

Influence of water status on mineral composition of berries in 'Grenache Noir' (*Vitis vinifera* L.)

F. ETCHEBARNE^{1),2)}, H. OJEDA²⁾ and A. DELOIRE^{1),3)}

¹⁾INRA, UMR 1083 Sciences for the Enology, Montpellier, France

²⁾INRA, UE 0999 Pech Rouge, Gruissan, France

³⁾SupAgro, Plant Sciences Department, Montpellier, France

Summary

The influence of vine water status on the seasonal changes of fresh weight, dry matter and the levels of potassium and calcium in grape-berries on field vines of 'Grenache Noir' (*Vitis vinifera* L.), was studied over a two-year period. Two levels of water status, irrigated and non-irrigated, were investigated using a single level of total leaf surface – each primary shoot was confined to ten leaves, one grape bunch, and the secondary shoots were removed as they appeared. The mineral element contents were determined separately in different fruit compartments, i.e. the skin, flesh and seeds. Potassium and calcium accumulate independently of one another, but their seasonal change in the fruit and their final quantities in the berry depend principally on plant water status. The accumulation of potassium parallels the change in fruit fresh weight; approximately 50 % of the final content was accumulated pre-veraison and loading continued during berry ripening. This report shows that a small quantity of calcium may accumulate throughout fruit ripening phases in situations where water supply is not a limiting factor. These results imply that fruit xylem is functioning partially during ripening. Moreover, in both water status situations, the quantity of calcium in the skin increases during ripening, which suggests apoplastic and/or symplastic migration in the berry.

Key words: Berry, *Vitis vinifera*, potassium, calcium, water status, fresh weight, dry matter.

Introduction

Mineral ions are of prime importance in determining the fruit nutritional value. Grape berries are very rich in potassium which is an essential macronutrient for grapevine and grape berry growth and development (MPELASOKA *et al.* 2003). This cation is an important compound which is involved in must and wine composition (MPELASOKA *et al.* 2003, MORRIS *et al.* 1983). In the tissue of many fruits, calcium is one of the minerals believed to be an important factor governing the quality of fruit storage. The calcium content of berry skins is linked to the fruit's resistance to pathogenic bio-agressors (CHARDONNET and DONÈCHE

1995). It is known that mineral elements are transported by the xylem and phloem vascular systems; while the water flow in many fleshy fruits changes from mainly xylemic to being mainly phloemic during development (CHATELET *et al.* 2008). In grapes (*Vitis vinifera* L.), this transition appears to occur around véraison (LANG and THORPE 1989, GREENSPAN *et al.* 1994, 1996, ROGIERS *et al.* 2001, MATTHEWS and SHACKEL 2005).

The objective of this study was to investigate the influence of vine water status on the accumulation of potassium and calcium in whole berries and in their compartments during berry growth and ripening. The experimental conditions of the study were such that the leaf-fruit ratio was balanced at the level of the primary shoot for all vines studied. Changes in the levels of these mineral elements in terms of their quantity per berry provides new information on the kinetics of mineral element accumulation in the grape berry of vines under conditions of water deficit and of pre- and post-veraison functioning of the fruit xylem and phloem.

Material and Methods

Vineyard experimental design: This study was carried out over two consecutive years (2006-2007) on young vines of 'Grenache Noir' (clone 134) grafted onto R-110 (planted in 2002) grown on clay limestone soil (dry Mediterranean limestone marl) at the Pech Rouge experimental vineyard at INRA-Gruissan, France. The vineyard is planted in a north-south orientation; the vinestocks are 1 x 3 m apart, trained in lyre, pruned in single cordon and watered by a drip irrigation system. Two levels of water status, irrigated and non-irrigated, were investigated using a single level of total leaf surface – each primary shoot was confined to ten leaves, one grape bunch, and the secondary shoots were removed as they appeared. Each treatment comprised four identical blocks within which 7 plants per block were used for sampling. The choice as to which plants would be sampled in each block was based on the weight of pruned wood and the trunk circumference in order to sample from plants of uniform vigor. Irrigation commenced from bunch closure onwards (stage 32, COOMBE 1995).

Determination of plant water status: The evolution of the pre-dawn leaf water potential (Ψ_{pd}) was monitored from berry-set to ripening (stages

29 and 38, COOMBE 1995) using the pressure chamber technique (SCHOLANDER *et al.* 1965). Measurements were carried out on 6 plants per treatment every 7-15 d according to climate conditions and the phenological stage of development.

Determination of meteorological data: Meteorological data were obtained from an automatic weather station, located at 43° 08' 35" latitude north and 3° 7' 59" longitude east (Pech Rouge experimental vineyard). The data are given as mean daily values.

Total leaf area and yield: Uniform growth of primary shoots was obtained by topping at ten primary leaves and by removal of secondary shoots (side shoots) from berry-set onwards. Second level bunches were removed to leave only one bunch per shoot. Total leaf area was determined by measuring the length of the main nervure of leaf, using the quadratic relationship defined for Grenache Noir at the end of vegetative growth, and which is $-y = 0.0134L^2 - 0.0762L$, $r^2 = 0.971$ - where 'L' is the total length of the main nervure of leaf at the time of measurement (LEBON *et al.* 2006). Total leaf area per vine was calculated by the product of "y", the number of leaves (10) and the number of shoot per plant (14).

Berry sampling: Two hundred berries – cut at the pedicel base – were sampled in quadruplicate, for each treatment at regular intervals from bunch closure onwards (stage 32, COOMBE 1995) until harvest-ripe (stage 38, COOMBE 1995) in 2006. In 2007, berry sampling began at pea-size (stage 31, COOMBE 1995) until the point when berries were considered to be over-ripe (stage 39, COOMBE 1995).

Quantification of K⁺ and Ca⁺⁺: Berry mineral elements were measured from the lag phase (before véraison: stage 33, COOMBE 1995) in 2006 and from pea-size stage (stage 31, COOMBE 1995) in 2007. Ten berries from each of the four replicates of each treatment were selected from the major class – the class containing the greatest number of berries, according to the volume – in order to quantify the mineral elements (K⁺ and Ca⁺⁺). The berries were rinsed in ultra-pure water, dried and frozen at -20 °C until analysis of the elements in each compartment (skin, flesh, seeds). For this purpose, the fresh and dry weights were determined. The latter was obtained af-

ter oven-drying at +80 °C (to constant weight) for periods varying between 48 and 168 h according to the phenological stage of the berry. The mineral elements were extracted from the dry matter (skin, flesh, seeds) by agitation in 10 ml HCl 0.1N for 7 d. For samples taken after véraison, 20 ml HCl was used for the skin and flesh as the mineral element concentrations are greater at this stage. The extracts were allowed to precipitate naturally, except in the case of post-veraison flesh samples for which sedimentation was obtained by centrifugation at 8000 rpm for 5 mins. Potassium was quantified by atomic emission spectroscopy and Ca⁺⁺ by atomic absorption spectroscopy using a spectrometer (Thermo S4 AA system, England).

Statistical analysis: An analysis of variance was performed using STATGRAPHICS Plus 4 program (StatPoint Inc., Northern Virginia, USA). Differences between treatment means were compared using the LSD (Fisher's least significant differences) test ($p = 0.05$).

Results and Discussion

Evaluation of water status: In 2006, the measurements of pre-dawn leaf water potential (Ψ_{pd}) during plant growth showed differences in water status between the irrigated (I) and non-irrigated (NI) treatments (Fig. 1 a). The I treatment maintained a water status close to -0.2 MPa until 60 DAA which then dropped to -0.3 to -0.5 MPa, as a result of a period of severe drought during August – corresponding to the stages of véraison-ripening. In parallel, the Ψ_{pd} values for the NI treatment dropped to approximately -0.9 MPa some days after véraison (66 DAA), which corresponds to a water stress situation, and consequently at 70 DAA, the plot was supplied with 8 mm of water to improve the general water status of the vines. This watering and the 43 mm of rain that fell on 78 DAA re-hydrated the plants, particularly for the NI treatment. In 2007, the seasonal change of pre-dawn leaf water potential showed significant differences between treatments during berry ripening (Fig. 1 b) but in contrast, Ψ_{pd} values were higher than in the 2006 experiments. Both treatments maintained high Ψ_{pd} values until véraison (about -0.2 MPa) and then values of the NI treatment became progressively lower towards the

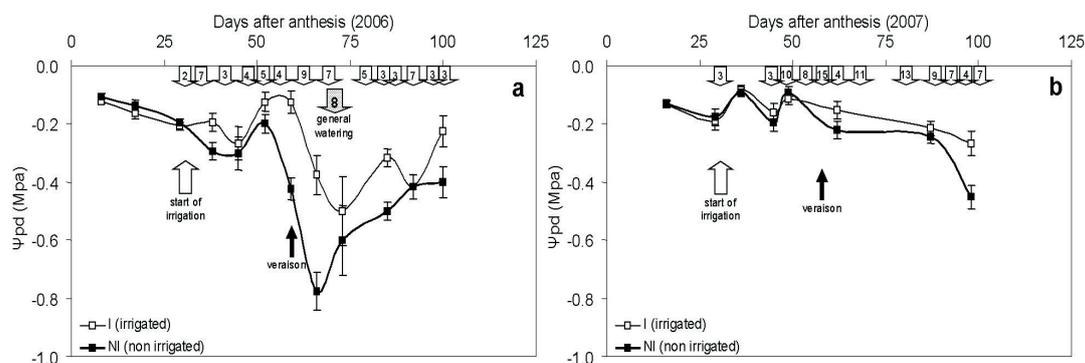


Fig. 1: Characterisation of pre-dawn leaf water potential (Ψ_{pd}) of 'Grenache Noir' from vines undergoing different irrigation treatments over the two-year experimental period (2006-2007). Arrows on the y-axis indicate the moment and the millimetres of water supplied by irrigation. Bars represent \pm limits of significance ($p = 0.05$).

Table 1

The water balance difference between 2006 and 2007 shows a water surplus of 101.9 mm for 2007 during the flowering to maturity period

Phenological stages	mean T° (°C)		ETP (mm)		Rainfall (mm)		Irrigation (mm)		Water balance (mm) = rainfall + irrigation - ETP	
	2006	2007	2006	2007	2006	2007	2006	2007	2006	2007
Flowering-veraison (0-59 daa)	23.4	20.8	360.9	311.2	6.5	58	25	24	-329.4	-229.2
Veraison-ripeness (60-100 daa)	22.8	22.0	214.7	196.5	50.5	12	48	70	-116.2	-114.5
Flowering-ripeness (0-100 daa)	23.1	21.4	575.6	507.7	57	70	73	94	-445.6	-343.7
difference between 2007 and 2006		-1.7		-67.9		+13		+21		+101.9

end of ripening (about -0.4 MPa at 100 DAA), which corresponds to moderate water deficit. This observed year-to-year variation is principally due to an overall water surplus of 101.9 mm in 2007, relative to 2006, which may be observed from meteorological data presented in Tab. 1.

Total leaf area measurements: The I and NI treatments in 2006 and 2007 were comparable in

Table 2

Total leaf area measurements of 'Grenache Noir' for 2006 and 2007. The training system is the Lyre

Season	2006 - 2007
No. leaves/primary shoot	10
No. primary shoot/vine	14
No. grappe/vinestock	14
SFT/primary shoot (m ²)	0.14
SFT/vine (m ²)	2

terms of the number of leaves and total leaf area per primary shoot and per plant (Tab. 2). The principal measured variable during fruit ripening was therefore vine water status (Fig. 1).

Berry growth and development: The increase in berry fresh weight showed a lag phase just prior to veraison. In 2006 it reached a maximum at 73 DAA (for NI) and 84 DAA (for I) and in 2007 for both treatments around 80 DAA. Veraison (berries soften and start to colour) took place at 60 DAA. In 2006 water deficit caused a significant reduction in fresh weight (Fig. 2 a1), dry weight (Fig. 2 b1) and berry water content (Fig. 2 c1). As water deficit was mild in 2007, there was no difference between treatments in terms of dry weight (Fig. 2 a2), but the greater availability of soil water in 2007 is reflected in fresh weight (Fig. 2 b2) and berry water content (Fig. 2 c2).

Accumulation of K⁺ and Ca⁺⁺ in whole berries: The accumulation of K⁺ and Ca⁺⁺ in grape-berries was affected by the vine water sta-

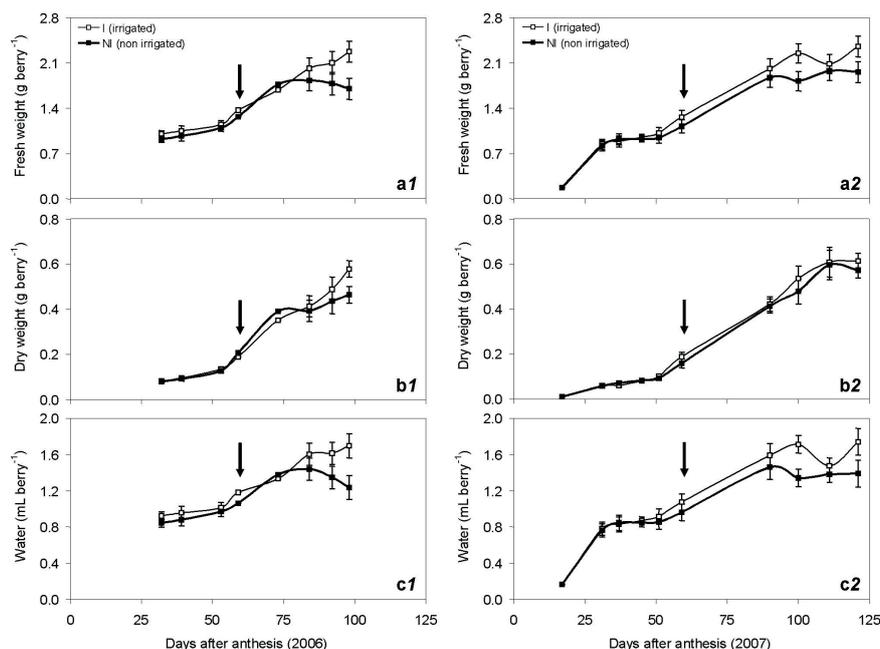


Fig. 2: Evolution of fresh (a) and dry (b) weight in g berry⁻¹ and the water level (c) of the berry in mL berry⁻¹, during growth and ripening ('Grenache Noir') from vines undergoing different irrigation treatments over the two-years (2006-2007). Arrows indicate veraison and bars represent ± limits of significance ($p = 0.05$).

tus and by the year-to-year variation. The difference in K^+ and Ca^{++} accumulation was most marked during the post-veraison period. The berry content of K^+ showed a steady upward trend throughout pre- and post-veraison periods. This work confirms the results of previous reports on this subject, namely that K^+ is the principal cation accumulated by the berry over the entire growth period (POSSNER and KLIEWER 1985, DONÈCHE and CHARDONNET 1992, SCHALLER *et al.* 1992, CREAMY *et al.* 1993, OLLAT and GAUDILLÈRE 1996, ROGIERS *et al.* 2000). However, this study also shows that the accumulation of K^+ in the berry seems to be linked to the accumulation of fruit fresh weight in relation with plant water status and to fruit dry weight in relation with vine photosynthetic activity. K^+ is the principal osmotically active cation in the berry's phloem and would appear to contribute to phloem flow (loading of soluble sugars), thus helping to establish an osmotic gradient between the leaves (source) and the berries (sink) (VÉRY and SENTENAC 2003). Before veraison (60 DAA) the berry accumulates approximately 50 % of total K^+ measured at maturity. In 2006 the rate of K^+ accumulation pre-veraison (until 60 DAA) was

0.03 - 0.04 $mg \cdot berry^{-1} \cdot d^{-1}$ for I and NI, respectively. Post-veraison (until 100 DAA) the accumulation rate was 0.09 - 0.04 $mg \cdot berry^{-1} \cdot d^{-1}$ for I and NI, respectively (Fig. 3 a1). In 2007, K^+ accumulation pre-veraison was similar to 2006, but the post-veraison accumulation was similar for both I and NI - approximately 0.04 - 0.05 $mg \cdot berry^{-1} \cdot d^{-1}$ respectively (Fig. 3 a2). The rate of accumulation of K^+ by the berry during ripening was related to plant water status. Unlike K^+ , the accumulation of Ca^{++} in 2006 occurred principally during the pre-veraison period, with 83 % of total Ca^{++} present at veraison for I and no Ca^{++} accumulation for NI post-veraison (Fig. 4 a1). In 2007 the Ca^{++} accumulation at veraison was around 70 % of total values for both treatments (Fig. 4 a2). Several studies have shown that Ca^{++} is accumulated in the berry throughout its development (SCHALLER *et al.* 1992, OLLAT and GAUDILLÈRE 1996, ROGIERS *et al.* 2000, CABANNE and DONÈCHE 2003). However, others indicate that the accumulation of Ca^{++} ceases after veraison (HRAZDINA *et al.* 1984, POSSNER and KLIEWER 1985, CREAMY *et al.* 1993). The results of this study suggest that the Ca^{++} content per berry may exhibit a steady upward

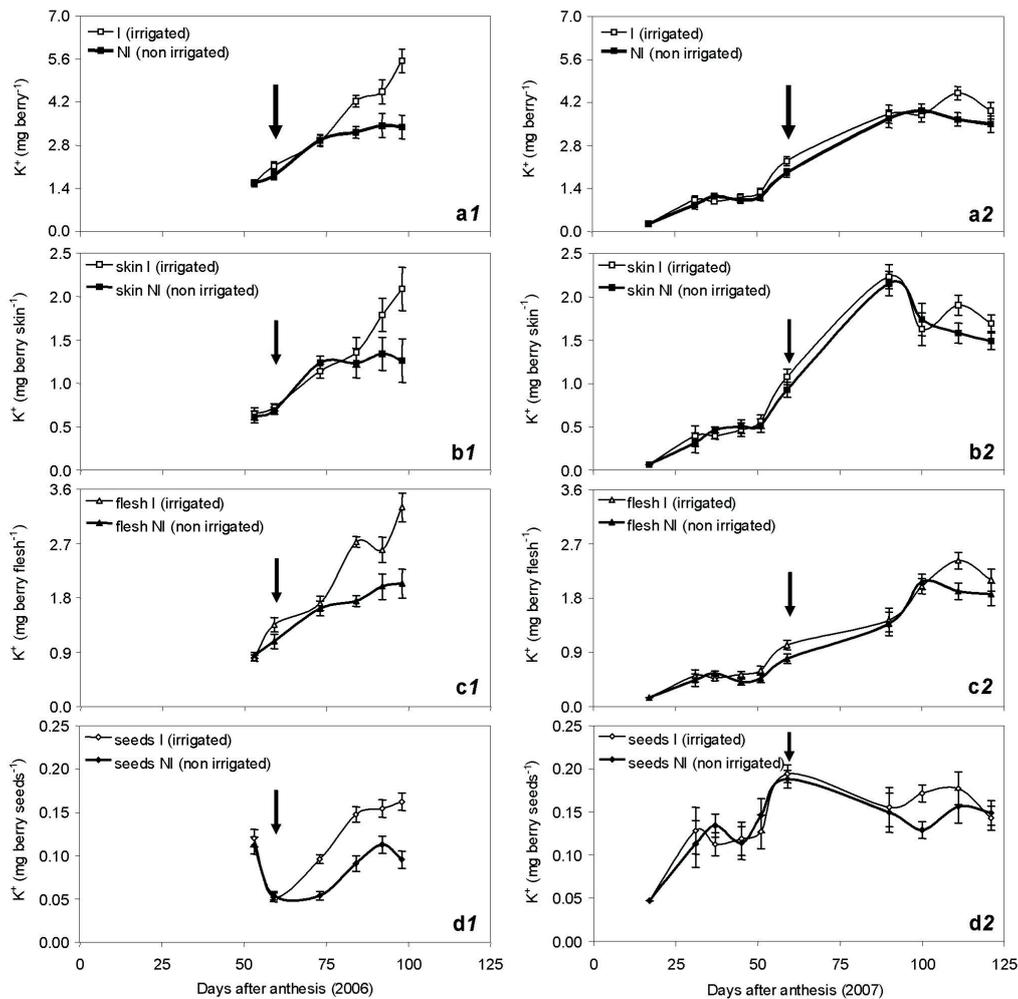


Fig. 3: Accumulation of potassium in whole berries and their distribution in the different compartments (skin, flesh, seeds) of 'Grenache Noir' during ripening from vines undergoing different irrigation treatments over two years (2006-2007). The most abundant cation per berry is K^+ . Vine water status and year-to-year variation change the accumulation of K^+ in the different berry compartments. Arrows indicate veraison. Results are expressed in $mg \cdot berry^{-1}$ and $mg \cdot berry \text{ compartment}^{-1}$ (skin, flesh and seeds). Bars represent \pm limits of significance ($p = 0.05$).

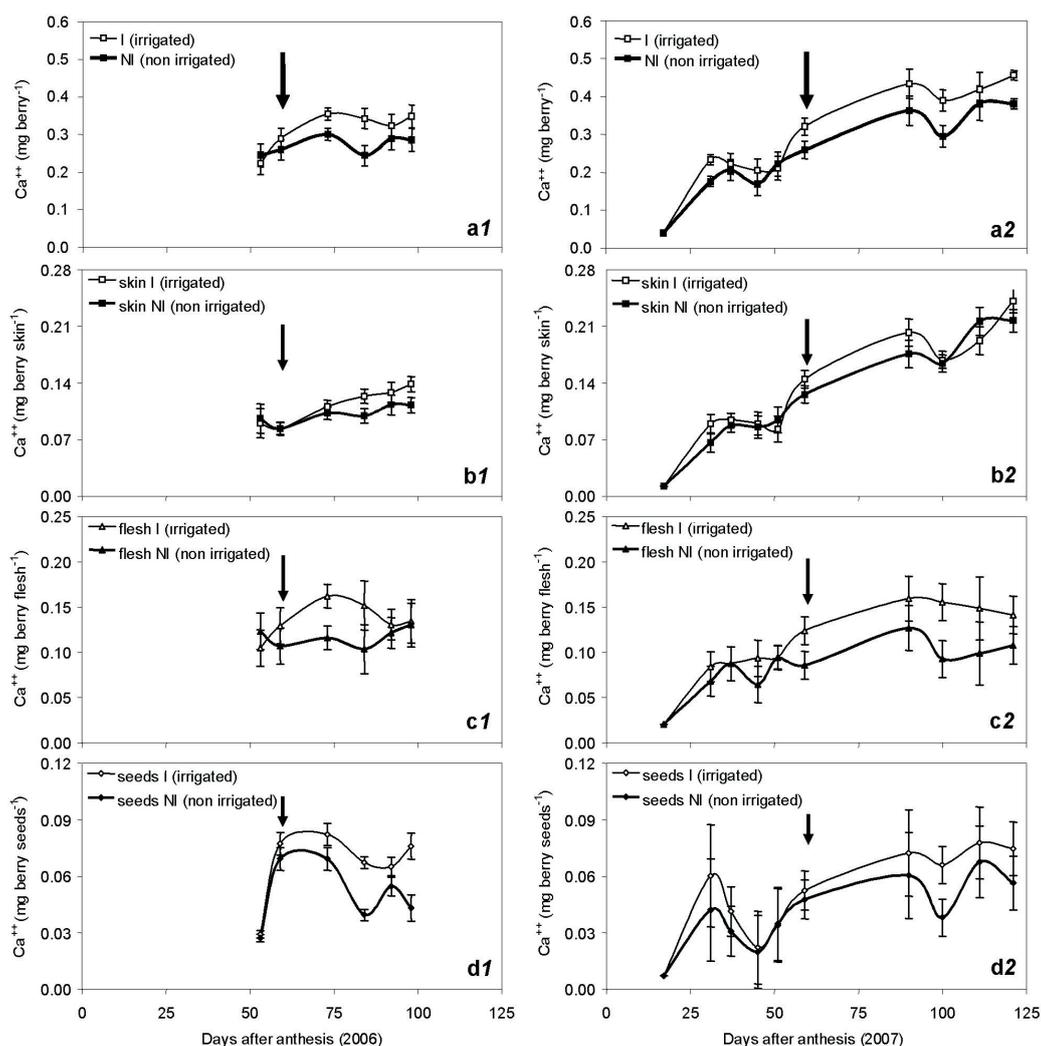


Fig. 4: Accumulation of calcium in whole berries and their distribution in the different compartments (skin, flesh, seeds) of 'Grenache Noir' during ripening from vines undergoing different irrigation treatments over the two-year experimental period (2006-2007). Berry content of Ca^{++} shows a steady upward trend during ripening under favorable water conditions. Vine water status and year-to-year variation changes the accumulation of Ca^{++} in the different berry compartments. Skin content of Ca^{++} increasing during ripening. Arrows indicates veraison. Results are expressed in mg berry^{-1} and $\text{mg berry compartment}^{-1}$ (skin, flesh and seeds). Bars represent \pm limits of significance ($p = 0.05$).

trend during the post-veraison period under certain conditions, e.g. non restrictive water supply to the plant and to the fruit. For both treatments, K^{+} was the more abundant cation in the mineral composition of the berry, followed by Ca^{++} .

Accumulation of K^{+} and Ca^{++} in different berry compartments: During pré-veraison and post-veraison, K^{+} and Ca^{++} are differentially distributed in the various berry compartments, *i.e.* the skin, flesh and seeds. It was shown in this study that water deficit either reduced or inhibited the accumulation of these cations in the fruit.

Skin and flesh: The accumulation of K^{+} and Ca^{++} in the skin increased during ripening but at different rates depending on the elements' response to water deficit and year-to-year variation. At maturity the skin contains 37 % of berry K^{+} in 2006 (Fig. 3 b1) and 43 % in 2007 (Fig. 3 b2), thus confirming the observations made by IL-AND and COOMBE (1988) for 'Syrah' and by DONÈCHE and

CHARDONNET (1992) for 'Cabernet Sauvignon'. The flesh contained 60 % of berry K^{+} at maturity in 2006 (Fig. 3 c1) and 53 % in 2007 (Fig. 3 c2). These percentages are not modified by plant water status. According to ROGIERS *et al.* (2006) the predominant accumulation of K^{+} in the flesh and in the skin confirms the role of this cation in cellular expansion. In particular, it was observed that during ripening there was a slight increase in Ca^{++} in the skin for both I and NI treatments in 2006 (Fig. 4 b1), and a significant increase in 2007 (Fig. 4 b2). Ca^{++} transport to skin cells during ripening could be explained by apoplastic and/or symplastic migration in the berry or by partial functioning of xylem after veraison. According to DONÈCHE and CHARDONNET (1992), there is a dramatic reduction in the concentration of Ca^{++} in cells of the flesh, whereas it is more abundant in the skin. However, this study shows Ca^{++} accumulation in berry flesh remained constant (Fig. 4 c1, c2).

Seeds: In 2006, the level of K^{+} in seeds continued to increase during the post-veraison period (Fig. 3 d1),

and again, the quantity of K^+ was lower in seeds of the NI treatment. In 2007, the quantity of K^+ remained constant throughout this period (Fig. 3d2). The quantity of Ca^{++} is variable for the same period for both 2006 and 2007 (Fig. 4d1, d2). As for K^+ , the seeds were a less important sink than skin or flesh for Ca^{++} , which was accumulated in the seeds prior to veraison; however there was a small but steady accumulative trend during ripening in 2007. Moreover, CABANNE and DONÈCHE (2003) and ROGIERS *et al.* (2006) reported that seed Ca^{++} content increases during ripening in several other grape-berry varieties. Pre-veraison xylem tracer studies indicated that xylem flow occurred not only via bundles supplying the skin and pulp of the berry, but also via the central bundles leading to the seeds, again suggesting continuous xylem flow to the seeds (ROGIERS *et al.* 2001). However, post-veraison the xylem tracers were limited to the brush region of the central bundles (DÜRING *et al.* 1987, FINDLAY *et al.* 1987, CREASY *et al.* 1993, ROGIERS *et al.* 2001).

The importance of grapevine water status and year-to-year variation on the accumulation of K^+ and Ca^{++} was demonstrated. The question of soil availability of these cations and the relationship between their root absorption and their distribution in the different plant organs (sink-source competition) justify further studies. This work indicates that the accumulation of Ca^{++} in the whole berry possibly continues during ripening under favorable water conditions, which in turn implies that there is partial functioning of xylem post-veraison. In parallel, a recent work has shown that grape berry peripheral xylem development continues further during berry maturation (CHATELET *et al.* 2008). In both treatments (irrigated and non irrigated) and seasons (2006 and 2007), the quantity of calcium in the skin increased during ripening; this would suggest that Ca^{++} migrates from other berry compartments especially from the flesh to the skin.

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