leaves was similar for both cultivars. Among grafting

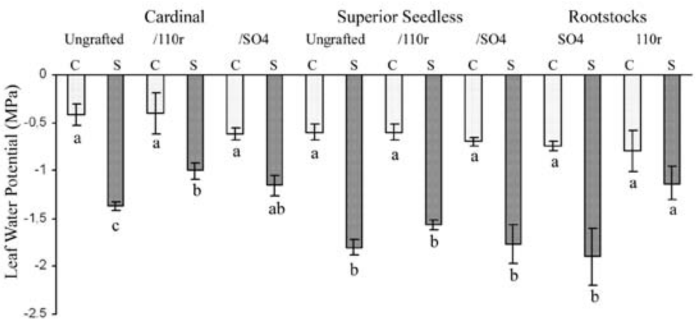

Figure 3 - Water potential of water deficit stressed and well watered grapevines cultivated under controlled conditions.

Vertical bars present ±standard deviations of the mean and different letters represent significant difference at the 5 % level using Duncan's test between controls and stressed of each cultivar (ungrafted and grafted) and both rootstocks, separately.

combinations, modifications of the accumulation of soluble sugars did not vary considerably, except of the combination of superior Seedless with 110R, were a decrease was recorded.

b) Proline

The contents of leaves in proline are presented in table 2. Generally, the well hydrated vines accumulated low amounts of free proline. However, under stress, some genotypes accumulated this osmolyte in higher amounts. Indeed, the accumulation of proline was significant in Superior Seedless grafted on 110R (4 times higher than controls) or on SO4 (6 times higher than controls), and in the self rooted Cardinal vines (5 times higher than controls, table 2).

According to these results, Cardinal accumulated both proline and soluble sugars, while Superior seedless accumulated the lowest contents of these compatible solutes in the leaves under the water deficit constraints.

The accumulation of these organic solutes plays important roles in the tolerance to osmotic stresses. According to Iacono *et al.* (2000), plants that maintain a high photosynthetic activity under water stress conditions allow metabolic stability and are therefore able to grow and adjust their metabolism processes according to the stressful situation. Thus, sugar accumulation during desiccation can be an efficient indicator of tolerance to this stress. On the contrary, the reduction of total soluble sugars concentration in the leaves of sensitive vines could be partially attributed to a reduced photosynthetic activity (Patakas *et al.*, 2002). As far as proline is concerned, its accumulation in plants was known to be specifically associated to abiotic stresses (Iannuci *et al.*, 2001; Folkert *et al.*, 2001; Sanchez *et al.*, 1998; Taylor 1996; Stines *et al.*, 1999; Harrak *et al.*, 1999). The concentration of

Table 2 - Leaf contents on soluble sugars and free proline in two grafted and ungrafted grapevine cultivars and two rootstcoks (*Vitis* sp.) submitted to prolonged water stress in greenhouses controlled conditions.

Values represent standard deviation between treatments at P < 0,05, letters represent statistical differences between controls and stressed analyzed for each cultivar (grafted and ungrafted) and the two roostocks, separately

			Soluble sugars ($mmol.g^{-1}DW$)	Proline ($mmol.g^{-1}FW$)
Cardinal	ungrafted	Control	**0,29** ±0,02 b	**0,37** ±0,01 b
		Stressed	**0,45** ±0,03 a	**1,51** ±0,72 a
	/110R	Control	**0,40** ±0,06 a	**0,32** ±0,01 b
		Stressed	**0,41** ±0,03 a	**0,39** ±0,07 b
	/SO4	Control	**0,39** ±0,02 a	**0,30** ±0,01 b
		Stressed	**0,33** ±0,03 b	**0,41** ±0,04 b
Superior Seedless	ungrafted	Control	**0,43** ±0,14 a	**0,48** ±0,29 b
		Stressed	**0,15** ±0,06 d	**0,38** ±0,21 b
	/110R	Control	**0,41** ±0,08 ab	**0,51** ±0,14 b
		Stressed	**0,20** ±0,10 cd	**2,02** ±1,16 a
	/SO4	Control	**0,36** ±0,08 ab	**0,27** ±0,14 b
		Stressed	**0,30** ±0,05 bc	**1,79** ±1,00 a
Rootstocks	110R	Control	**0,39** ±0,09 b	**0,26** ±0,04 b
		Stressed	**0,42** ±0,04 a	**0,34** ±0,02 a
	SO4	Control	**0,34** ±0,03 b	**0,28** ±0,01 b
		Stressed	**0,46** ±0,09 ab	**0,36** ±0,02 a

Table 3 - Potassium and sodium accumulation in the leaves, stemps and roots of two grated and ungrated grapevine cultivars and two rootstocks (*Vitis* sp.) exposed to prolonged water stress (in mmol.g^{-1}DW)

Letters represent statistical differences between controls and stressed calculated for each cultivar (grafted und ungrafted) and both rootstocks, separately. NS : non signficiant, *P< 0.05

			Na$^+$			K$^+$		
			Leaf	Stem	Root	Leaf	Stem	Root
Cardinal	ungrafted	Control	2,42 *b	2,40 *b	2,52 *b	0,83 *c	0,36 *b	0,78 NS
		Stressed	2,61 *a	2,44 *b	2,76 *ab	1,41 *a	0,35 *b	0,86 NS
	/110R	Control	2,15 *b	2,59 *a	2,85 *a	1,11 *b	0,72 *a	0,98 NS
		Stressed	2,20 *b	2,60 *a	2,93 *a	1,11 *b	0,73 *a	1,01 NS
	/SO4	Control	2,05 *b	2,51 *ab	2,64 *ab	0,93 *bc	0,58 *a	0,82 NS
		Stressed	2,10 *b	2,62 *a	2,88 *a	1,03 *bc	0,69 *a	0,95 NS
Superior Seedless	ungrafted	Control	1,26 *b	1,45 NS	1,31 NS	1,24 *bc	0,86 *a	0,60 NS
		Stressed	3,59 *a	1,24 NS	1,30 NS	1,72 *a	0,79 *a	0,37 NS
	/110R	Control	1,01 *b	1,13 NS	1,25 NS	1,02 *c	0,88 *a	0,35 NS
		Stressed	1,51 *b	1,17 NS	1,59 NS	1,38 *b	0,84 *a	0,34 NS
	/SO4	Control	1,20 *b	1,19 NS	1,12 NS	1,16 *bc	0,77 *a	0,41 NS
		Stressed	1,13 *b	1,45 NS	2,42 NS	1,18 *bc	0,61 *b	0,37 NS
Rootstocks	110R	Control	2,11 NS	2,22 *b	2,62 NS	0,87 *b	0,59 *a	0,79 NS
		Stressed	2,21 NS	2,42 *a	2,62 NS	1,13 *a	0,63 *a	0,94 NS
	SO4	Control	2,16 NS	2,26 *b	2,55 NS	0,61 *b	0,44 *b	0,77 NS
		Stressed	2,14 NS	2,27 *b	2,61 NS	0,77 *c	0,30 *c	0,65 NS

proline in the leaves of the tolerant cultivar Cardinal was higher than that of the sensitive cultivar Superior Seedless. These results are in accordance with those of Wang *et al.* (2004) who reported that the increase of proline in the leaves under salt stress was linked to plant resistance.

4. Distribution of Na^+, K^+ and Cl^- ions

In the control vines, the contents of Na^+ in the leaves ranged between 1 and 2.4 mmol.g^{-1}DW. They are generally higher than those of K^+ (table 3). Cardinal cultivar (self rooted or grafted) as well as the rootstocks 110R and SO4 accumulated higher Na^+ amounts in their leaves than Superior Seedless ungrafted and grafted. Following the stress application, Na^+ distribution in the different vine organs was not affected and remained steady in the majority of genotypes. Nevertheless, an accumulation of Na^+ in the leaves was recorded in Superior Seedless self rooted (3.59 mmol.g^{-1}DW, table 3).

Unlike Na^+, a significant increase of K^+ was recorded in the leaves of the stressed vines; especially in Cardinal, Superior Seedless and 110R (table 3).

Drought affected neither the content nor the distribution of Cl^- in the different organs (data not shown). Besides, Cl^- amounts were much lower than those of Na^+ and K^+ ions and did not exceed 0.5 mmol.g^{-1}DW.

Thus, mineral contents were analysed to investigate ionic transports among the different organs of grapevines and to follow up the eventual modifications in the leaf uptake. K^+ is one of the most common osmoticums that increases significantly under water stress (Patakas *et al.*, 2002). This ion was accumulated in both Cardinal and Superior Seedless; the accumulation of Na^+ in the leaves of Superior Seedless was higher than that of K^+. As these two cultivars present different tolerance potentials, the accumulation of Na^+ in Superior Seedless leaves, as a sign of ionic transport dysfunction, would be attributed to the susceptibility of this cultivar to drought. In the rootstocks, as well as the grafted cultivars, the ionic composition remained steady in the different organs. These results confirm the efficiency of the root system in the mineral uptake and homeostasis, especially under water shortage.

CONCLUSION

The response of grapevine to the prolonged drought stress was variable among the cultivars and rootstocks as well as among the grafting associations. Cardinal was able to maintain a steady water status, showed the least pronounced growth deterioration and leaf area reduction and accumulated organic metabolites. It was considered as a resistant cultivar to drought. Superior Seedless showed a different and reverse behaviour. Its growth and metabolic machinery were inefficient when exposed to the stress. It was classified as susceptible to drought. Among rootstocks, 110R revealed to be the most vigorous in normal conditions but responded negatively to the water stress. The grafting seemed to be dependent on the intrinsic potentialities of both variety and rootstock but also on their interactions under drought. The excessive vigour seems to be restrictive for vine survival when exposed to a severe abiotic stress like prolonged water deficit.

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