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Water Potential, Osmotic Potential, and Cell Turgor in Developing European Plums

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Abstract. **Neck shrivel is a fruit disorder of european plum (*Prunus domestica* L.). We investigate whether an asymmetrical distribution of osmolytes might explain the observations of a turgid stylar end and a flaccid stem end, in a selection of 17 plum cultivars sourced from two sites. The osmotic potential (Ψ_Π) of the juices expressed from stem or stylar end fruit samples decreased (became more negative) during development. The cell turgor (Ψ_P) slightly increased during development up to 352 ± 42 kPa at 78 days after full bloom (DAFB) in the stem end and up to 331 ± 51 kPa at 92 DAFB in the stylar end, and then decreased. At maturity, Ψ_P averaged 22 ± 3 kPa in the stem end and 22 ± 4 kPa in the stylar end. These values are negligibly low compared with the very negative values of Ψ_Π in the stylar end (−3188 ± 73 kPa) and stem end (−3060 ± 74 kPa). There was a transient gradient in Ψ_Π between stylar end and stem end that almost disappeared by maturity. Marked differences in Ψ_Π and its distribution were measured across 17 cultivars. In the majority (14), Ψ_Π was more negative at the stylar end than at the stem end. A more negative Ψ_Π in the stem was only detected in 'Aprimira', 'Topfive', and 'Tophit'. Our results demonstrate that cell Ψ_P is very low and is essentially independent of Ψ_Π in developing european plums. In most cultivars, Ψ_Π in the stylar end is more negative than in the stem end. The absence of an axial gradient in Ψ_P and the small differences in Ψ_Π between the stem and stylar end make both factors unlikely candidates for explaining neck shrivel.**

Neck shrivel is a fruit disorder of european plum. Shriveled fruit is perceived as of low quality so there is a marked decrease in value at market. Susceptibility to neck shrivel varies among cultivars and between seasons. This complicates systematic research on cause-and-effect relationships. Earlier studies have established an elevated skin permeability to water vapor due to an increased frequency of microcracks at the stem end of the fruit, and this may contribute to neck shrivel in symptomatic fruit of susceptible 'Hauszwetsche' clones. The water vapor permeability of the nonshriveled, stylar end of the same cultivar was lower and had only a few, randomly oriented, microcracks. There were no differences in microcracking or in skin permeance in the stem and stylar ends of fruit of a nonsusceptible cultivar (Knoche et al. 2019). It is not known if microcracking is the only factor involved in neck shrivel. A backflow of xylem water (from fruit to the tree) has been excluded as a factor (Khanal et al. 2021; Winkler and Knoche 2021).

An alternative explanation for neck shrivel is an asymmetric distribution of the osmotic potential (ψ_Π) within the plum tissues. Assuming the fruit to be at equilibrium water potential (ψ), a more negative ψ_Π at the stylar end, as compared with the stem end, would result in a higher turgor potential (ψ_P) at the stylar end, compared with the stem end. This could lead to a turgid stylar end and a flaccid stem end.

The objective of this study was to establish (1) whether there is a gradient in ψ_Π within plums, and (2) whether changes in ψ_Π during development, are related to changes in ψ_P. We focused on the stylar end and stem end regions of the fruit because a differential response in these regions could contribute to neck shrivel.

Materials and Methods

Plant material. Mature fruit of *Prunus domestica* L. were sampled in orchards of the Federal Fruit Variety Office at Wurzen (lat. 51°22′ N; long. 12°45′ E) (cultivars Auerbacher, Bühler Frühzwetsche, Cacaks Schöne, Chrudiminer Zwetsche, Czernowitzer, Elena, Hauszwetsche Wolff, Hauszwetsche zum Felde, Italienische Zwetsche, Katinka, Lützelsachser, Oullins Reneclaude, and Tegera) or in orchards of the Horticultural research station of the Leibniz-University at Ruthe (lat. 52°14′ N, long. 9°49′ E) (cultivars Aprimira, Auerbacher, Cacaks Schöne, Elena, Hanita, Hauszwetsche Wolff, Topfive, Tophit, and Toptaste). All trees were cultivated according to current regulations for integrated fruit production. Fruit were sampled randomly from a minimum of three trees per cultivar, and held for no longer than 36 h at 2 °C.

Analyses. Fruit used in the experiments was characterized by determining fruit mass and skin color (CM-2600d; Konica Minolta, Osaka, Japan). For determination of the ψ_Π values, the fruit was cut longitudinally into halves along the suture. The pit was removed. Juice was expressed from one of the halves using a garlic press. Assuming radial (or at least bilateral) symmetry, this value represents the fruits' mean ψ_Π. To determine if an axial gradient in ψ_Π existed within the fruit, the remaining half-fruit was sliced perpendicularly to its longitudinal axis. It was cut into two slices of equal thickness until 105 DAFB or into four slices of equal thickness after 105 DAFB, until maturity. Fruit from the cultivar comparison were also cut into four slices. The juice was expressed from each slice. The osmolarity of each juice sample was determined by water vapor pressure osmometry (VAPRO 5520 and 5600; Wescor, Logan, UT, USA) and the value of ψ_Π was calculated.

The value of ψ_P was quantified in the stem end and the stylar end of developing 'Hauszwetsche Wolff' and 'Elena' fruit using a cell pressure probe (CPP) (Steudle 1993). The CPP comprised a glass capillary filled with silicone oil and was connected to a pressure transducer (26PCGFA6D; Honeywell Sensing and Control, MN, USA). The CPP was mounted on a micromanipulator. To determine the ψ_P, the glass capillary was carefully inserted into a parenchyma cell in the outer mesocarp under a horizontal microscope (≈200 to 400 μm below the skin surface). Upon insertion into a cell, the pressure inside the capillary equilibrated with the cell's internal ψ_P. The peak pressure of the system was recorded as described previously (Knoche et al. 2014, Schumann et al. 2014). We analyzed only those insertions that (1) maintained a leak-free seal between capillary and the cell, when subjected to a small, transient, increase in pressure, and (2) where the pressure returned to atmospheric (i.e., the pressure just before the insertion) immediately after the capillary had been withdrawn from the fruit. Only when these two conditions had been met, was the peak pressure recorded and taken as an estimate of the cell's ψ_P. A minimum of five fruit were measured in the two regions, per sampling date, and per cultivar.

Statistics. Data are presented as means ± standard errors. Data were analyzed by analysis of variance using the statistical software package SAS (version 9.4; SAS Institute, Cary, NC, USA).

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Results and Discussion

The time course of increase in fruit mass revealed the classical double-sigmoid growth pattern characteristic of stone fruit (Fig. 1A). The initial stage I is accompanied by a small increase in fruit mass due to cell division in the pericarp. During stage II, the endocarp and the embryo develop with little overall change in fruit mass. During stage III (also known as final swell), fruit mass increases rapidly due to cell expansion in the mesocarp (Lilleland and Newsome 1934; Tukey 1934) (Fig. 1A). Based on the changes in fruit mass and in skin color in 'Hauszwetsche Wolff', the stage I/II transition occurred at ≈55 DAFB, and the stage II/III transition at about 100 DAFB.

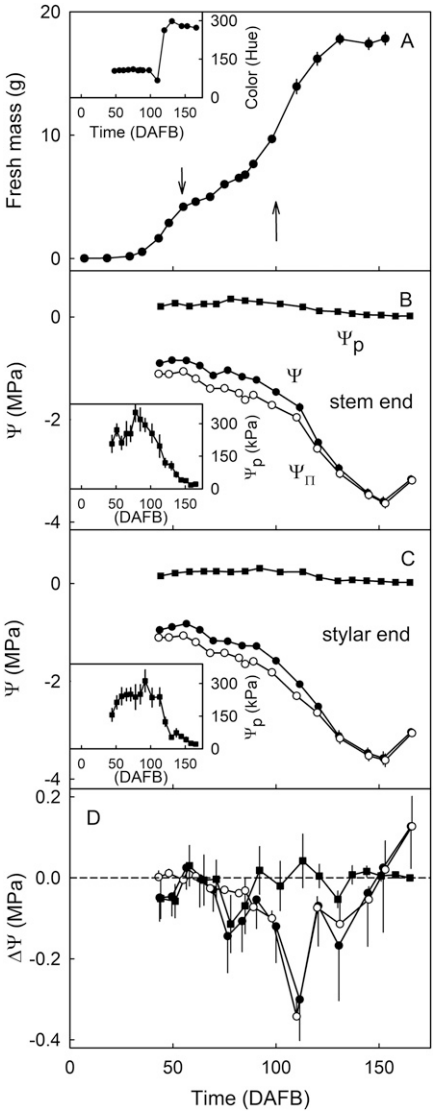

Fig. 1. Time course of change in fruit mass (**A**), in skin color as indexed by the Hue angle (inset in **A**), in change in osmotic potential (ψ_Π), in turgor (ψ_P) and in calculated water potential (ψ) in the stem end (**B**) and the stylar end (**C**) of 'Hauszwetsche Wolff' european plum. Arrows in (**A**) indicate the phase I/II and phase II/III transition. Insets in (**B**) and (**C**) represent the ψ_P redrawn on a different scale. Differences between the stem and stylar ends of the same fruit in their water potential ($\Delta\psi$), and in their water potential components, osmotic potential ($\Delta\psi_\Pi$) or turgor potential ($\Delta\psi_P$) (**D**). The Δ values were calculated by subtracting the stem end values of ψ_Π, ψ_P, and ψ from their respective stylar end values. Because both ψ and ψ_Π have negative signs, negative values for $\Delta\psi$ and $\Delta\psi_\Pi$ indicate that the stylar end of the fruit is more negative than the stem end. The number of replicates were as follows: 20 to 30 for mass and color, 8 to 10 for ψ_Π, and 10 for turgor potential.

The ψ_Π value of the juice expressed from the stem end and stylar end regions generally decreased (become more negative) throughout fruit development. The rate of decrease was slower during stages I and II, but increased markedly during stage III (Fig. 1B,C). The values of ψ_P recorded either in the stem end or in the stylar end slightly increased to a maximum of ≈352 ± 42 kPa at 78 DAFB in the stem end and 313 ± 51 kPa at 92 DAFB in the stylar end region. Thereafter, the value of ψ_P decreased rapidly again during stage III and was the same in the stem end (22 ± 3 kPa) and the stylar end (22 ± 4 kPa) at maturity. The ψ_P values at maturity were negligibly low compared with the very negative values of ψ_Π at the stylar (−3188 ± 73 kPa) and stem ends (−3060 ± 74 kPa). That is, numerically, ψ_P was only ≈0.7% of ψ_Π, hence, the calculated value for ψ (where $\psi = \psi_\Pi + \psi_P$) was essentially the same as that for ψ_Π. Similar results were obtained for 'Elena' (data not shown). Neither 'Hauszwetsche Wolff' nor 'Elena' showed any symptoms of neck shriveling in the season in which these measurements were made. The ψ_Π were in the same range as those reported earlier for plums (Grappadelli et al. 2019; Knoche et al. 2019; Winkler and Knoche 2018).

The low mean values for ψ_P, and the transient increase in ψ_P at the stage II/III transition, and the essential equivalence of ψ_Π and ψ are not unique features of a developing plum. These three have also been reported for developing grapes (Thomas et al. 2006; Matthews et al. 2009) and sweet cherries (Knoche et al. 2014; Schumann et al. 2014). It is interesting that the transient increase in ψ_P in plums, in grapes, and in sweet cherries occurs when the phase of rapid solute import begins. The following explanation may be offered. The initial increase in ψ_P results from a more negative ψ_Π at a constant ψ. The reason for the subsequent decrease in ψ_P while ψ_Π keeps decreasing until maturity is not clear. A low value of ψ_P in fleshy fruits with very negative ψ_Π is accounted for by an accumulation of apoplastic solutes (Wada et al. 2008, 2009). Apoplastic solutes decrease the gradient in ψ_Π between symplast and apoplast, thereby decreasing turgor. Apoplastic solutes, in turn, may result from an apoplastic unloading of the phloem or a mismatch between phloem unloading and the loading of solutes into the cells. To our knowledge, there are no published studies on the mechanism of phloem unloading in european plum (for recent reviews see Falchi et al. 2020; Ma et al. 2019); however, in japanese plum (*Prunus salicina* L.) apoplastic and symplastic phloem unloading coexist (Grappadelli et al. 2019). In hybrid grape berries (*Vitis vinifera* ×*Vitis labrusca* L.), unloading of the phloem switches from symplastic to apoplastic unloading at or immediately before veraison, when the rapid accumulation of solutes begins (Zhang et al. 2006). If this also occurred in european plum, it would account for an accumulation of apoplastic solutes and the decrease in ψ_P while ψ_Π decreases continuously until maturity.

Calculating the difference in the value of ψ_Π between the stylar end and the stem end of the fruit revealed a transient gradient in ψ_Π and ψ during stage II, but this rapidly disappeared. The gradient resulted from a more negative ψ_Π at the stylar end that reflected an earlier accumulation of osmolytes in the stylar end, as compared with the stem end. This observation has also been reported for grapes and is explained by a basipetal wave of maturation and ripening: the stylar end being more advanced than the stem end (Castellarin et al. 2011). As in grape, maturation is apparently initiated in the stylar end of a plum. An additional factor could be the decrease in xylem functionality during stage III development that also occurs in european plum and this too progresses basipetally: the stylar end first, then toward the stem end (Khanal et al. 2021; Winkler and Knoche 2021). It is worth noting that there was no gradient in ψ_P between stylar end and stem end.

The cultivar comparison at maturity revealed marked differences in the values of ψ_Π and their spatial distributions (Table 1). The most negative values of ψ_Π were in 'Hauszwetsche Wolff' and 'Topfive', whereas the least negative ones were in 'Katinka' and 'Lützelsachser'. In most cultivars, ψ_Π was more negative at the stylar end of the fruit than at the stem end. In 'Chrudiminer Zwetsche', 'Elena' (site Ruthe), 'Hauszwetsche Wolff' (site Ruthe), 'Hauszwetsche zum Felde', 'Katinka', 'Lützelsachser', and 'Oullins Reneclaude' there were no significant gradients. A reverse gradient, where ψ_Π in the stem end was more negative than in the stylar end, was measured in 'Aprimira', 'Topfive', and 'Tophit'. The latter was also observed in our earlier study, particularly for fruit that suffered from neck shriveling (Knoche et al. 2019). It may therefore be hypothesized that a more negative ψ_Π in the stem end could result from excessive transpiration leading to a concentration of the osmolytes in the stem end region of the fruit. The excessive transpiration, in turn, resulted from severe microcracking of the stem end that probably was causal in neck shrivel.

Based on the data in this and our earlier study, a direct role of gradients in ψ_P or ψ_Π in neck shrivel is unlikely. First, based on our hypothesis, a flaccid stem end (low ψ_P) and a turgescent stylar end (high ψ_P) would account for neck shrivel. However, there is no evidence for a gradient in ψ_P between the stylar end and stem end region. Also, the ψ_P of mature fruit were negligibly low in both regions. Second, a gradient in ψ_Π toward the stem end can be accounted for by excessive transpiration through microcracks. This gradient, however, is in the opposite direction as the one expected if the ψ_Π was causal (Knoche et al.

Table 1. Distribution of osmotic potentials of expressed juice (ψ_Π) of selected cultivars of european plum along the stem/stylar scar axis. The values of ψ_Π represent the mean ψ_Π of the fruit at maturity. The distribution ψ_Π within the fruit is indexed as the gradient of ψ_Π values in a series of tissue slices taken along the stem/stylar scar axis, minus the mean ψ_Π of the same fruit. Four slices of equal thickness were cut perpendicular to the longitudinal axis of the fruit. These slices are termed stem end, stem end equatorial, stylar end equatorial, and stylar end, respectively. The slice ψ_Π values were normalized by subtracting the fruit mean ψ_Π from the ψ_Π of the slice. The range of ψ_Π within a fruit ($\Delta\psi_\Pi$) of a cultivar was calculated as the difference in ψ_Π value of the stylar end slice minus that of the stem end slice. The number of replicates was 8 to 10.

			$\Delta\psi_\Pi$ (MPa)				
Cultivar		ψ_Π (MPa)	Stem end	Stem end equatorial	Stylar end equatorial	Stylar end	Range in $\Delta\psi_\Pi$ (MPa)
Aprimira	Ruthe	−2.3 ± 0.1	−0.17 ± 0.05 a	−0.10 ± 0.04 a	0.14 ± 0.04 b	0.33 ± 0.03 c	0.50 ± 0.05
Auerbacher	Ruthe	−3.0 ± 0.1	0.09 ± 0.07 a	0.07 ± 0.06 a	−0.05 ± 0.05 ab	−0.25 ± 0.05 b	−0.35 ± 0.06
Bühler Frühzwetsche	Wurzen	−2.3 ± 0.0	0.12 ± 0.04 a	0.06 ± 0.03 ab	−0.02 ± 0.02 b	−0.20 ± 0.03 c	−0.32 ± 0.06
Cacaks Schöne	Ruthe	−2.2 ± 0.1	0.11 ± 0.04 a	0.07 ± 0.04 ab	−0.01 ± 0.03 ab	−0.07 ± 0.04 b	−0.18 ± 0.04
Cacaks Schöne	Wurzen	−2.4 ± 0.1	0.28 ± 0.06 a	0.08 ± 0.07 ab	−0.19 ± 0.09 bc	−0.40 ± 0.10 c	−0.68 ± 0.10
Chrudiminer Zwetsche	Wurzen	−2.9 ± 0.1	−0.04 ± 0.06 ns	−0.04 ± 0.07 ns	−0.08 ± 0.08 ns	−0.14 ± 0.09 ns	−0.09 ± 0.05
Czernowitzer	Wurzen	−3.3 ± 0.1	0.50 ± 0.08 a	0.14 ± 0.07 b	−0.29 ± 0.06 c	−0.62 ± 0.06 d	−1.11 ± 0.09
Elena	Ruthe	−2.3 ± 0.1	0.03 ± 0.04 ns	−0.03 ± 0.04 ns	−0.08 ± 0.04 ns	−0.06 ± 0.03 ns	−0.10 ± 0.03
Elena	Wurzen	−2.8 ± 0.1	0.22 ± 0.05 a	0.03 ± 0.05 ab	−0.08 ± 0.06 b	−0.17 ± 0.07 b	−0.39 ± 0.09
Hanita	Ruthe	−2.7 ± 0.1	0.17 ± 0.10 a	0.06 ± 0.09 ab	−0.10 ± 0.08 ab	−0.22 ± 0.07 b	−0.40 ± 0.11
Hauszwetsche Wolff	Ruthe	−3.1 ± 0.1	−0.09 ± 0.05 ns	−0.09 ± 0.02 ns	−0.00 ± 0.03 ns	0.03 ± 0.04 ns	0.13 ± 0.08
Hauszwetsche Wolff	Wurzen	−3.8 ± 0.1	0.42 ± 0.10 a	−0.06 ± 0.05 b	−0.11 ± 0.03 b	−0.14 ± 0.05 b	−0.56 ± 0.13
Hauszwetsche zum Felde	Wurzen	−3.0 ± 0.1	−0.09 ± 0.05 ns	−0.05 ± 0.03 ns	−0.05 ± 0.03 ns	−0.04 ± 0.02 ns	0.05 ± 0.06
Italienische Zwetsche	Wurzen	−3.4 ± 0.1	0.27 ± 0.09 a	−0.04 ± 0.11 ab	−0.25 ± 0.11 b	−0.34 ± 0.11 b	−0.61 ± 0.06
Katinka	Wurzen	−1.6 ± 0.0	−0.02 ± 0.03 ns	0.02 ± 0.03 ns	0.04 ± 0.04 ns	−0.05 ± 0.04 ns	−0.03 ± 0.04
Lützelsachser	Wurzen	−2.1 ± 0.1	0.10 ± 0.06 ns	0.08 ± 0.06 ns	0.04 ± 0.05 ns	−0.07 ± 0.05 ns	−0.16 ± 0.06
Oullins Reneclaude	Wurzen	−2.8 ± 0.1	0.09 ± 0.07 ns	0.07 ± 0.07 ns	0.03 ± 0.06 ns	−0.01 ± 0.05 ns	−0.10 ± 0.04
Tegera	Wurzen	−2.6 ± 0.1	0.24 ± 0.07 a	0.16 ± 0.09 a	0.01 ± 0.11 ab	−0.34 ± 0.11 b	−0.59 ± 0.09
Topfive	Ruthe	−3.8 ± 0.1	−0.10 ± 0.04 a	0.04 ± 0.03 ab	0.11 ± 0.05 b	0.08 ± 0.03 b	0.18 ± 0.04
Tophit	Ruthe	−2.9 ± 0.1	−0.20 ± 0.10 a	−0.08 ± 0.12 ab	0.17 ± 0.09 ab	0.28 ± 0.08 b	0.48 ± 0.08
Toptaste	Ruthe	−3.7 ± 0.1	0.16 ± 0.06 a	0.03 ± 0.05 ab	−0.05 ± 0.07 ab	−0.12 ± 0.09 b	−0.27 ± 0.11
Grand Mean		−2.8 ± 0.0	0.10 ± 0.02	0.02 ± 0.02	−0.04 ± 0.02	−0.12 ± 0.02	−0.23 ± 0.03

Analysis of variance revealed significant interaction, hence means were compared within cultivars. Means within rows followed by the same letter are not significantly different based on a Tukey's studentized range test, $P < 0.05$. ns = nonsignificant.

2019). Third, the lack of symptomatic fruit in the present study demonstrates that a more negative ψ_Π in the stylar end is not sufficient to dehydrate the stem end. If the stylar end was dehydrating the stem end, we would expect the ψ_P of the stylar end to be higher than that of the stem end. This, however, was not the case, indicating that hydraulic resistance of the flesh to water movement is significant. Unfortunately, in the season in which this study was conducted, there was no fruit with neck shriveling. Thus, it is inconclusive for this hypothesis that there was no significant correlation between the gradient in ψ_Π of the fruit or absolute ψ_Π and the occurrence of microcracks (Knoche, unpublished data).

It is interesting that for the three cultivars, 'Cackaks Schöne', 'Elena', and 'Hauszwetsche Wolff', obtained from two different sites, Ruthe and Wurzen, the fruit from Wurzen recorded more negative values of ψ_Π and steeper gradients in ψ_Π than those from Ruthe. These observations do demonstrate that site factors (soil, or management, or microenvironment, etc.) can affect gradients in ψ_Π (Falchi et al. 2020).

Conclusion

Our results demonstrate that cell ψ_P is consistently low and is essentially independent of ψ_Π in developing european plums. This observation aligns closely with nearly all fleshy fruit species so far investigated. As expected, ψ_Π becomes increasingly negative during fruit development, the decrease being more rapid during stage III than during stages I and II. The absence of significant levels of ψ_P throughout fruit development means that the values of ψ_Π and of ψ are closely similar numerically. There were no significant differences in ψ_P recorded between stylar end and stem end. In most cultivars examined here, ψ_Π in the stylar end is more negative than in the stem end. The absence of an axial gradient in ψ_P and the small differences in ψ_Π between the stem and stylar end make both factors unlikely candidates for explaining neck shrivel.

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