Characterizing Neck Shrivel in European Plum

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Abstract. Neck shrivel is a physiological disorder of European plum (Prunus domestica L.) fruit, characterized by a shriveled pedicel end and a turgent granular stylar end. Affected fruit are perceived as of poor quality. Little is known of the mechanistic basis of neck shrivel, but microcracking of the cuticle has been implicated. The objective of our study was to quantify transpiration through the skin surfaces of European plums with and without symptoms of neck shrivel. Cumulative transpiration increased linearly with time and was greater in the susceptible European plum cultivar Hauszwetsche Wolff with neck shrivel, compared with fruit of the same cultivar but without neck shrivel and compared with fruit of the non-susceptible unnamed clone PS-112. Cumulative transpiration of epidermal skin segments (ES) excised from symptomatic ‘Hauszwetsche Wolff’ from near the pedicel end exceeded that from ES excised from near the stylar end. The permeance of ES from near the pedicel end of ‘Hauszwetsche Wolff’ with neck shrivel (12.4 ± 2.6 × 10⁻⁴ m s⁻¹) exceeded that of ES from near the stylar end (2.9 ± 0.8 × 10⁻⁴ m s⁻¹) 4.3-fold. However, in the clone PS-112, the same difference was only 1.6-fold (1.3 ± 0.8 × 10⁻⁴ m s⁻¹ vs. 0.8 ± 0.3 × 10⁻⁴ m s⁻¹). Microscopy revealed numerous microcracks near the pedicel end of symptomatic ‘Hauszwetsche Wolff’ fruit but markedly fewer microcracks near the stylar end. The microcracks near the pedicel end were located parallel to the pedicel/style axis, whereas those near the stylar end were randomly oriented. Juices extracted from near the pedicel end of susceptible cultivars had consistently more negative osmotic potentials [ψ5 (e.g., for Doppelte Hauszwetsche −5.1 ± 0.1 MPa)] than those from near the stylar end (e.g., for Doppelte Hauszwetsche −4.0 ± 0.1 MPa) or that from fruit without symptoms of neck shrivel (e.g., for pedicel end and stylar scar regions of Doppelte Hauszwetsche −3.8 ± 0.1 vs. −3.3 ± 0.1 MPa, respectively). Our results indicate that increased transpiration through microcracks near the pedicel end may contribute to neck shrivel but that the causes of neck shrivel are likely more complex.

Neck shrivel is a nonpathogenic, physiological disorder of European plum that occurs preharvest during late fruit development and that continues to develop postharvest. Symptomatic fruit is perceived to be of poor quality so has reduced commercial value (Widmer and Stadler, 2003). Visual symptoms are a loss of turgescence in the pedicel (proximal) end of the fruit, whereas the stylar (distal) end remains turgent. Cultivars differ in susceptibility to neck shrivel, but several commercial cultivars are susceptible. In Germany, these include several clones of ‘Hauszwetsche’.

There has been no systematic research on neck shrivel in European plum. Causes of the disorder are unknown. The lack of a mechanistic understanding makes it difficult to derive effective counterstrategies for breeders or to develop cultural practices for its mitigation. European plum is not the only fruit susceptible to neck shrivel. European plums (e.g., for Doppelte Hauszwetsche −5.1 ± 0.1 MPa)] than those from near the stylar end (e.g., for Doppelte Hauszwetsche −4.0 ± 0.1 MPa) or that from fruit without symptoms of neck shrivel (e.g., for pedicel end and stylar scar regions of Doppelte Hauszwetsche −3.8 ± 0.1 vs. −3.3 ± 0.1 MPa, respectively). Our results indicate that increased transpiration through microcracks near the pedicel end may contribute to neck shrivel but that the causes of neck shrivel are likely more complex.

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Materials and Methods

PLANT MATERIAL. Ripe fruit of European plum cultivars (Hauszwetsche Wolff, Doppelte Hauszwetsche, Hauszwetsche Etscheid, Toptaste) and of the unnamed clone P5-112 were sampled from experimental orchards at the horticultural research stations of the State Education and Research Center of Viticulture, Horticulture and Rural Development Rheinpfalz, Ahrweiler, Germany (lat. 50°17'32"N, long. 7°05'E) and of the research station of the Leibniz University Hannover in Ruthe, Germany (lat. 52°14'14"N, long. 9°49'E). The cultivars Hauszwetsche Wolff, Doppelte Hauszwetsche, Hauszwetsche Etscheid, and Toptaste are considered susceptible to neck shrivel, whereas the unnamed clone P5-112 is not. All trees were grafted on ‘GF 655’ rootstocks. Fruit were selected for uniformity of size and color and were processed fresh or held at 4°C for no longer than 7 days before processing.

TRANSPIRATION ASSAYS. For transpiration assays, fruit with and without neck shrivel symptoms were selected. Transpiration was quantified on a whole-fruit basis or using ES mounted in stainless-steel diffusion cells (Knoche et al., 2000). ES were excised using a razor blade, carefully blotted, and then mounted on diffusion cells using high-vacuum grease (Korasilon Paste hochviskos; Kurt Obermeier, Bad Berleburg, Germany). Diffusion cells were filled with deionized water and then sealed with clear transparent tape. Whole fruit and the diffusion cells were then placed in a closed polyethylene box above dry silica gel at 22°C. The diffusion cells were placed upside down such that the ES in the orifice faced the silica gel. Fruit and/or ES were weighed repeatedly. The rate of transpiration ($F$) was then determined as the slope of a regression line fitted through a plot of cumulative mass vs. time. The permeance ($p$) was calculated using Fick’s law of diffusion:

$$p = \frac{F}{A \times \Delta C} = \frac{F}{A \times (C_i - C_o)}$$

The $F$ of water vapor across the skin per unit time was divided by the product of the transpiring skin surface area of the ES ($A$) and the driving force ($\Delta C$) for water transport; i.e., the difference in water vapor concentration between the cut inner surface of the ES ($C_i$) and the outer surface of the ES ($C_o$). Because the water vapor concentration above dry silica gel is essentially zero (Geyer and Schönheit, 1988), the concentration of water vapor on the inner surface of the ES represents the driving force for transpiration. The $C_i$ equals the water vapor concentration at saturation at the respective temperature. Values for $C_i$ are tabulated for various temperatures (Nobel, 1999). The permeance estimate so obtained

Table 1. Permeance of epidermal skin segments excised from pedicel end and stylar end regions of the cultivar Hauszwetsche Wolff and the unnamed clone P5-112 of European plums. Fruit of ‘Hauszwetsche Wolff’, but not of P5-112, showed typical symptoms of neck shrivel near the pedicel end.

| Cultivar/clone     | Pedicel end | Stylar end | Mean region |
|--------------------|-------------|------------|-------------|
| Hauszwetsche Wolff | 12.4 ± 2.6  | 2.9 ± 0.4  | 6.0 a*      |
| P5-112             | 1.3 ± 0.8   | 0.8 ± 0.3  | 1.0 b       |
| Mean cultivar      | 3.4 a       | 1.4 b      |             |

*Main effects but not interaction significant by analysis of variance. Main effects differ according to the Tukey Studentized range test, $P \leq 0.05$. 

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is a material constant that is characteristic for a particular fruit surface and, hence, is independent of experimental settings such as surface areas or driving forces. Thus, it is a useful parameter for comparisons of cultivars and treatments.

Using this experimental setup, time courses of whole fruit transpiration of susceptible ‘Hauszwetsche Wolff’ with or without neck shrivel and of the nonsusceptible clone P5-112 were established. Subsequently, the time courses of transpiration of ES excised from near the pedicel and stylar ends of symptomatic ‘Hauszwetsche Wolff’ and from P5-112 (no shrivel) were determined as described previously.

In another experiment, transpiration of excised fruit skins of susceptible ‘Hauszwetsche Etscheid’ with and without neck shrivel were compared. For this experiment, fruit from the same batch were selected for the presence and absence of neck shrivel.

To identify the role of the pedicel in transpiration, transpiration of whole fruit of ‘Doppelte Hauszwetsche Wolff’ with and without the pedicel attached was quantified as described previously (Athoo et al., 2015). To summarize, fruit without pedicels were prepared by cutting the pedicel and sealing the cut end of the pedicel stub (including the pedicel/fruit junction) using epoxy glue (UHU plus schnellfest; UHU, Bühl/Baden, Germany). Subtracting the mean rate of transpiration of fruit without pedicels from the mean rate of fruit with pedicels yielded the mean transpiration rate of the pedicels. Excised detached pedicels were used as a control.

Microcracks. Microcracks were inspected using the procedure described by Peschel and Knoche (2005). To summarize, fruit of susceptible ‘Hauszwetsche Wolff’, ‘Doppelte Hauszwetsche’, and of the nonsusceptible clone P5-112 were immersed for a minimum of 5 min in an aqueous solution containing 0.05% acridine orange. Thereafter, fruit were removed, rinsed with deionized water, and then carefully blotted. ES were excised from the pedicel end and the stylar end such that the orientation of the ES relative to the pedicel/style axis was known. The ES were inspected using a fluorescence microscope (MZ10F and GFP filter module; Leica Microsystems, Wetzlar, Germany). Calibrated images were taken in incident and fluorescent light (DP 73; Olympus, Hamburg, Germany). The lengths and numbers of microcracks per unit area and the orientation of microcracks relative to the pedicel/style axis were quantified using image analysis (cellSens Dimension 1.7.1; Olympus).

Isolation of cuticular membranes (CMS). Epidermal discs were excised from susceptible ‘Hauszwetsche Wolff’ with and without neck shrivel and from nonsusceptible P5-112 using a cork borer (15 mm in diameter). Discs were incubated in 50 mM citric acid buffer containing pectinase [90 mL.L⁻¹ (Panzym Super E flüssig; Novozymes, Bagsvaerd, Denmark)]
and cellulase [5 mL·L⁻¹ (Cellubrix L, Novozymes)] (Orgell 1955). The pH was adjusted to pH 4.0 using NaOH. Microbial growth was prevented by adding NaN₃ at a final concentration of 30 mM. The isolation medium was refreshed periodically until CMs separated. The isolated CMs were carefully cleaned from adhering cellular debris using a soft, camel-hair brush, desorbed in deionized water (at least five changes), air-dried, and then weighed on an analytical balance.

**Osmotic Potential.** To investigate whether the stylar end of fruit with neck shrivel may have dehydrated the pedicel end due to a more negative $\psi_S$, juice was extracted from fruit with or without neck shrivel and the $\psi_S$ quantified. Fruit were cut perpendicular to the pedicel/style axis into three sections of about equal height. $\psi_S$ of the expressed juice from the pedicel-end and the stylar-end sections were determined, and the equatorial sections were discarded. Juice was extracted using a garlic press and analyzed by water vapor pressure osmometry (Vapro 5520; Wescor, Logan, UT). Preliminary experiments established that $\psi_S$ did not differ significantly between crude juice, the supernatant, or the pellet of centrifuged juice (M. Knoche, unpublished data).

**Data Analysis and Terminology.** Data for permeances were log transformed before analysis of variance (ANOVA) to obtain normal distributions. The ANOVA and mean comparisons (Proc. GLM) were carried out using SAS (version 9.1.3; SAS Institute, Cary, NC). We refer to the mass loss that occurs when incubating intact fruit or ES mounted in diffusion cells above dry silica gel as transpiration. The mass loss attributable to respiration is negligibly small. Furthermore, transpiration comprises the loss of water along several parallel pathways, including the cuticle, stomata, microcracks, and—if present—the pedicel surface. Because the density of water at room temperature is $\approx 1$ kg·L⁻¹ (Nobel, 1999) and transpiration was quantified gravimetrically, the data are given in units of mass.

**Results**

The cumulative amount of water transpired increased with time and was significantly larger in susceptible ‘Hauszwetsche Wolff’ and in fruit exhibiting neck shrivel, compared with fruit of the same cultivar without neck shrivel or to fruit of the nonsusceptible clone P5-112 (Fig. 1A).

Also, transpiration of ES excised from symptomatic ‘Hauszwetsche Wolff’ was larger when ES were obtained from near the pedicel end compared with those from near the stylar end. Compared with susceptible ‘Hauszwetsche Wolff’, transpiration through ES of nonsusceptible P5-112 was markedly lower (Fig. 1B). In ‘Hauszwetsche Wolff’, permeance of the ES from neck shrivel fruit taken near the pedicel end exceeded that of those from near the stylar end 4.3-fold, but in P5-112, the pedicel end/stylar end difference was only 1.6-fold (Table 1).

Comparison of fruit with and without neck shrivel within the susceptible ‘Hauszwetsche Etscheid’ revealed consistently greater transpiration for those ES excised from near the pedicel end compared with near the stylar end. In addition, transpiration of skins from symptomatic fruit exceeded that from fruit without neck shrivel, regardless of skin region (Fig. 1C). These differences were all significant at $P \leq 0.05$.

Visual inspection and fluorescence microscopy revealed numerous microcracks in the skin near the pedicel end of symptomatic ‘Hauszwetsche Wolff’ fruit but markedly less near the stylar end of the same fruit. There were only few microcracks in the nonsusceptible P5-112, either near the pedicel or stylar ends (Fig. 2). Furthermore, in ‘Hauszwetsche Wolff’, microcracks near the pedicel end differed from those near the stylar end. The former was more frequent, as indexed by their larger cumulative crack length per unit area and a greater length of microcracks (Table 2). Furthermore, a striking difference was the high degree of orientation of microcracks near the pedicel end of ‘Hauszwetsche Wolff’ fruit with neck

| Position          | n'   | Cumulative crack length per unit area [mean ± SE (mm·mm⁻²)] | Length per crack [mean ± SE (μm)] |
|-------------------|------|-------------------------------------------------------------|-----------------------------------|
| Pedicel end       | 1384 | 0.63 ± 0.08 a'                                              | 256 ± 12 a                        |
| Stylar end        | 25   | 0.16 ± 0.03 b                                               | 226 ± 16 b                        |

Note: Number of microcracks inspected.

Mean separation within columns by the Tukey Studentized range test, $P \leq 0.05$.

**Fig. 3. Frequency distribution of microcracks in European plum of mature ‘Doppelte Hauszwetsche’ European plum. The fruit had typical symptoms of neck shrivel near the pedicel end.**

**Table 2. Cumulative length of microcracks per unit area and length per microcrack in pedicel end and stylar end regions of ‘Doppelte Hauszwetsche’ European plum.**
shrink (Figs. 2 and 3). Frequency distributions of crack orientation indicate essentially all cracks near the pedicel end run parallel to the pedicel/style axis and hence, viewed from the pedicel end, appear oriented like the spokes in a wheel (with the pedicel being the hub).

Generally, the cuticle of the susceptible ‘Hauszwetsche Wolff’ had a greater mass per unit area compared with the nonsusceptible P5-112 (Table 3). Furthermore, in symptomatic ‘Hauszwetsche Wolff’, cuticle mass per unit area near the pedicel end exceeded that near the stylar end of the same fruit and also that near the pedicel end of nonsymptomatic fruit of the same cultivar (Table 3).

For fruit of susceptible european plum cultivars, the $\psi_S$ of juice extracted from near the pedicel end and also from near the stylar end was consistently more negative for fruit with neck shrink than for asymptomatic fruit of the same cultivar (Table 4). Furthermore, whether fruit was symptomatic, the $\psi_S$ of juice from near the pedicel was more negative than that from near the stylar end. Also, the difference in $\psi_S$ between pedicel end and stylar end was greater for fruit with neck shrink than for fruit without neck shrink. ‘Toptaste’ was an exception, where this difference was not significant.

It is particularly interesting that pedicel transpiration also contributed to the water lost by a detached fruit (Fig. 4). Cumulative fruit transpiration increases linearly with time up to 120 h but was slightly greater for fruit with the pedicel attached than with the pedicel detached. Similarly, transpiration from the pedicel (calculated by subtracting the cumulative transpiration of fruit without pedicels from the cumulative transpiration of fruit with pedicels) also increased about linearly up to 120 h (Fig. 4A). In contrast, cumulative transpiration of detached pedicels continued only for about 24 h, the rate (slope) decreasing to zero over this period; i.e., cumulative transpiration asymptomed as the isolated pedicel dried out (Fig. 4B).

Discussion

Our paper establishes that 1) skin permeance is greater near the pedicel end than near the stylar end—particularly so in fruit exhibiting neck shrink symptoms; 2) the high skin permeance of the skin near the pedicel end is likely the result of extensive cuticular microcracking; and 3) in fruit with neck shrink, the $\psi_S$ of the expressed juice is generally more negative near the pedicel end than near the stylar end.

In fruit with neck shrink, the skin near the pedicel end has greater permeance. The cuticle forms the primary barrier to transpiration, and microcracks impair this barrier function. Hence, cuticular microcracking results in increased water vapor permeance in european plum. This is also true in apple [Malus xdomestica Borkh. (Maguire et al., 1999)] and sweet cherry (Knoche and Peschel, 2006). In european plum, the vascular water inflow to the pedicel end does not keep pace with the transpiration water outflow from this part of the fruit. This may contribute to neck shrink and also to the more negative $\psi_S$ of the flesh of the pedicel end of the fruit, compared with that of the stylar end. This observation was consistent among the three cultivars investigated.

It is particularly interesting that the tendency for flesh cell contents to be more concentrated ($\psi_S$ more negative) by increased skin transpiration near the pedicel end was not offset by a redistribution of water from the flesh cells near the stylar end ($\psi_S$ less negative). The axial osmotic gradient would be expected to favor such a basipetal water movement.

Fruit exhibiting neck shrink had more negative $\psi_S$ near both pedicel and stylar ends, compared with nonsymptomatic fruit. Because mature european plum does not have significant turgor, fruit water potential is essentially equal to fruit $\psi_S$ (Knoche et al., 2014). Thus, it is intriguing that within a european plum fruit, there appears to be a standing gradient of water potential between the stylar end (less negative) and the pedicel end (more negative). This indicates the existence of a high internal resistance to water movement that somehow prevents establishment of water potential equilibrium within the flesh of a european plum fruit.

We suggest increased transpiration near the pedicel end of the fruit is not the only factor involved in neck shrink of european plum. Empirical observations indicate that vascular transport also may be involved. For example, it has been reported for a number of fruit crops, [e.g., sweet cherry (Grimm et al., 2017; Winkler et al., 2016)] that a wave of increasing xylem dysfunctionality progresses basipetally from the stylar end of the fruit to the pedicel end. If this was also the case in european plum, a diurnal backflow of xylem water from fruit to tree, under daytime conditions of high foliar evaporative demand, may dehydrate the pedicel end of the fruit (via its still-functional xylem), but not the stylar end of the fruit (which is protected by its now-dysfunctional xylem) (Lang and Volz, 1993, 1998).

Similarly, the pedicel transpiration that occurs postharvest in detached fruit also dehydrates the fruit by pulling water out of it. Hence, the fruit serves as a water reservoir for transpiration that supports the continuing turgescence of the pedicel tissues. Whether the dehydration of the fruit is limited to the pedicel end also will depend on the spatial distribution in the fruit of (still) functional and (now) dysfunctional xylem.

Microcracking pattern. We observed a drastic difference in the patterns of cuticular microcracking between the pedicel end and the stylar end of european plum. The skin near the pedicel end had numerous microcracks per unit area, and these were almost all orientated parallel to the fruit’s pedicel/style axis. Meanwhile, the microcracks in the stylar end were much fewer and were oriented more or less at random. This observation was unexpected, as the european plum cultivars investigated here were essentially symmetrical in shape about the equatorial plane. This symmetry indicates the historical growth trajectories (and thus the patterns of skin strain and stress) in the proximal and distal parts of the fruit would have been very similar. Hence, the reason for the differential pattern of microcracking remains obscure. Several factors may be involved.

Table 3. Mass of cuticle per unit skin area of the european plum cultivar Hauszwetsche Wolff (susceptible) with and without neck shrink and of the unnamed clone P5-112 (nonsusceptible).

| Cultivar/clone | Symptoms | n  | Mass of cuticle per area [mean ± SE (g m⁻²)] |
|---------------|----------|----|------------------------------------------|
|               |          |    | Pedicel end | Stylar end | Pedicel end | Stylar end |
| Hauszwetsche Wolff | None | 25  | 9.6 ± 0.4 a  | 7.8 ± 0.3 b  |
| P5-112 | Shrivels | 25  | 10.4 ± 0.4 a  | 8.7 ± 0.3 b  |
| P5-112 | None | 5   | 5.1 ± 0.2 a  | 4.5 ± 0.1 a  |

*Mean separation within rows by the Tukey Studentized range test, $P \leq 0.05$. 
Microcracking of the cuticle can result from a mismatch between the rate of surface area expansion and that of cuticle deposition as demonstrated in sweet cherry (Lai et al., 2016), grape (Becker and Knoche, 2012), and apple (Lai et al., 2016). This also applies to the equatorial region of European plum, where decreased cuticle deposition, the onset of elastic strain, and the beginning of microcracking all coincide (Knoche and Peschel, 2007). However, to account for differential microcracking between pedicel and stylar ends, one would anticipate that surface expansion and/or cuticular deposition also must differ between the two regions. There is no conclusive evidence for differential cuticle depositions in pedicel and stylar end regions of European plum. In our present study, the pedicel end of the susceptible “Hauszwetsche Wolff” fruit with neck shrivel tended to have a thicker cuticle than the stylar end. The greater mass per unit area of cuticle near the pedicel end of a shrunken fruit (compared with that near the turgescent stylar end) may be the result of a release of elastic strain and thus skin shrinkage during shriveling. This is consistent with the smaller thickness difference between pedicel and stylar ends of nonshriveled fruit of “Hauszwetsche Wolff” fruit with neck shrivel; it is also consistent with the absence of a basal/distal gradient in cuticle deposition in our earlier study (Knoche and Peschel, 2007). Nothing is known of the distribution of growth stresses and strains across the surface of European plums. However, the symmetry of this prolate spheroid makes differential growth stresses and strains between the two poles rather unlikely (see above).

Previous studies established that surface moisture induces microcracks in the cuticle of sweet cherry (Knoche and Peschel, 2006) and apple fruit (Knoche and Grimm, 2008). The surfaces of both crops, however, lack a delicate fine structure in their epicuticular wax. This makes both surfaces easy-to-wet in contrast to European plum. In the latter, the bloom of the epicuticular wax renders the surface difficult-to-wet. This, and the absence of a pedicel cavity to harbor raindrops, makes moisture-induced microcracking less likely in European plum.

Using the theory of plates and shells, Considine and Brown (1981) developed a physical model that predicts the distribution of mechanical stress and the associated failure pattern in a fleshy fruit. For a prolate spheroid, such as the European plum, the model predicts a lengthwise fracture pattern; i.e., the microcracks near the equator will run parallel to the long axis of the fruit. Meanwhile, any cracking near the pedicel and stylar ends will take the form of concentric rings, centered on the pedicel and stylar scar. Again, the observed differential microcracking between the two poles of the symmetric fruit is not accounted for. Clearly, further study is needed to identify the mechanistic basis of the observed highly differential incidence and orientation of cuticular microcracking in European plum.

**Conclusions**

Increased transpiration through microcracks near the pedicel end of susceptible European plum cultivars is an important factor that contributes to neck shriveling. Whether this is the only factor or whether dehydration of the pedicel end while still on the tree via pedicel xylem efflux is also involved remains to be investigated. Furthermore, the mechanistic basis of the pattern of microcracking near the pedicel end is unknown. The “stress relaxation analysis” of fruit skins, as recently proposed, may be helpful in identifying the mechanisms underlying microcracking (Knoche and Lang, 2017; Lai et al., 2016).

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Table 4. Osmotic potential of juice expressed from near the pedicel and stylar ends of susceptible European plum cultivars with and without symptoms of neck shrivel.

| Cultivar         | Symptoms | n  | Pedicel end | Stylar end | Difference |
|------------------|----------|----|-------------|------------|------------|
| Doppelte Hauszwetsche | None     | 20 | 3.8 ± 0.1   | 3.3 ± 0.1  | 0.5 ± 0.1 a |
|                  | Shrivel  | 20 | 5.1 ± 0.1   | 4.0 ± 0.1  | 1.0 ± 0.1 b |
| Hauszwetsche Etscheid | None     | 20 | 3.5 ± 0.1   | 3.3 ± 0.1  | 0.3 ± 0.0 a |
|                  | Shrivel  | 20 | 4.2 ± 0.1   | 3.7 ± 0.1  | 0.4 ± 0.1 b |
| Toptaste         | None     | 20 | 2.5 ± 0.1   | 2.3 ± 0.1  | 0.2 ± 0.0 NS |
|                  | Shrivel  | 5  | 3.8 ± 0.3   | 3.5 ± 0.4  | 0.3 ± 0.2 NS |

*Mean separation within the column “Difference” and within cultivars by the Tukey Studentized range test, *P* ≤ 0.05.
NS = nonsignificant.

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Fig. 4. (A) Time course of cumulative transpiration of susceptible ‘Hauszwetsche Etscheid’ European plum with and without the pedicel and of the pedicel only. Transpiration of the pedicel was determined from detached pedicels or calculated by subtracting the cumulative transpiration of a fruit with its pedicel, from that without it. Data are presented as means ± se. Where error bars are not visible, they are smaller than the plotting symbols. (B) Same data for pedicel transpiration as those shown in A, but now redrawn on a different y-axis scale. se bars were omitted in B for clarity.

Microcracking of the cuticle can result from a mismatch between the rate of surface area expansion and that of cuticle deposition as demonstrated in sweet cherry (Lai et al., 2016), grape (Becker and Knoche, 2012), and apple (Lai et al., 2016). This also applies to the equatorial region of European plum, where decreased cuticle deposition, the onset of elastic strain, and the beginning of microcracking all coincide (Knoche and Peschel, 2007). However, to account for differential microcracking between pedicel and stylar ends, one would anticipate that surface expansion and/or cuticular deposition also must differ between the two regions. There is no conclusive evidence for differential cuticle depositions in pedicel and stylar end regions of European plum. In our present study, the pedicel end of the susceptible “Hauszwetsche Wolff” fruit with neck shrivel tended to have a thicker cuticle than the stylar end. The greater mass per unit area of cuticle near the pedicel end of a shrunk fruit (compared with that near the turgescent stylar end) may be the result of a release of elastic strain and thus skin shrinkage during shriveling. This is consistent with the smaller thickness difference between pedicel and stylar ends of nonshriveled fruit of “Hauszwetsche Wolff”; it is also consistent with the absence of a basal/distal gradient in cuticle deposition in our earlier study (Knoche and Peschel, 2007). Nothing is known of the distribution of growth stresses and strains across the surface of European plums. However, the symmetry of this prolate spheroid makes differential growth stresses and strains between the two poles rather unlikely (see above).

Previous studies established that surface moisture induces microcracks in the cuticle of sweet cherry (Knoche and Peschel, 2006) and apple fruit (Knoche and Grimm, 2008). The surfaces of both crops, however, lack a delicate fine structure in their epicuticular wax. This makes both surfaces easy-to-wet in contrast to European plum. In the latter, the bloom of the epicuticular wax renders the surface difficult-to-wet. This, and the absence of a pedicel cavity to harbor raindrops, makes moisture-induced microcracking less likely in European plum.

Using the theory of plates and shells, Considine and Brown (1981) developed a physical model that predicts the distribution of mechanical stress and the associated failure pattern in a fleshy fruit. For a prolate spheroid, such as the European plum, the model predicts a lengthwise fracture pattern; i.e., the microcracks near the equator will run parallel to the long axis of the fruit. Meanwhile, any cracking near the pedicel and stylar ends will take the form of concentric rings, centered on the pedicel and stylar scar. Again, the observed differential microcracking between the two poles of the symmetric fruit is not accounted for. Clearly, further study is needed to identify the mechanistic basis of the observed highly differential incidence and orientation of cuticular microcracking in European plum.

**Conclusions**

Increased transpiration through microcracks near the pedicel end of susceptible European plum cultivars is an important factor that contributes to neck shriveling. Whether this is the only factor or whether dehydration of the pedicel end while still on the tree via pedicel xylem efflux is also involved remains to be investigated. Furthermore, the mechanistic basis of the pattern of microcracking near the pedicel end is unknown. The “stress relaxation analysis” of fruit skins, as recently proposed, may be helpful in identifying the mechanisms underlying microcracking (Knoche and Lang, 2017; Lai et al., 2016).
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