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Growth and Water Transport in Fleshy Fruit

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Fruit volumetric growth is primarily the result of water accumulation, and hence maintenance of fruit growth requires coordination between long-distance water and solute transport through the vascular tissue, and short-distance water and solute uptake at the level of individual cells. One hypothesized coordinating principle is that for fruit growth to occur, there must be a favorable difference in total water potential between the fruit and the rest of the plant (e.g., Grange and Andrews, 1994). Essentially all of the previous studies of fruit water relations, including our own, have been based on whole fruit measurements of total water potential, and many of these are consistent with this principle. The current understanding of fruit water relations, however, particularly at the cellular level, is quite rudimentary, and it may be premature to generalize about the water relations of the fruit as a whole before we have a clear understanding of the water relations of the component cells. In this chapter we give a brief overview of the water relations of fleshy fruits as they relate to the process of fruit growth, particularly in grapes, and present experimental measurements of fruit water balance, whole fruit osmotic potential, and intact fruit cell turgor in the grape berry. Our turgor measurements indicate that fruit cell turgor is substantially depressed by the presence of solutes in the apoplast. The consequences that apoplastic solutes may have on water exchange between the fruit and the plant are discussed, as well as questions and directions for future research.

Fleshy Fruit Growth, Expansion, and Contraction

Fleshy fruit arise from a wide range of tissues (see Coombe, 1976), and in some respects the interaction between xylem and phloem transport during fruit growth is similar to that experienced by most other growing plant

structures. Diurnal variations in size (expansion and contraction), and hence volume, of fleshy fruit are common (Elfving and Kaufmann, 1972; Johnson *et al*, 1992; Tromp, 1984), superimposed on an overall size increase over time. The diurnal variations are usually attributed to changes in hydration, presumably due to changes in fruit cell turgor; under these conditions it is difficult, or perhaps impossible, to unequivocally separate growth (by definition the irreversible change in volume) from these reversible changes in volume. We assume that growth of the fruit reflects growth of the component cells (in the case of the grape berry these are mostly mesocarp cells), that growth occurs when nighttime expansion exceeds daytime contraction (in some cases daytime contraction may be absent), and that both processes arise from water flows into and out of the fruit. Hence, one approach to describing fruit growth is to quantify these flows as a "water balance" (net growth = flow in – flow out). We will further assume that the exchange of water between the fruit and the parent plant occurs primarily, if not exclusively, through the phloem and xylem tissues in the fruit pedicel. Inflow must come from the parent plant, but outflow can occur either via fruit transpiration or, in some cases (e.g., cowpea, Pate, 1988; apple, Lang, 1990) via water "backflow" through the xylem, although the prevalence in fleshy fruits of this kind of water flow, sometimes referred to as "water recycling," has not been established. This is an important phenomenon since a water potential gradient generated both by transpiration (Lee *et al*, 1989; Lee, 1990) and by an osmotic gradient (Lang and Düring, 1991) has been implicated in the control of fruit growth and water economy.

Multiphasic Growth Habit

Growth of many fleshy fruit, including *Prunus* sp. and *Vitis* sp., exhibit a double-sigmoid pattern in which there are two periods of rapid growth. The growth phases are separated by a period of variable length during which little or no expansive growth occurs. The growth habit of grape berries has long been divided arbitrarily into three stages (e.g., Connors, 1919) (Fig. 9.1A). Stage I extends from anthesis to the slowed growth of stage II, and stage III extends from the onset of the second growth phase until maturity. During stage I there is some cell division, but by stage III, all fruit growth is due to the expansion of existing cells (Coombe, 1976; Ojeda *et al.*, 1999). The duration of stage II is under both genetic and environmental control (Coombe, 1976), and in grape, much attention is given to the relatively abrupt transition from stage II to stage III, referred to as veraison. In addition to the rapid changes in growth rate at veraison (Fig. 9.1A), around this time the fruit ripening process begins, identified by the appearance of red color in red and black grape varieties, fruit softening, and a decline in fruit solute potential, with the decline in solute potential reflecting the accumulation of substantial concentrations of

sugars (Fig. 9.1B). Hence the relatively abrupt transition from little or no growth to rapid growth is associated with an apparently abrupt increase in the rate of transport of sugars into the berry. The increase in sugar transport is substantial because both volume and solute concentration are increasing. Coombe (1992) has observed the resumption of growth to follow by a few days a measurable increase in hexose concentrations in berries at veraison.
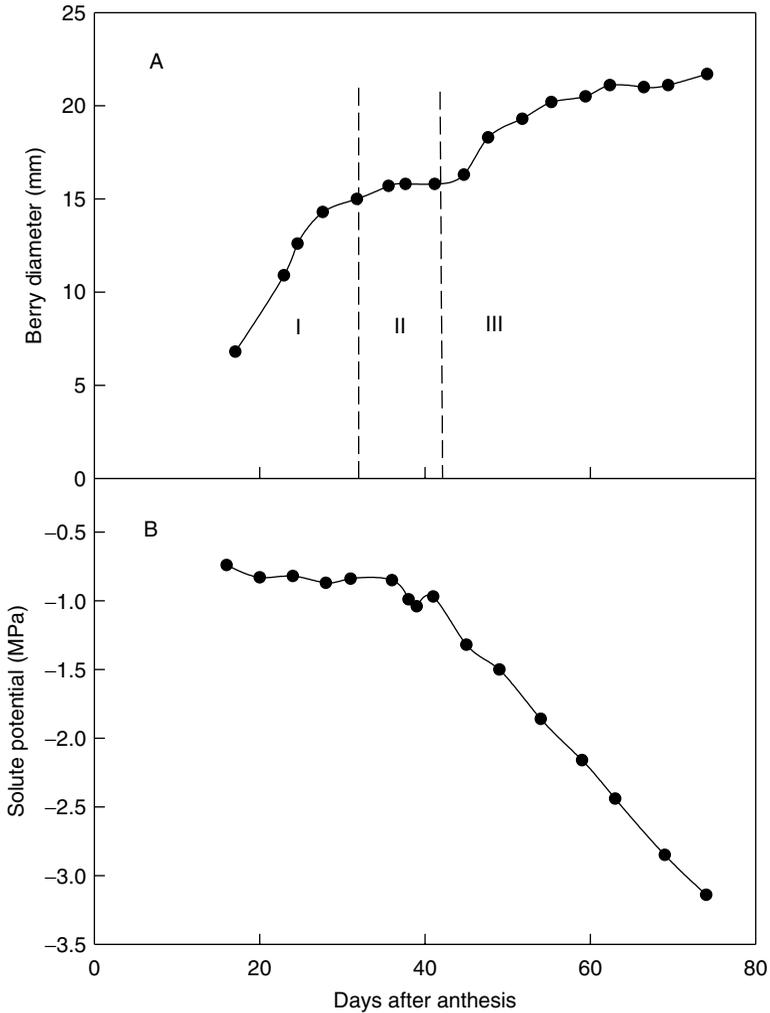
Figure 9.1   Developmental pattern of (A) fruit diameter and (B) fruit solute potential for grape (*Vitis vinifera* L. cv Cardinal). The arbitrary designation of growth stages (I, II, and III) is described in the text. (from Matthews *et al.*. 1987)

It is axiomatic that expansive cell growth requires the presence cell turgor, and in many, although not in all instances, a direct relation between turgor and the rate of growth has been found (e.g., Serpe and Matthews, 2000). It is also generally believed, however, that at any given turgor, the rate of growth is determined by the rate of weakening of the structure of the cell wall (e.g., Cosgrove, 2000). Hence the resumption of berry growth at veraison could, in theory, be associated with an increase in berry cell turgor, possibly as a result of solute accumulation in the absence of a change to cell wall strength, or to a weakening of the cell wall in the absence of a turgor change, or to a combination of both processes. It should be noted here that each of these processes would have different consequences for whole fruit water potential, and they may also have different consequences for the transport of water from the plant to the fruit, depending on which water transport pathway (phloem or xylem) is predominant. For instance, if turgor increases because of an increase in solute accumulation by mesocarp cells, then this may occur without any change in fruit total water potential, and hence no change in the water potential gradient between the fruit and the parent plant. In fact, if the sugar concentration in the mesocarp cells is higher than that of the phloem, then there may be an increase in fruit water potential owing to the presence of excess phloem-derived water, and water may flow from the fruit to the plant through the xylem, as occurs in other systems (Pate, 1988; Lang, 1990).

The steady state value of fruit cell turgor and total water potential during growth would depend on the hydraulic conductivity of the vascular pathway between the fruit and the parent plant. If there is excess phloem-derived water and the pathway for water return to the parent plant (presumably the xylem) had a low conductivity, then both cell turgor and cell total water potentials would substantially increase. If growth resumption were due to a weakening of the cell wall, however, then an initial decline would be expected in either cell turgor or cell total water potential (or both). The steady state value reached by these potentials would also depend on the hydraulic conductivity of the vascular pathway connecting the fruit and the parent plant, but, in this case, a low conductance xylem pathway would be associated with a substantial decrease in cell turgor and/or total water potential. These two alternative scenarios (turgor increase versus wall loosening) to explain increased fruit growth at veraison illustrate the importance of considering both short- and long-distance transport processes and their possible interaction.

Diurnal Expansion and Contraction

Many fleshy fruit exhibit a diurnal pattern of expansion and contraction even when well watered (Shimomura, 1967; Coombe and Bishop, 1980; Nakano, 1989; Johnson *et al.*, 1992). Figure 9.2 shows the diurnal behavior

of grape berry diameter around veraison. Virtually all berry growth occurs during the night; day periods are characterized by either contraction or absence of expansion. Initially (i.e., during stage II) daily contraction and nightly expansion are approximately equal, and little net growth is observed. The transition to stage III is characterized by a dramatic reduction in the daily contractions over 2 to 3 days. The contractions decreased from approximately 0.125 mm/day on days −5 and −4 to less than 0.025 mm/day on days 0 and 1 (Fig. 9.2). Nightly expansion also increased approximately 50% compared to the preveraison expansion. That this transition occurred before color development indicates that the resumption of growth and altered diurnal water relations are early events in the transition from stage II to stage III. What causes expansion to increase and daily contraction to be reduced at this stage?

Daily contraction of fleshy fruit is generally well correlated with decreasing leaf water potential, as was the case in citrus (Elfving and Kaufmann, 1972; Maotani *et al.*, 1977) and apple (Tromp, 1984). This is also the case in preveraison grape, where the daily contraction increased from about 4% to 10% as midday leaf water potential declined from about −1.0 to −1.5 MPa (Fig. 9.3). When shoot transpiration was restricted before veraison, a marked reduction of diurnal contraction also occurred (Greenspan *et al.*, 1994). Hence, it is generally assumed that fruit contraction simply indicates that a conductive apoplastic pathway (i.e., xylem) is connecting the fruit to
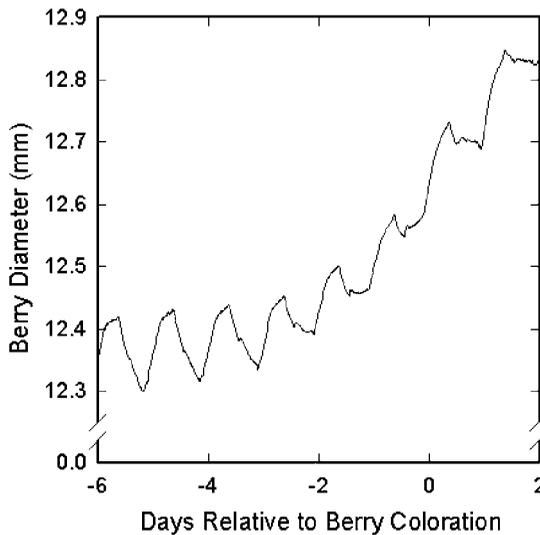

Figure 9.2   Diurnal pattern of fruit diameter in grape (*Vitis vinifera* L. cv. Cabernet Sauvignon) at the transition of stage II to stage III (veraison).

the rest of the plant, and that when soil drying or plant transpiration cause a decline in overall plant water potential, a decrease in berry cell total water potential (and hence berry cell turgor pressure) is a direct result. Assuming that soil drying has minimal effect on berry transpiration, however, the increased diurnal contraction of berries during pre-veraison soil water deficits (Fig. 9.3) could be due either to backflow out of the fruit to the parent plant through the xylem, or to a reduced net vascular inflow to the fruit. In contrast to pre-veraison fruit, however, for the same range of midday leaf water potential, the daily contraction in fruit diameter of the post-veraison berry was about 1% and insensitive to changes in midday leaf water potential (Fig. 9.3). The relative insensitivity of post-veraison berries may indicate an improved water transport to post-veraison berries or a hydraulic isolation that prevents the berry from experiencing the diurnal water deficits occurring in the stem.

Leaf, Stem, and Fruit Water Potential

Fruits and leaves can be considered as competing sinks for water, and in some cases it has been assumed that the difference between fruit and leaf water potential determines the directionality of water exchange between
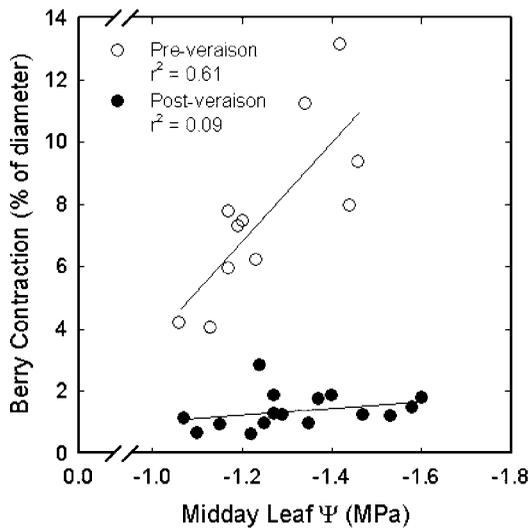
Figure 9.3 Amplitude of diurnal berry contraction at various midday Ψ leaf for pre- and post-veraison Cabernet Sauvignon berries. Pre-veraison correlation is significant for $P < 0.01$; post-veraison correlation is not significant.

the fruit and the parent plant. For instance, backflow of vascular water from fruit to transpiring leaves has been suggested from diurnal measurements in which $\Psi_{leaf} < \Psi_{fruit}$ during midday for various crops (Klepper, 1968; Tyvergyak and Richardson, 1979; Syvertsen and Albrigo, 1980; Yamamoto, 1983), including grape (van Zyl, 1987). However, since fruits and leaves only share the stem portion of the water transport pathway, it is the fruit-to-stem water potential difference that is appropriate for this analysis. In grapes, cluster water potential ($\Psi_{peduncle}$) was lower than stem water potential at most times in the diurnal cycle and under wet and dry soil conditions (Greenspan *et al.*, 1996), indicating that a favorable gradient for water flow existed, at least from the stem to the cluster. Using *in situ* psychrometers, Guichard *et al.* (1999) showed a close and straightforward relation between the fruit-to-stem water potential gradient and the rate of water flow through the fruit pedicel in tomato over a diurnal course, with the lowest flow through the pedicel at midday, when fruit and stem water potentials were essentially equivalent. Tomatoes are unusual, however, in that they show little or no midday contraction (Johnson *et al.*, 1992) compared to pre-veraison grapes (Fig. 9.2) and other fruits (e.g., apple, Tromp, 1984). Consistent with the lack in midday contraction in tomato, however, Guichard *et al.* (1999) also found little diurnal change in fruit total water potential. Hence the pre-veraison diurnal oscillations in fruit size that are observed in grape may indicate that diurnal changes do occur in fruit total water potential and in fruit cell turgor (but see the section Fruit Turgor and Apoplastic Solutes) during this period. These pre-veraison diurnal oscillations in fruit size are also consistent with those expected on the basis of the diurnal pattern in stem and cluster total water potential.

The transition to little or no midday fruit contraction at veraison suggests that an uncoupling of fruit water potential from cluster or stem water potential occurs at this time, but the basis for this change is not clear. A similar change has been observed in cotton fruit (bolls, Anderson and Kerr, 1943), but in this case the rapid growth period with no midday contraction occurs first, and is followed by a period of no growth and marked midday contraction. The absence of midday contraction in growing organs may be difficult to interpret, however, as it may indicate either that the turgor and possibly the total water potential of the organ is stable over the diurnal course, or that organ growth is simply adjusting to the relatively gradual diurnal changes in cell turgor (e.g., Shackel *et al.*, 1987). A diurnally stable fruit water potential would result if fruit and plant water potential were uncoupled, and such uncoupling has been hypothesized in a number of systems, mostly based on the assumption that close coupling in the first place is due to xylem water transport. In grape, the apparent change in coupling at veraison has been studied using dye uptake methods and attributed to an irreversible disruption of xylem transport by many

authors (Delrot *et al.*, 2001), although there is some evidence that the xylem remains functional in post-veraison berries (Rogiers et al., 2001). Hence, it is not yet clear whether the apparent change in coupling *in situ* is due to the xylem becoming irreversibly disrupted, or indirectly due to another mechanism, such as a reduction in the driving force that is responsible for xylem transport (hydrostatic gradient) between the fruit and the stem (see later).

Vascular Flows in Developing Fruit

Net flows into and out of fruit have been estimated using various mass balance approaches. From measurements of fruit transpiration and mass, and assumptions about phloem and xylem composition, Pate and co-workers estimated that water was supplied by xylem and phloem, approximately 60:40 (v/v), to white lupin fruit (Pate *et al.*, 1977), and that the phloem supply was greater than 100% of daily fruit water gain in cowpea (Peoples *et al.,* 1985; Atkins *et al.*, 1985). From measurements of fruit mass, transpiration, and Ca influx, Ho *et al.* (1987) estimated that the water supply to tomato fruit was predominately via the phloem, increasing from approximately 85% to approximately 95% of the total water uptake during fruit development. Lang and Thorpe (1989) introduced a novel approach to analysis of the fruit water budget in which the xylemic, phloemic, and transpirational flows can be separated. Diurnal measurements of intact (all 3 flows), detached (transpiration only), and phloem girdled (Ts and xylem {au: pls flow) fruit allow all three flows to be obtained by subtraction. This approach clarify Ts} assumes independence of xylem and phloem transport, and a sensitivity analysis indicated that the assumption leads to little error except at very low flow rates (Fishman *et al.*, 2001). In apple, which typically exhibits daytime contraction, Lang (1990) found that the xylem contribution to overall fruit water balance progressively decreased as fruit developed.

Using the approach of Lang and Thorpe (1989), Matthews and colleagues evaluated the diurnal water budget of the grape berry before and after veraison (Greenspan *et al.*, 1994) and in comparison with leaf and stem water status during water deficits (Greenspan *et al.*, 1996). Before veraison and under well-watered conditions, the bulk of vascular water flow from parent plant to the berry occurs via the xylem, and the phloem contributes less than 10% of total inflow (Fig. 9.4). After veraison, phloem becomes the primary source of berry water, contributing more than 80% of total inflow under well-watered conditions. In apple, tomato, and grape, particularly late in fruit development, most authors have attributed the relatively small xylem contribution to the development of a high xylem

hydraulic resistance within the fruit, often as a result of growth-induced xylem stretching or breakage (Lang and Ryan, 1994; Malone and Andrews, 2001; Düring *et al.,* 1987; Findlay *et al.*, 1987). In many of these studies (1) staining of lignin in the berry revealed evidence of stretching or gaps in the xylem appearing at or after veraison; and (2) dye uptake from cut pedicels and transport into the berry was diminished after veraison. Disrupted xylem within the berry would presumably contribute to a reduced conductance to the parent plant, but the direct implication of these observations within berries on water exchange between berry and parent plant are not clear. For instance, in the study of Düring *et al.* (1987), dye movement declined gradually over 2 weeks, whereas based on the diurnal patterns of expansion and contraction (Fig. 9.2), the transition from xylemic to phloemic transport is apparently rapid, occurring over 2 days. Xylem flow is also reduced, but not eliminated, at veraison, and the xylem appears to contribute to the recovery of berry volume during the night, as indicated by the positive nighttime xylem flow in the irrigated, post-veraison vine (Greenspan *et al.*, 1994). Hence, a purely anatomical explanation (i.e., xylem disruption) for the change from xylemic to phloemic transport at veraison may be oversimplified.

In addition to vascular flow estimates using intact/girdled/excised fruit, the diurnal behavior of berry size when restricting transpiration of leaves or fruit, and when imposing water deficits, all are consistent with an abrupt
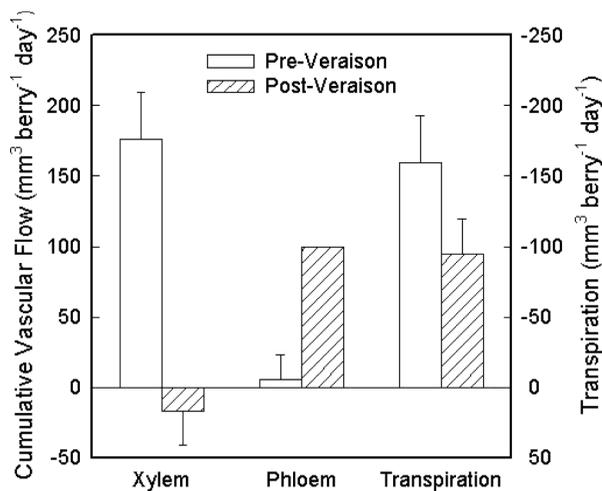
Figure 9.4   Calculated cumulative daily vascular flow and transpiration for pre- and post-veraison berries of irrigated vines. Water flow was estimated from a linear combination of cumulative diurnal volume changes in intact, excised, and girdled berries (as in Fig. 9.6). Error bars indicate 1 SE,n = 3. (from Greenspan *et al.*, 1996)

shift from xylem-to-phloem-sourced water at veraison. It is clear, however, that at this time there is also an increased rate of sucrose translocation to the fruit (Brown and Coombe, 1985; Coombe *et al.*, 1987), and this must be associated with either an increased transport of the solvent water through the phloem or a greatly increased concentration of sucrose in the phloem sap. The estimated inflow rate through the phloem increased approximately 10-fold after veraison (Greenspan *et al.*, 1994). Although hexose accumulation during ripening constitutes osmotic adjustment, it is unlikely that the observed change in water flow patterns is primarily due to increasing sugar concentrations because berry osmotic potentials decrease only approximately 0.067 $MPa.d^{-1}$ (Fig. 9.1B; Matthews *et al.*, 1987). Furthermore, the water budget data indicate a decrease in xylem inflow after veraison, whereas an effective increased osmotic gradient should increase flow. Consequently, the post-veraison insensitivity of the berry-to-plant water deficits (Fig. 9.3) may be a manifestation of a strong phloem component at veraison, rather than a loss of xylem conductance. Using the same methods in prune (*Prunus domestica*), xylem flows to fruits were clearly dominant during stage II (mid-June), and phloem flows were becoming dominant at the start of stage III (early July) (Shackel, unpublished). However, later in stage III (mid-July) both flows were comparable again, implying the presence of functional xylem. These data suggest that the patterns exhibited during fruit development, in the relative importance of xylem or phloem flows, may be reversible, perhaps depending more on source and/or sink behavior than on a physical loss in xylem continuity/conductance.

Fruit Turgor and Apoplastic Solutes

One important aspect of water relations in fleshy fruits is that substantial levels of solutes, primarily sugars, are accumulated toward the end of fruit development. This is particularly true in grapes, with many varieties reaching solute potentials as low as −3 MPa (Fig. 9.1B). With such low solute potentials, it is reasonable to hypothesize that there may be a mechanism that prevents the development of excessive fruit cell turgor, particularly under environmental conditions that would favor the occurrence of high total water potentials in the plant, such as wet soil and low evaporative demands. Indirect estimates of turgor in Cardinal grapes indicated that turgor was relatively constant (0.2 to 0.4 MPa), because the marked decline in solute potential during development was matched by a parallel decline in fruit total water potential (Matthews *et al*, 1987). Direct measurements of turgor with the cell pressure probe in Cabernet Sauvignon grapes indi-

cated that turgor was within this range (0.3 MPa) at 50 to 60 days after anthesis, but that a marked decline in turgor occurred after this time, with values stabilizing at about 0.03 MPa by 70 days after anthesis (Fig. 9.5). For these berries, the decline in turgor with fruit development was apparently uniform for cells from 100 μm to almost 1 mm below the fruit surface (Fig. 9.6). If fruit cell turgor is low as a result of low fruit total water potential, then it should be possible to hydrate fruit artificially and increase cell turgor. Excised grape berries will hydrate through the fruit pedicel, and after a 24-hour hydration period there was a clear increase in fruit cell turgor (Table 9.1). This indicates that one of the reasons for low cell turgor was a low total water potential (water deficit) in the fruit as a whole, consistent with the low solute potential data shown in Fig. 9.1B. However, the low cell turgor that occurred late in fruit development was also apparent after 24 hours of hydration (Table 9.1), indicating either that full hydration requires substantially longer than 24 hours, or that some other mechanism is responsible for low cell turgor in fruit cells.

One mechanism that has been proposed to explain lower than expected turgor in tomato fruit pericarp cells, despite tissue hydration, is the presence of apoplastic solutes (Shackel *et al.*, 1991). Evidence for the presence of apoplastic solutes has also been found in growing stems of pea, soybean, and cucumber (Cosgrove and Cleland, 1983) and in stems of sugarcane (Welbaum and Meinzer, 1990), which, like fruit tissue, accumulate substantial concentrations of sugars as a normal part of development.
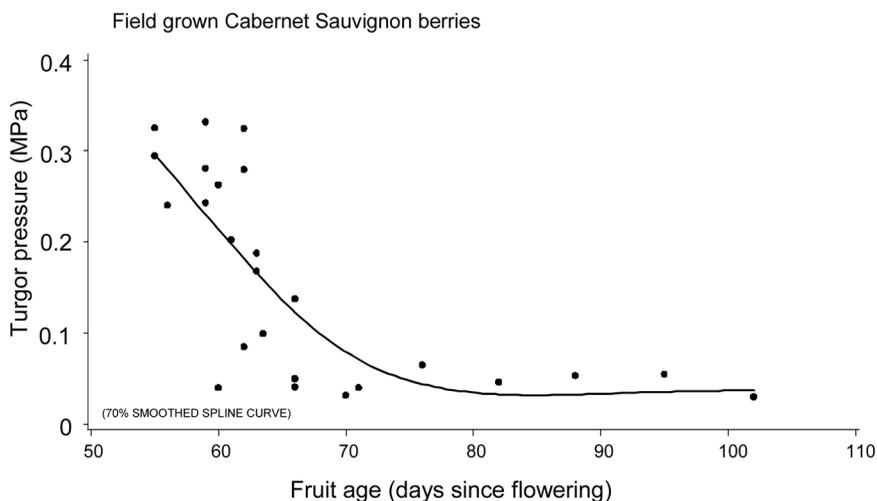
Figure 9.5   Mesocarp cell turgor at various days after flowering for Cabernet Sauvignon berries.
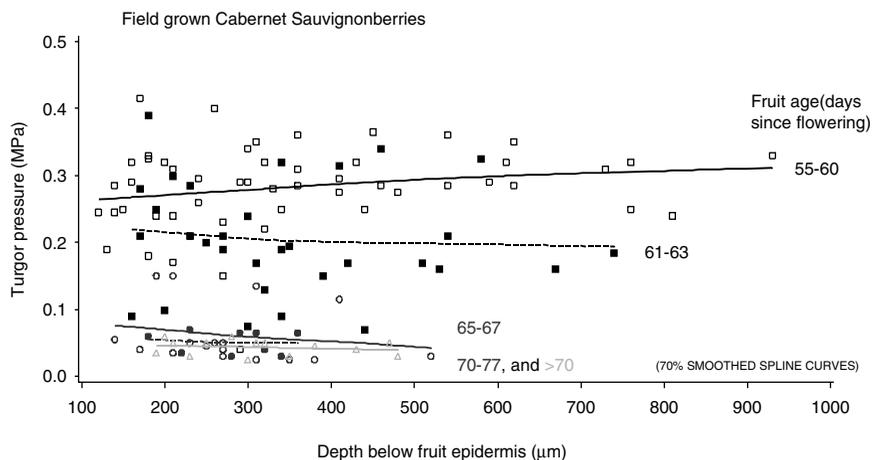
Figure 9.6 Mesocarp cell turgor at various depths beneath surface of Cabernet Sauvignon berries. Curves are for data collected at different days after flowering.

The presence of solutes in the apoplast of a sink tissue, such as a fruit, are broadly consistent with models of phloem transport that involve an apoplastic sugar unloading step from the phloem, and are also consistent with the Münch pressure-flow hypothesis in that phloem turgor will be reduced, and hence phloem transport increased, by the presence of apoplastic solutes; however, the consequences of apoplastic solutes for water transport in the xylem are less clear. It may be that there must be a favorable stem-to-fruit total water potential gradient (fruit lower than stem) for growth to occur. However, even though apoplastic solutes will

Table 9.1 Increase in berry weight after a 24-hour hydration period with the fruit pedicel immersed in tap water and the turgor of berry cells before and after hydration

Berry Age (Days from Anthesis)	24-Hour Increase in Berry FW (mg)	Cell Turgor Pressure (MPa)	
		Prehydration	Posthydration
30	56	0.31	0.44
45	64	0.25	0.42
60	56	0.23	0.34
75	32	0.09	0.19
90	26	0.02	0.07

Hydration was performed in a humidified chamber under laboratory conditions (20 -25˚ C).

reduce fruit total water potential and also fruit cell turgor, they should not contribute to a matric (tension) gradient in the xylem, and hence should not directly influence water transport through the xylem. Unfortunately, when fruit total water potential is measured psychrometrically (Matthews *et al.*, 1987), it is impossible to separate apoplastic solute effects from apoplastic matric effects.

A key unresolved issue is the spatial scale at which apoplastic solutes may be regulated in plant reproductive tissues such as fruits and seeds. Bradford (1994) proposed the concept of a localized semipermeable apoplast barrier near the embryo, so that unloaded solutes would be confined to the apoplast in the vicinity of the embryo, rather than being free to flow back toward the leaves in the xylem. In the case of seeds, which convert most of the imported soluble carbohydrate into starch or other insoluble compounds, most evidence indicates that excess water arrives via phloem import, and that this excess water is recirculated back to the stem via the xylem (Pate *et al.*, 1985). In the case of fruits, however, particularly grapes, most of the imported carbohydrate remains soluble and is at high concentrations throughout essentially all of the fruit flesh. Hence, a similar mechanism would require either for the majority of the fruit apoplast to be semipermeable or for the barrier to be between the plant and the fruit as a whole, perhaps associated with the fruit pedicel. In theory, the presence of a semipermeable apoplast would solve the problem of xylem tension causing backflow of solutes from the fruit to the plant, but under conditions of minimal xylem tension (wet soil, low evaporative demand) such a barrier should also cause an osmotic pressure to develop within the fruit apoplast, presumably causing either apoplastic swelling or a phenomenon such as guttation.

It may be possible that the entire fruit xylem and apoplastic space do experience a normal diurnal range in tension, but that a low and consistent turgor is maintained by an exchange of solutes between the symplast and the apoplast at the cellular level. Because the volume of the apoplast is very small relative to the symplast, a minimal export or import of a suitably mobile solute (potassium?) across the plasma membrane would be required to cause a substantial change in apoplastic solute potential for any given cell. Under conditions of increasing water potential (declining apoplastic tension), solute export would prevent cell turgor from increasing, and even though the exported solutes would begin diffusing into the vascular system, the loss of solute from the fruit as a whole would be limited by the relatively long distance and limited cross section of the vascular pathway, compared to the size of the fruit. As water potential decreased (apoplastic tensions increase), either during the daytime or as a result of limited soil moisture, solute import from the apoplast would maintain turgor. If fruit cell turgor were maintained in this way, then fruit volume would

also be maintained, and this should limit the quantity of water (and solute) that may be withdrawn from the fruit via the xylem as xylem tensions increase. Hence, a localized process of apoplastic solute regulation, perhaps based simply on cell turgor homeostasis, could account for a number of important aspects of post-veraison fruit water relations in grape: (1) low cell turgor and fruit tissue water potential that are largely independent of changes in plant (and cluster) water potential (uncoupling hypothesis), (2) inability to substantially increase fruit cell turgor by artificial hydration, and (3) a substantial reduction in the flows of water through the xylem. This conceptual model predicts that the sum of the tension (hydrostatic potential) and the osmotic potential in the apoplast will be maintained at a relatively constant value, either with soil drying or with normal diurnal changes in plant transpiration, by compensating changes in both components. It should be possible to test at least one of these components if direct measurements of xylem tension (Wei *et al.*, 2001) can be accomplished in the tracheids of grape berries.

Conclusions

Fleshy fruit growth and development is of great practical importance, as well as representing a challenge for our understanding of long and short distance water and solute transport. Based on many lines of evidence, the water transport that is required for fruit growth changes from a xylem to a phloem-dominated pathway over the course of fruit development, and in grape this change in the relative importance of the two pathways appears to occur rather abruptly. This change is associated with an apparent uncoupling of fruit water status from plant water status, and may play a role in the well-known ability of grapes to continue to accumulate substantial concentrations of solutes (sugars) under limited soil water conditions, but the basis for the change in pathway dominance and for water status coupling is unclear. Direct measurements have demonstrated that fruit cell turgor is relatively low in grape, and that it declines progressively during development, despite a progressive increase in whole fruit, and presumably fruit cell, solute concentration. Because cell turgor also remains low after a 24-hour hydration, we propose that turgor is being depressed by the presence of apoplastic solutes. We further suggest that a regulated partitioning of these solutes between the symplast and apoplast, for the purposes of turgor homeostasis, may account for the change in vascular pathway dominance and the apparent uncoupling of fruit from plant water status.

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