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PHOTO 1. Different berry shrivelling stages within a Shiraz bunch.

GRAPE BERRY SHRIVELLING – CHANGES IN PHYSIOLOGY AND QUALITY

DEHYDRATION/SHRINKING OF GRAPE BERRIES DURING LATE RIPENING IS A COMMON DISORDER OF GRAPEVINE CULTIVARS AND HAS DELETERIOUS IMPLICATIONS FOR YIELDS AND GRAPE QUALITY. **BY KOBUS HUNTER, A. CARLOMAGNO, NEELS VOLSCHENK, A. FERRANDINO, C. LOVISOLO, A. GENRE & V. NOVELLO**

The cultivar Shiraz is particularly sensitive for this disorder and often displays large variation in physical and physiological condition of berries between and within bunches (Photo 1). Essentially, softening and deformability of fruit are due to breakdown of cortex parenchyma cell walls, the latter which are mainly composed of cellulose, hemicellulose and pectin (polysaccharides). Cell wall composition and behaviour are complex and still far from fully understood. During grape ripening and the processing of grapes (e g during skin contact and pressing), berry cell walls are "barriers" to the diffusion and integration of many components essential to wine quality. Studies already revealed the complex orchestration of metabolic, transport and control processes during the whole cycle of the developing berry. It showed the phenotypic plasticity of the grapevine under field conditions. It also demonstrated the environment-sensitivity of the expression and function of berry transcriptomes related to secondary metabolism that leads to the compounds in the berry that are commonly associated with berry disease resistance and wine quality/style.

Although dehydration and direct sun exposure are plausibly commonly associated with the shrinking disorder, specific mechanisms or events leading to shrinking of berries are not yet fully elucidated and research is continuing globally. Source:sink relationships (supply and demand) and sap flow are implicated in this disorder and have steering effects on grapevine growth and development and carbon and water distribution to grapes. Understanding of sap flow is incomplete, but critically needed under current (unfavourably) changing environmental conditions (i e increasing temperatures and decreasing water availability). Water arrives to the berry via xylem (plus minerals, etc) and phloem (plus minerals, amino acids, sugars, etc). Water balance (maintenance of water relations and turgor) is most likely determined by growth in volume, soluble solid transport and accumulation, transpiration and return of water to the plant through the xylem. The latter may temporarily occur on a hot day when, e g leaves transpire excessively, thereby surpassing water absorption by the roots and leading to what is known as 'xylem backflow'. Berries are more sensitive towards vine water relations during pre-véraison than during post-véraison. Berry transpiration has a significant role to play during both periods. At véraison, in correspondence with an apparent xylem disruption, phloem sap becomes the source of water and solutes for the berry until maximum berry weight is attained. The 'phloem water pathway' becomes dominant compared to the 'xylem water pathway'. The continuation of berry transpiration and progressive isolation of the berry from vascular transport pathways, then lead to shrinking of the berry and/or solute concentration, depending on physiological activity of the canopy (vine) and environmental conditions.

The mechanism of late season berry dehydration is not clear and the dilemma in understanding concerns the role of the xylem during post-véraison (peripheral vs axial flow); the existence and timing of xylem backflow; and the functionality of the phloem. Despite many attempts based on berry dimension responses after transport disruption by means of girdling and heat treatment; flow of xylem and phloem dyes and tracers; monitoring of xylem and phloem mobile mineral transport; hydraulic conductance measurements; measuring of berry turgor and hydraulic dynamics; and xylem tracheary element analyses, the mechanisms involved in the shrinking of the berry at a specific ripeness level are not completely resolved.

Essentially, two likely scenarios are generally debated:

a) From véraison through ripening the berry gradually gets isolated from the mother plant, i e both xylem and phloem become impeded;

b) From véraison through ripening the berry remains hydraulically connected to the vine, but the roles of berry xylem and phloem change: pre-véraison the xylem supplies water to the berry, whereas post-véraison it is used to drain phloem water supply surplus (because water is supplied to the berry essentially via the phloem during this period).

Indications are that sucrose and water transport to the grapes and berry water loss are regulated by a combination of photosynthetic activity, canopy and berry microclimate, osmotically driven transport, berry evapotranspiration, sucrolytic enzyme activity (splitting sucrose into glucose and fructose), membrane degeneration/permeability and a change in the ratio of xylem:phloem import, primarily after véraison. Many aspects, such as cellular compartmentation and xylem embolism, are however disputed. Some regulatory processes between canopy and grapes during ripening are summarised in Figure 1.

Water deficit experiments were performed on seven-year-old VSP Shiraz (clone SH1A)/R99 (clone RY2A) on a Glenrosa soil with Western aspect at ARC Infruitec-Nietvoorbij, Stellenbosch [15 treatments of different water volumes (no irrigation and soil volume filled to 75% and 100%, respectively, of field water capacity {FWC}) applied as either single or different combinations of irrigations at different growth stages, i e berry set, pea size berry, véraison and post-véraison] in combination with three grape ripeness levels (23, 25 and 27°B). Results showed that apical leaves generally outperformed basal leaves on either primary or secondary shoots. Being younger, apical primary leaves and secondary leaves generally respond better to decreasing photosynthetic active radiation during ripening and would be more involved in metabolic processes to satisfy sucrose and osmotic balance demands from the rest of the plant during this time.

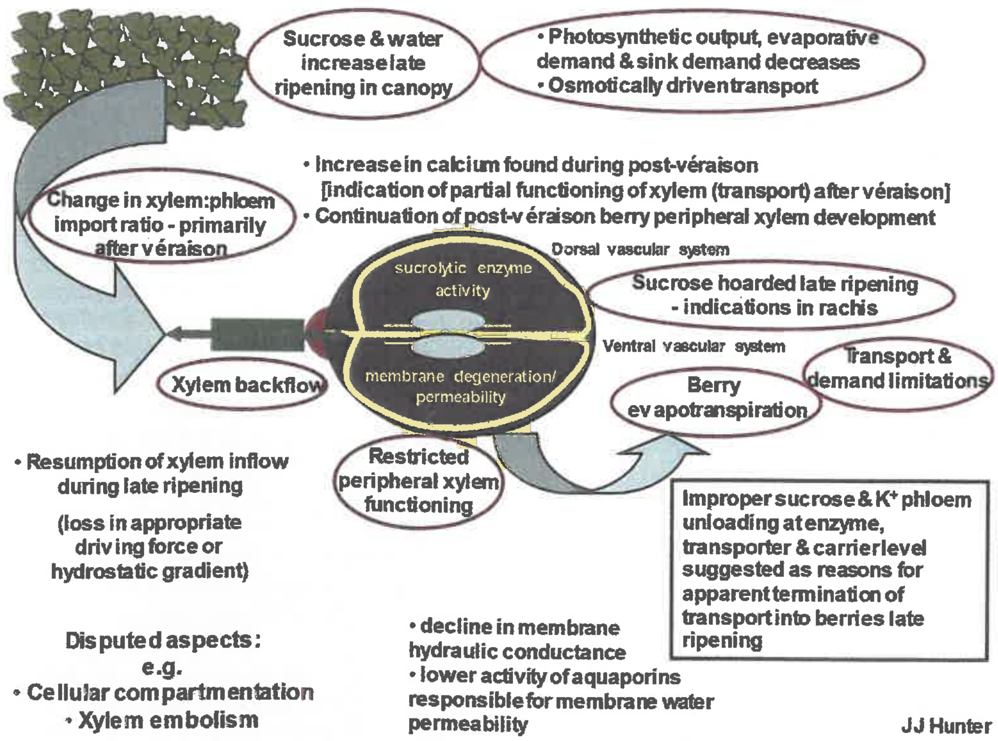

FIGURE 1. Schematic representation of some regulatory processes between and within canopy and grapes during the ripening period.

Although the capability for osmo-regulation is almost the same in mature and immature leaves, younger leaves have more elastic cell walls, rendering them an ability to maintain positive cell turgor under lower leaf water conditions and a higher potential to buffer the impact of unfavourable environmental conditions, such as high temperatures and dry conditions, on grape development and ripening. Pre-véraison initiation of secondary leaves by judicious canopy management is therefore important in order to maintain the canopy photosynthetic capacity and increase the potential of the canopy to continue supporting the grapes when adverse environmental conditions may occur during ripening. This may extend the harvesting window by continued translocation/ contribution to grapes by the canopy, as well as contribute to reserve accumulation after harvest. Irrigation (volume and growth season stage), in combination with a definitive ripeness level, may contribute largely to a required style of wine. Restricted irrigation (75% of FWC) at pea berry size and at post-véraison (approx three weeks after véraison at maximum berry size) (as single stage treatment or in combination) featured prominently as being favourable to grape and wine composition, as well as wine sensorial quality, albeit resulting in different grape and wine styles.

During late ripening, photosynthetic activity continues despite the senescing canopy (and cooler day and night temperatures), although at a lower rate, and sucrose normally build up in leaves as a result of reduced transport to the rest of the vine, including the berries. Vines tend to recuperate/stabilise during this time, maintaining water balances to, amongst others, support reserve accumulating compartments. Not transpiration, phloem flow or xylem flow seem able to sustain influx during late ripening and maintain berry turgor. Water relation gradients, along with photosynthetic activity, sucrose accumulation patterns and enzyme activity in leaves and berries during this time, do not support active water transport dynamics and flow to berries. Our earlier ^{14}C-translocation studies also showed that grape berries are the major sinks in the canopy between berry set and véraison stages, but that this focus fades after that.

Sucrose is hoarded in the rachis during late ripening, indicating independent development and/or senescence for berry and rachis during this period (Figure 2). Transport into the berries is restricted, despite a favourable gradient for accumulation and a decreasing osmotic potential in the berry, because of the concentration of glucose and fructose. The behaviour of rachis and berry is not concerted and the rachis displays typical vegetative tissue characteristics. The linear relationship between sugar transport and accumulation is broken during this time; this was also found when water deficit was induced in vines. The berry therefore concentrated during this period, but at the same time lost mass as a result of continued water loss and reduced phloem sugar and water transport (active sources and sinks are required for high phloem sap velocity); it became at least partly isolated. Not only is the berry less sensitive to soil water deficit during late ripening, but it also seems not to be affected by high volumes of water during this time. Efforts to prevent further shrinking would therefore not be successful following this route. A continued loss of water from the berry finally leads to a reduction in both mass and volume, which further leads to physico-chemical changes.

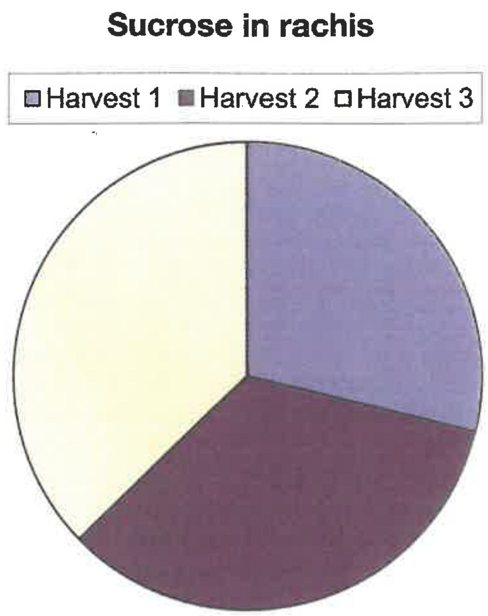

FIGURE 2. Hoarding of sucrose in the rachis of Shiraz during different stages of ripening.

Xylem-dye and phloem- (fluorescent) tracer experiments (Photo 2 – showing inflow into the whole berry and mesocarp staining by transpiration) were done with field-grown VSP Shiraz/101-14 Mgt. Results showed reverse xylem flow from berry to plant until, but not after véraison (around 24°B and beyond towards 27°B). The experiments could not clarify whether this is due to a vessel/tracheid breakage or not, but it showed that xylem back-flow in late post-véraison intact, as well as shrivelled berries, is unlikely. The phloem transport marker also demonstrated the absence of flow from berry to plant (despite a perfect distribution inside the berry) and *vice versa* (despite transport through leaves, petioles and shoots) during berry ripening of intact and shrivelled berries. This means that the mutual attraction between berry and vine was already very limited/absent/ passive. Results further showed that after fruit-set water flowed straight to the seeds via central bundles, meaning that at this stage the seeds are major sinks in terms of water/mineral/hormone uptake, but this behaviour switched after their growth has stopped. During the ripening stages peripheral bundles seemed the preferential way by which the water entered the berry, until it completely ceased at the late ripeness stage.

Environmental factors seem to play a larger role in establishing final soluble solid concentration during late ripening, despite the concurrent array of very complex processes (involving enzymes, transporters, carriers, osmotic agents, etc). The water status of the berry is not solely determined by sugar, but many compounds, including amino acids, organic acids, inorganic cations and anions, and other taste and flavour compounds,

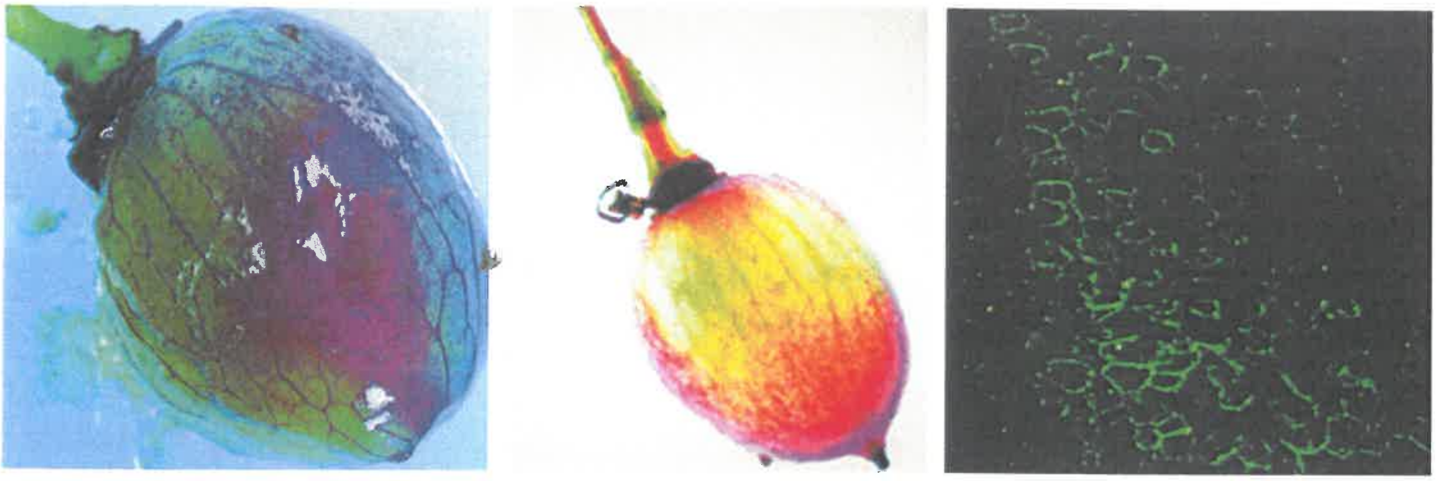

PHOTO 2. Xylem-dye and phloem- (fluorescent) tracing showing inflow into the whole berry and mesocarp staining by transpiration in field-grown Shiraz.

contribute to the soluble solid/osmotic status of the berry. Although partial degeneration seems more evident, the viability of the internal structure of the berry (mesocarp) changes during this time, be it because of compartmentation/membrane breakdown and/or cell death, hence the decrease in firmness and observed shrivelling. Apart from the concentration of sugar, abundance of potassium in the berry at this time causes a real danger of organic (tartaric) acid salt formation, a pH increase and a concomitant decrease in colour intensity. Extraction during maceration will also be affected detrimentally despite the softer berry and lower skin:pulp ratio. Berry shrivelling therefore causes both physical and physiological changes that cannot be associated with high quality grapes and wine.

CONCLUSIONS

- Neither berry transpiration forces, nor sap flux velocity of phloem and xylem, seem able to prevent isolation of the berry, sustain influx and maintain a fully intact berry without shrivel during late ripening stages.
- Decreased vascular flow of water into the berry, coupled with continued transpiration, promote pre-harvest berry weight loss and shrinking.
- During late grape ripening, water is supplied to the perennial/permanent parts in order to sustain turgor balances/recuperate water relations, build up reserves and support root growth activity, essentially "bypassing" the berry.
- At high grape ripeness level and with berry shrivelling, differences induced with special manipulation treatments during the growth season that were aimed at grape composition/wine style changes, would largely diminish.
- If grapes are forced to ripen or allowed to ripen to over-ripeness, expected outcomes of seasonal cultivation efforts to produce unique wines per terroir may be tempered and even negatively affected; this is not conducive to economic viability/sustainability.
- Terroir factors, such as soil type and environmental conditions (including climatological patterns), would be major steering factors for vine water status, vegetative and reproductive growth characteristics, grape ripening dynamics and eventual wine style.
- Judicious viticulture practices are essential to support seasonal grape development and perennial consistency.

ABSTRACT

Shrivelling of grape berries during late ripening is common under field conditions, particularly for Shiraz. It generally affects yields and grape quality deleteriously. Decreased vascular inflow of water and continued transpiration promote pre-harvest berry weight loss and shrinking. During late grape ripening water essentially "bypasses" the berry. Forced grape ripening and over-ripeness may nullify seasonal efforts to create unique grape and wine styles and increase sustainability. Grape physical and chemical ripening dynamics are complex and seem intimately linked to terroir factors, such as soil type and environmental conditions (including climatological patterns). Judicious viticulture practices across the perennial spectrum are required to buffer grape disorders, sustain consistency in seasonal berry dynamics and reach objectives aimed at specific wine styles.

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