J. Amer. Soc. Hort. Sci. 127(3):325–332. 2002.

Studies on Water Transport through the Sweet Cherry Fruit Surface: V. Conductance for Water Uptake

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Additional index words. permeability, water absorption, transpiration, cuticle, cracking, *Prunus avium*

Abstract. **Rain-induced cracking of sweet cherry (*Prunus avium* L.) fruit is thought to be related to water absorption through the fruit surface. Conductance for water uptake ($g_{tot.\ uptake}$) through the fruit surface of 'Sam' sweet cherry was studied gravimetrically by monitoring water penetration from a donor solution of deionized water through segments of the outer pericarp into a polyethyleneglycol (PEG) containing receiver solution. Segments consisting of cuticle plus five to eight cell layers of epidermal and hypodermal tissue were mounted in stainless steel diffusion cells. Conductance was calculated from flow rates of water across the segment and the difference in osmotic potential between donor and receiver solution. Flow rates were constant up to 12 hours and decreased thereafter. A log normal distribution of $g_{tot.\ uptake}$ was observed with a median of 0.97×10^{-7} m·s^{-1}. Further, $g_{tot.\ uptake}$ was not affected by storage duration (up to 71 days) of fruit used as a source of segments, thickness of segments (range 0.1 to 4.8 mm), or segment area exposed in the diffusion cell. Osmolality of the receiver solution in the range from 1140 to 3400 mmol·kg^{-1} had no effect on $g_{tot.\ uptake}$ ($1.45 \pm 0.42 \times 10^{-7}$ m·s^{-1}), but $g_{tot.\ uptake}$ increased by 301% ($4.37 \pm 0.46 \times 10^{-7}$ m·s^{-1}) at 300 mmol·kg^{-1}. $g_{tot.\ uptake}$ was highest in the stylar scar region of the fruit ($1.44 \pm 0.16 \times 10^{-7}$ m·s^{-1}) followed by cheek ($1.02 \pm 0.21 \times 10^{-7}$ m·s^{-1}), suture ($0.57 \pm 0.17 \times 10^{-7}$ m·s^{-1}) and pedicel cavity regions ($0.22 \pm 0.09 \times 10^{-7}$ m·s^{-1}). Across regions, $g_{tot.\ uptake}$ was related positively to stomatal density. Extracting total cuticular wax by dipping fruit in chloroform/methanol increased $g_{tot.\ uptake}$ from $1.18 \pm 0.23 \times 10^{-7}$ m·s^{-1} to $2.58 \pm 0.41 \times 10^{-7}$ m·s^{-1}, but removing epicuticular wax by cellulose acetate stripping had no effect ($1.59 \pm 0.28 \times 10^{-7}$ m·s^{-1}). Water flux increased with increasing temperature (range 20 to 45 °C). Conductance differed between cultivars with 'Hedelfinger' sweet cherry having the highest $g_{tot.\ uptake}$ ($2.81 \pm 0.26 \times 10^{-7}$ m·s^{-1}), followed by 'Namare' ($2.68 \pm 0.26 \times 10^{-7}$ m·s^{-1}), 'Kordia' ($0.96 \pm 0.14 \times 10^{-7}$ m·s^{-1}), 'Sam' ($0.87 \pm 0.15 \times 10^{-7}$ m·s^{-1}), and 'Adriana' ($0.33 \pm 0.02 \times 10^{-7}$ m·s^{-1}). The diffusion cell system described herein may be useful in analyzing conductance in water uptake through the fruit surface of sweet cherry and its potential relevance for fruit cracking.**

Rain-induced cracking of sweet cherry fruit (*Prunus avium*) is a limitation in crop production world wide (Christensen, 1996; Verner and Blodgett, 1931). Fruit cracking is thought to result from increased turgor caused by water uptake into the fruit (Andersen and Richardson, 1982; Considine and Kriedemann, 1972).

The cuticular membrane (CM) represents the primary barrier for water transport (Franke, 1967; Martin and Juniper, 1970). In sweet cherry fruit, water transport across the CM has been studied under defined conditions by monitoring transpiration through segments excised from the outer pericarp (Knoche et al., 2000, 2001). These segments comprise the exocarp including the CM plus several cell layers of adhering tissue. Total conductance for transpiration ($g_{tot.\ transp.}$) was calculated from the amount of water transpired (J) per unit surface area of segment ($A_{segment}$) and time by dividing by the driving force for penetration (ΔC), i.e., the difference in water vapor concentration across exocarp segments (Knoche et al., 2000). This approach offers significant advantages over studies employing detached, intact fruit. First, the system permits a high level of control in that A and ΔC may be standardized using diffusion cells and defined donor and receiver media. Second, since A and ΔC are known, $g_{tot.\ transp.}$ may be calculated. Since it is independent of A and ΔC, $g_{tot.\ transp.}$ is a suitable parameter for comparing water transport for example between treatments or cultivars. Third, A and ΔC may be manipulated even beyond the range occurring under natural conditions. Fourth, following a diffusion experiment, number of stomata on exocarp segments may be determined by light microscopy. This allows establishment of relationships between conductance and stomatal number, which is difficult on a whole fruit basis. Also, segments may be inspected for microscopic cracks in the CM that are often observed on sweet cherry fruit (Glenn and Poovaiah, 1989; Knoche et al., 2000). Lastly, using exocarp segments, transport experiments may be focused on a particular region of the fruit surface.

Up to now the aforementioned system has been used to quantify conductance in transpiration ($g_{tot.\ transp.}$) in sweet cherry fruit (Knoche et al., 2000, 2001) and no information is available on conductance for water uptake ($g_{tot.\ uptake}$) which is the reverse and relevant process in fruit cracking. Hence, it is not known whether $g_{tot.\ transp.}$ equals $g_{tot.\ uptake}$ as would be expected for an ideal system with a homogenous membrane and no interaction between water and membrane permeability. Therefore, the objectives of this study were to 1) establish an in vitro system that allows us to monitor and analyze mechanistically water uptake through the sweet cherry fruit exocarp under controlled conditions and 2) identify factors affecting conductance for water uptake.

Materials and Methods

Plant material. Mature sweet cherry fruit ('Hedelfinger', 'Kordia', and 'Sam', all grafted on 'Alkavo' rootstocks) were

Received for publication 10 Sept. 2001. Accepted for publication 28 Jan. 2002. We thank Monika Möhler, Kurt Ehm, Wolfgang Meyer, and Erhardt Sonnenkalb for providing fruit samples, Ruth Richter and Matthias Hinz for technical assistance, Stefanie Peschel for useful discussion, Dieter Reese for building experimental equipment, Peter Petracek and Randy Beaudry for critical comments of an earlier version of this manuscript, and the Deutsche Forschungsgemeinschaft (grant KN402/4) and the Gisela Foundation for financial support.

collected in a commercial orchard (planting year 1989) located near Eisleben (lat. 51°31'N and long. 11°44'E) in 1999 and 2000. Fruit of 'Namare' (rootstock 'Alkavo', planting year 1995) were obtained from the Bundessortenamt, Prüfstelle Marquardt, Marquardt, (lat. 52°31'N and long. 12°51'E), those of 'Adriana' (rootstock 'F12/1', planting year 1993) from an experimental orchard at the Horticultural Research Center LVG Erfurt, Erfurt, Germany (lat. 50°58'N and long. 11°01'E). Fruit selected for uniformity of development and freedom from defects by visual inspection were transferred to the laboratory within 3 h and held at 1.4 ± 0.6 °C, 89.0% ± 9.0% relative humidity (RH), and CO_2- and O_2-concentrations of 18.1% ± 0.3% and 17.1% ± 0.1%, respectively. Fruit were removed from storage at weekly intervals and held at 1 ± 1 °C and 90% ± 5% RH until initiation of the experiment.

General experimental procedures. Fruit were allowed to equilibrate to 25 ± 2 °C. Segments of the outer pericarp were excised with a razor blade. Parenchyma tissue of the mesocarp was removed by gentle scraping (Price et al., 2000). Segments thus obtained consisted of cuticle plus five to eight cell layers of epidermal and hypodermal tissue and will be referred to as exocarp segments. Thickness of exocarp segments ranged from 100 to 200 µm (determined by light microscopy). Unless otherwise specified, segments from the cheek region were mounted in stainless steel diffusion cells using a high vacuum grease (Hochvakuumfett schwer; Wacker-Chemie, München, Germany; Fig. 1A). Dimensions of diffusion cells were 7 mm orifice diameter, 24 mm outer diameter, 24 mm height, 61 g without segment and without receiver and donor solutions. Diffusion cells were filled with a receiver solution containing polyethylene glycol (PEG-6000; Merck Eurolab GmbH, Darmstadt, Germany) via a sampling port in the bottom. The osmolality of the receiver solution was 1140 mmol·kg^{-1} (model 5520 vapor pressure osmometer; Wescor, Inc., Logan, Utah) which corresponded to the average osmolality of cell sap extracted from mesocarp tissue of the same batch of fruit. Subsequently, diffusion cells were sealed with tape (Tesa Film; tesa-Werke Offenburg, Germany). Experiments were initiated by applying 0.10 to 0.15 mL of donor solution, usually deionized water, to the orifice of the diffusion cell such that the entire area of the exposed exocarp segment (38.5 mm^2) was covered. Diffusion cells were incubated in an upright position at 25 °C (see Fig. 1A). Water uptake was monitored gravimetrically. Unless otherwise specified, the donor was removed quantitatively at 0, 1, 2, and 3 h by blotting with soft tissue paper (Kimwipes, Lite 200; Kimberley-Clark Corp., Roswell, Ga.), the diffusion cell weighed to determine water uptake (microbalance BP 211 D, Sartorius AG, Göttingen, Germany), and the donor solution subsequently reapplied. Preliminary experiments established that water conductance was not affected by 1) the type of sealant used for mounting segments in diffusion cell [$0.74 \pm 0.15 \times 10^{-7}$ m·s^{-1} and $0.75 \pm 0.18 \times 10^{-7}$ m·s^{-1} for high vacuum grease (Hochvakuumfett schwer) and silicone RTV 3140 (Dow Corning 3140 RTV Coating; Dow Corning Corp., Midland, Mich.), respectively], 2) agitating diffusion cells at 150 rotations/min during incubation ($0.79 \pm 0.24 \times 10^{-7}$ m·s^{-1} and $0.85 \pm 0.17 \times 10^{-7}$ m·s^{-1} for without and with agitation, respectively), and 3) orientation of diffusion cells ($0.81 \pm 0.25 \times 10^{-7}$ m·s^{-1} and $0.98 \pm 0.08 \times 10^{-7}$ m·s^{-1} for upright and inverted orientation of diffusion cells with tape covered donor solutions, respectively). Further, transpiration losses from entirely tape-sealed diffusion cells with exocarp segments mounted were negligibly small (Knoche et al., 2000). In some experiments, exocarp segments were investigated for microscopic cracks by light microscopy and the number of stomata was determined as described in Knoche et al. (2000). Exocarp segments having cuticular cracks were excluded from data analysis.

Experiments

Evaluating the system. Initial experiments were conducted to optimize the operating conditions of the water uptake test. Time course of water uptake through exocarp segments was established during a 48-h period (n = 20 segments).

The effect of holding fruit in controlled atmosphere storage for up to 71 d after harvest was investigated by analyzing control treatments of all experiments conducted in that time period under standard conditions, i.e., cheek segments of 'Sam' sweet cherry, PEG receiver solution at an osmolality of 1140 mmol·kg^{-1}, deionized water as the donor, and a temperature of 25 °C.

To quantify the effect of thickness of segments (0.1 to 4.8 mm) on water conductance, successive portions of mesocarp tissue were removed from exocarp segments with a razor blade. Water uptake was determined as described above (n = 26 segments).

The effect of surface area of the exocarp segment exposed in the diffusion cell was studied by monitoring water flow through segments having 0%, 25%, 50%, 75%, or 100% of the exposed area sealed by silicone (Dow Corning 3140 RTV coating; n = 10 segments). The relationship between water conductance and osmolality of the receiver solution was established using PEG-solutions at 0, 300, 1140, 2730, or 3400 mmol·kg^{-1} (n = 25 segments). In a further experiment, PEG and sucrose solutions were compared at equal osmolality (1140 mmol·kg^{-1}; n = 12 segments).

The effect of an inhibitor of metabolism was established using a PEG receiver solution that contained NaN_3 at 1 mM. PEG-solution without NaN_3 served as a control (n = 10 segments).

To quantify potential effects of the direction of water transport on conductance, deionized water was used as the donor solution inside the diffusion cell and 0.1 mL of PEG-solution (osmolality 1140 mmol·kg^{-1}) as the receiver on top of the cell. Using this setup, water penetrated from the inside of the diffusion cell through the exocarp segment into the PEG-receiver on the CM surface. Diffusion cells with PEG-receiver solution (osmolality 1140 mmol·kg^{-1}) inside the cell and deionized water as a donor solution on the CM surface (see Fig. 1A) served as controls (n = 20 segments).

Factors affecting conductance. To establish uniformity of water conductance across the sweet cherry fruit surface, conductance of segments excised from cheek, suture, pedicel cavity, and stylar region was determined. Pedicel cavity segments were taken from the mantle of the cavity close to the rim on the cheek side. Segments from the stylar region comprised the scar and a concentric portion of the surrounding surface. Conductance and number of stomata per region were determined as described above (n = 11 segments). The effect of the cultivar on conductance and stomatal density was evaluated using exocarp segments excised from the cheek of mature 'Adriana', 'Hedelfinger', 'Kordia', 'Namare', and 'Sam' fruit (n = 13 to 25 segments).

Epicuticular or total cuticular wax was removed from sweet cherry fruit by cellulose-acetate-stripping (Silcox and Holloway, 1986) or by dipping fruit in 1 chloroform : 1 methanol (v/v) (five dips for 30 s each), respectively. Exocarp segments were excised and mounted on diffusion cells as described above. Nontreated segments served as controls (n = 15 segments). Tem-

perature effects on water conductance were established by incubating diffusion cells at 20, 30, or 45 ± 2 °C (n = 25 segments).

Data analysis and presentation. The flow of water (F) across exocarp segments was calculated on an individual segment basis from the slope of a linear regression line fitted through a plot of the increase in weight of diffusion cells vs. time (0 to 3 h). For some segments (10.8% of the population investigated), coefficients of determination (r^2) were <0.90. In these instances time courses were often characterized by an initially (0 to 1 h) rapid increase in water uptake which leveled off and approached an asymptote within the 3-h observation period. Several arguments suggested that these segments were not sealed properly. First, the frequency of atypical time courses increased for segments excised from firm fruit during early stages of development and in particular from those regions that exhibit marked curvature, e.g., stylar scar region, stem cavity region (M. Beyer, unpublished data). Second, when applying a solution containing the fluorescent tracer acridine orange to mounted segments, dye solution was found occasionally between top and bottom of diffusion cells having atypical penetration time courses, but not in cells with linear penetration time courses. Dye movement between the top and the bottom of the diffusion cell would be indicative of an improperly sealed cell. Thus, data for segments having atypical time-courses of water uptake characterized by $r^2 < 0.90$ were excluded from data analysis. For the remaining observations ('Sam') coefficients of determination averaged $r^2 = 0.97$. Conductance ($g_{tot.\ uptake}$) was calculated according to Eq. [1] (Nobel, 1991)

$$F = A_{segment} \times J = A_{segment} \times g_{tot.uptake} \times \frac{\overline{V}_w}{RT} \times \Delta\Psi \qquad [1]$$

where F represents the water flow per unit time, $A_{segment}$ the area of the exposed segment in the diffusion cell ($A_{segment}$ = 38.5 mm^2) and J the flux per unit area and time.

The conductance for water uptake equals $g_{tot.\ uptake}$ and the term ($\overline{V}_w$/RT) the partial molar volume of water ($\overline{V}_w$) divided by the product of the universal gas constant (R) times the absolute temperature (T). The gradient in water potential across the exocarp segment is represented by $\Delta\Psi$. According to Nobel (1991) the water potential (Ψ) is related to the chemical potential of water (μ_w) relative to a reference state (μ^*_w) and comprises several components (Eq. [2], Nobel, 1991):

$$\Psi = \frac{\mu_w - \mu^*_w}{\overline{V}_w} = \Psi_P + \Psi_\Pi + \Psi_h = \Psi_P + \Psi_\Pi + \rho_w \times g \times h \qquad [2]$$

In this equation Ψ_P equals the turgor and Ψ_Π the osmotic potential. The Ψ_h represents the gravitational potential and equals the product of the density of water (ρ_w), the gravitational acceleration (g) and the height of the water column (h). Introducing don and rec as sub-subscripts referring to the respective donor and receiver compartments, the difference in water potential ($\Delta\Psi$) between donor and receiver is given by Eq. [3]:

$$\Delta\Psi = \Psi_{don} - \Psi_{rec} = \Delta\Psi_P + \Delta\Psi_\Pi + \Delta\Psi_h = \Psi_{P_{don}} - \Psi_{P_{rec}} + \Psi_{\Pi_{don}} - \Psi_{\Pi_{rec}} + \rho_w \times g \times (h_{don} - h_{rec}) \qquad [3]$$

In our system, the donor and, within the typical duration of an uptake experiment (<12 h), the receiver were at atmospheric pressure and hence, $\Psi_{Pdon} - \Psi_{Prec} = 0$. Furthermore, since water was used as a donor solution, $\Psi_{\Pi don} = 0$. The $\Psi_{\Pi rec}$ may be derived from Eq. [4] (Schönherr, 1976)

$$-\Psi_{\Pi_{rec}} = \Pi_{rec} = RT \times \Phi c_{PEG} \qquad [4]$$

where Π_{rec} is the osmotic pressure, Φ the osmotic coefficient that corrects for nonideal behavior, and c_{PEG} the concentration of PEG-6000.

Alternatively, Φc_{PEG} may be determined directly for example by vapor pressure osmometry as was done in the present study. At 25 °C and $|\Psi_{\Pi rec}|$ = 522.7 g PEG/kg of water, Φc_{PEG} = 1140 mmol·kg^{-1} and $|\Psi_{\Pi rec}|$ equaled 2.83 MPa. Calculating $|\Psi_{\Pi rec}|$ for 25 °C using the relationship reported by Michel and Kaufmann (1973) yielded 2.93 MPa which is close to our estimate when considering the polydispersed nature of PEG-6000.

The gravitational term in Eq. [3] accounted for the pressure exerted by the water donor droplet covering the exocarp segment. Assuming $h_{don} - h_{rec}$ = 4 mm as a conservative estimate, the pressure imposed by the water droplet equaled 3.91 × 10^{-5} MPa. This is small and negligible (<0.01% of $|\Psi_{\Pi rec}|$ relative to the osmotic potential of the receiver solution ($|\Psi_{\Pi rec}|$ = 2.83 MPa) suggesting that $|\Psi_{\Pi rec}|$ was the only factor determining the gradient in water potential and hence, the driving force for water uptake in our system. Inserting $|\Psi_{\Pi rec}|$ in Eq. [1] and rearranging yields $g_{tot.\ uptake}$.

Since water conductance of the sweet cherry fruit cuticle had a log normal distribution (Knoche et al., 2000), data in text and tables are presented as medians ± SE. For figures, asymmetric SE bars were calculated using the following procedure: First, data were log-transformed to obtain normal distributions. Second, means ± SE were calculated then back-transformed by taking the exponent. This procedure produced asymmetric error bars that accounted for the log-normal distribution of the data. Log-transformed data were subjected to analysis of variance (ANOVA) where appropriate and means were compared using Tukey's Studentized range test (Proc GLM; SAS program package version 6.12; SAS Inst., Inc., Cary, N.C.). Regression analysis was carried out using treatment medians unless otherwise specified. Significance of coefficients of determination at $P \leq$ 0.05, 0.01, or 0.001 is indicated by *, **, or ***, respectively.

Results

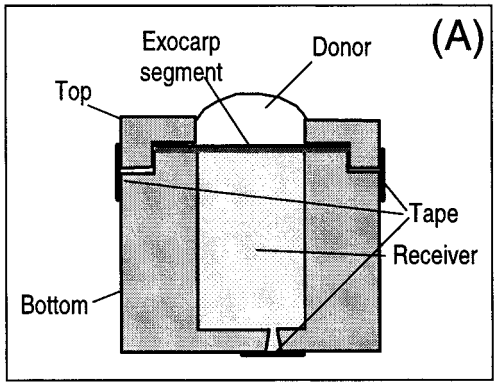
Water uptake increased linearly with time up to 12 h (mean r^2 = 0.95 ± 0.02 for all observations) and thereafter occurred at a decreasing rate (Fig. 1B). Uptake did not reach an equilibrium within 48 h. The frequency distribution of $g_{tot.\ uptake}$ was characterized by marked tailing at high $g_{tot.\ uptake}$. Upon log transformation, a symmetrical distribution was obtained indicating that $g_{tot.\ uptake}$ had a log normal distribution with a median of 0.97 × 10^{-7} m·s^{-1} and 0.66 × 10^{-7} m·s^{-1} and 1.57 × 10^{-7} m·s^{-1} as the 25% and 75% quartiles, respectively (n = 302, Fig. 1C).

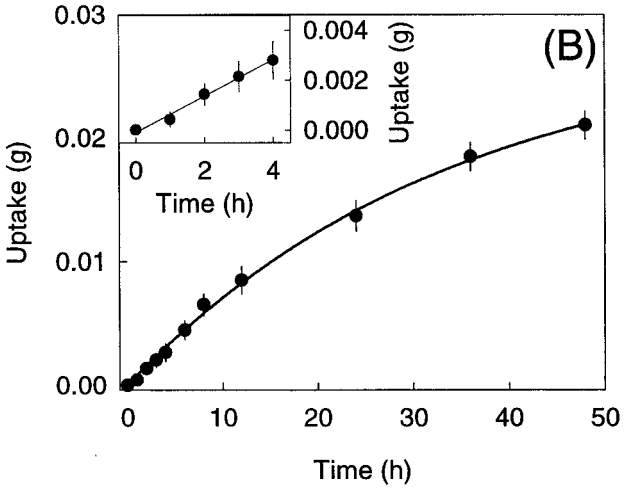
Holding fruit in storage for up to 71 d had no effect on $g_{tot.\ uptake}$ (r^2 = 0.01; data not presented). Also, $g_{tot.\ uptake}$ was not affected by thickness of segments (r^2 = 0.01; data not presented).

Reducing the cross sectional area for uptake by sealing portions of exocarp segments with silicone resulted in a proportional reduction in F. There was no significant effect on $g_{tot.\ uptake}$ (Fig. 2).

Increasing the osmolality of the receiver solution from 0 to 3400 mmol·kg^{-1} increased F from 10.80 ± 2.84 × 10^{-5} g·h^{-1} to 122.54 ± 37.08 × 10^{-5} g·h^{-1} (Fig. 3A). The highest $g_{tot.\ uptake}$ was at 300 mmol·kg^{-1}, then decreased and remained constant at higher osmolality (1140 to 3400 mmol·kg^{-1}; Fig. 3B). There was no significant difference in $g_{tot.\ uptake}$ between receiver solutions containing PEG or sucrose at equal osmolality (0.73 ± 0.34 × 10^{-7} m·s^{-1} vs. 0.85 ± 0.09 × 10^{-7} m·s^{-1} for PEG vs. sucrose at 1140 mmol·kg^{-1}, respectively) or between water transport from the outside into the diffusion cell vs. from the inside out (1.28 ± 0.45 × 10^{-7} m·s^{-1} vs. 0.76 ± 0.16 × 10^{-7} m·s^{-1} for outside in vs. inside out, respectively).

Π





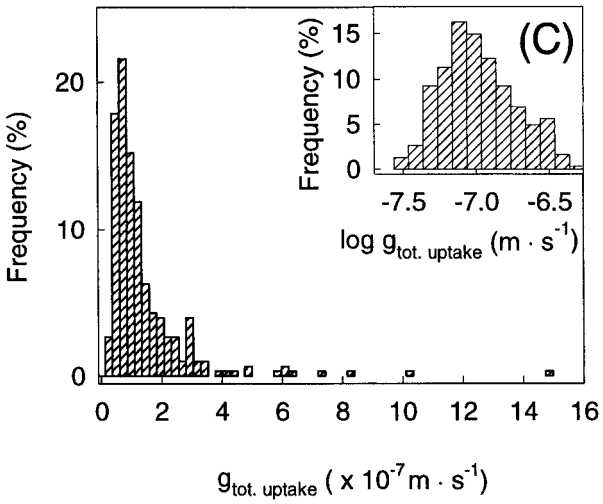


Fig. 1. (**A**) Schematic diagram of diffusion cell for determining conductance for water uptake ($g_{tot.\ uptake}$) through the sweet cherry fruit cuticle using exocarp segments. (**B**) Time course (0 to 48 h) of water uptake through exocarp segments excised from the cheek of 'Sam' sweet cherry fruit. Inset: short-term time course (0 to 4 h). Vertical bars = SE (n = 20). (**C**) Frequency distribution of $g_{tot.\ uptake}$ in the cheek region of 'Sam' sweet cherry. Inset: frequency distribution of log transformed $g_{tot.\ uptake}$.

Furthermore, adding NaN_3 to PEG receiver solutions had no effect on $g_{tot.\ uptake}$ ($0.73 \pm 0.34 \times 10^{-7}$ $m \cdot s^{-1}$ vs. $0.70 \pm 0.21 \times 10^{-7}$ $m \cdot s^{-1}$ for PEG only vs. PEG plus NaN_3, respectively).

Significant differences in $g_{tot.\ uptake}$ and stomatal density ($d_{sto.}$) were observed between regions of the sweet cherry fruit surface. In the pedicel cavity region $g_{tot.\ uptake}$ and $d_{sto.}$ were lowest and increased towards the stylar region of the fruit (Table 1; Fig. 4B). Sealing the stylar scar with silicone did not affect $g_{tot.\ uptake}$ ($1.44 \pm 0.16 \times 10^{-7}$ $m \cdot s^{-1}$ vs. $1.37 \pm 0.41 \times 10^{-7}$ $m \cdot s^{-1}$ for segments from stylar regions having the scar open vs. sealed, respectively). Generally, the relationship between $g_{tot.\ uptake}$ and $d_{sto.}$ was not or only weakly significant for individual regions of the fruit surface (see Fig. 4A for cheek region), but a significant linear relationship (r^2 = 0.93***) was obtained when data for regions were pooled (Fig. 4B).

Differences in $g_{tot.\ uptake}$ and $d_{sto.}$ were noted among the sweet cherry cultivars. The lowest $g_{tot.\ uptake}$ and $d_{sto.}$ were observed in 'Adriana', the highest in 'Hedelfinger' (Table 2; Fig. 4C). There was a significant positive linear relationship between $g_{tot.\ uptake}$ and $d_{sto.}$ (Fig. 4C).

Removing epicuticular wax by cellulose-acetate-stripping had no significant effect on $g_{tot.\ uptake}$ ($1.59 \pm 0.28 \times 10^{-7}$ $m \cdot s^{-1}$ vs. $1.18 \pm 0.23 \times 10^{-7}$ $m \cdot s^{-1}$ for stripped segments vs. control, respectively). Extracting total wax by dipping fruit into chloroform/methanol increased $g_{tot.\ uptake}$ 2.2-fold to $2.58 \pm 0.41 \times 10^{-7}$ $m \cdot s^{-1}$.

Water flux per unit area and time (J) increased 1.3- and 1.5-fold when temperature increased from 20 to 30 and 30 to 45 °C, respectively (Fig. 5). From this, the respective computed

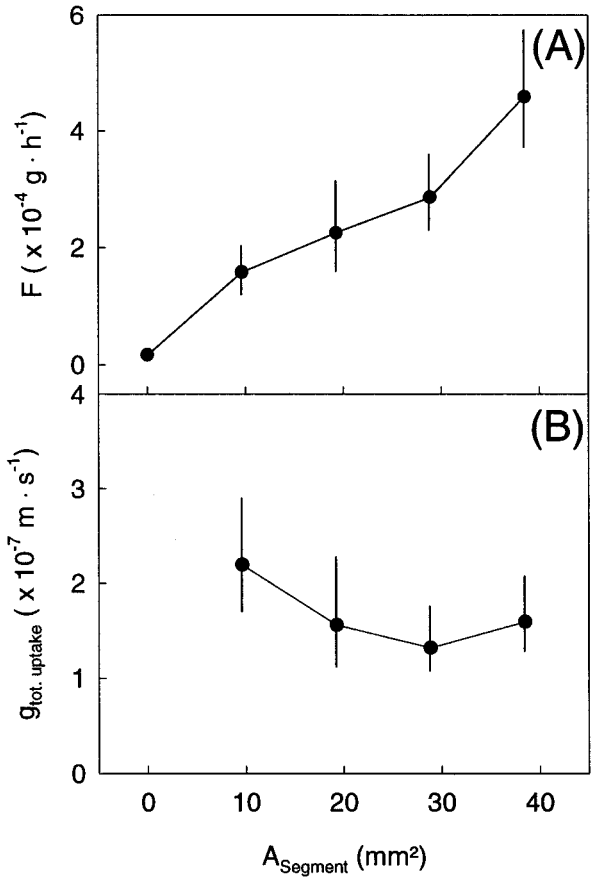


Fig. 2. Effect of cross-sectional area for transport on the (**A**) flow rate of water (F) and (**B**) conductance for water uptake ($g_{tot.\ uptake}$) through exocarp segments excised from the cheek of mature 'Sam' sweet cherry fruit. Vertical bars = SE (n = 10).

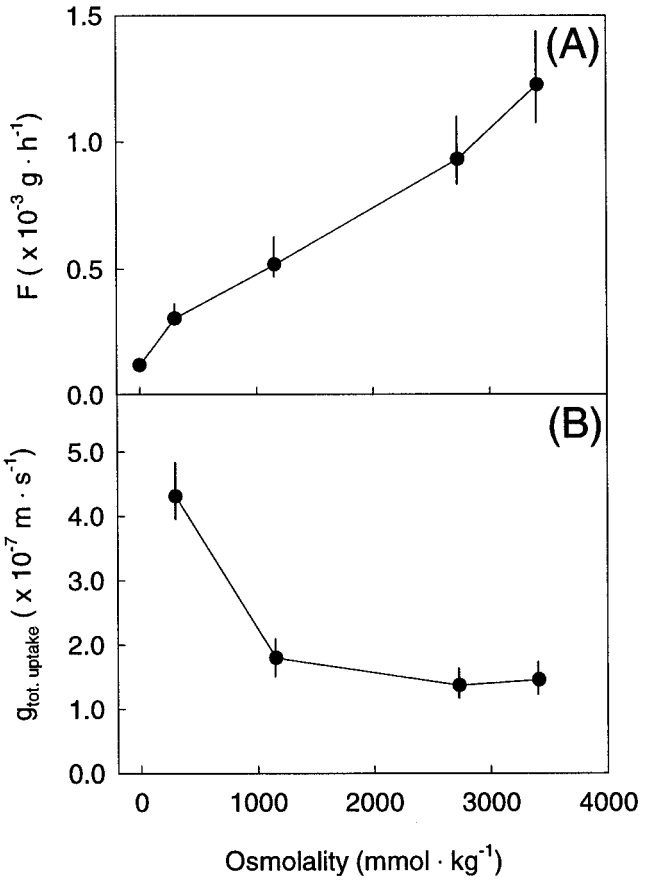


Fig. 3. Effect of osmolality of the receiver solution on the (**A**) flow rate of water (F) and (**B**) conductance for water uptake ($g_{tot. uptake}$) through exocarp segments excised from the cheek of mature 'Sam' sweet cherry fruit. Vertical bars = SE (n = 25).

Q_{10}-values were 1.30 and 1.29. The energy of activation (Ea) calculated from the slope of a linear regression equation fitted through a plot of ln (J) or ln ($g_{tot. uptake}$) vs. the inverse of the absolute temperature (range 20 to 45 °C) averaged 19.8 and 20.1 kJ·mol^{-1} for J and $g_{tot. uptake}$, respectively.

Discussion

Theoretical model for water uptake in an osmotic system. In our system the driving force for water uptake represented the difference in osmotic potential between the aqueous donor and the PEG containing receiver solution. Since PEG is a large molecule (average molecular weight 6000) and therefore does not penetrate the CM (Baur, 1999), only water will penetrate in significant amounts. Thus, diffusion cells with exocarp segments resembled an osmotic system. In this system different mechanisms of penetration may be operative. Penetration may occur by diffusion through the CM polymer and through any pores that may exist and form a liquid continuum through the CM (Schönherr, 2000; Schönherr and Bukovac, 1970). Furthermore, in the presence of an (osmotic) potential gradient such pores would provide pathways for viscous flow (Schönherr, 1982). Thus, the conductance $g_{tot. uptake}$ represented an osmotic conductance comprising a diffusion and possibly a viscous flow component.

Table 1. Total conductance for water uptake ($g_{tot. uptake}$) and stomatal density ($d_{sto.}$) ± SE of exocarp segments excised from pedicel cavity, cheek, ventral suture, and stylar region of mature 'Sam' sweet cherry fruit.

Region	$g_{tot. uptake}$ ($\times 10^{-7}$ m·s^{-1})^z	$d_{sto.}$ (mm^{-2})^y
Pedicel cavity	0.22 b^y (± 0.09)	0.00 c (± 0.02)
Cheek	1.02 a (± 0.21)	1.14 b (± 0.07)
Ventral suture	0.57 a (± 0.17)	0.97 b (± 0.06)
Stylar scar	1.44 a (± 0.16)	1.90 a (± 0.13)
Grand median	0.98 (± 0.19)	1.09 (± 0.10)

^{z}Data log-transformed before ANOVA.
^{y}Mean separation (n = 11) within columns by Tukey's studentized range test, $P < 0.05$.

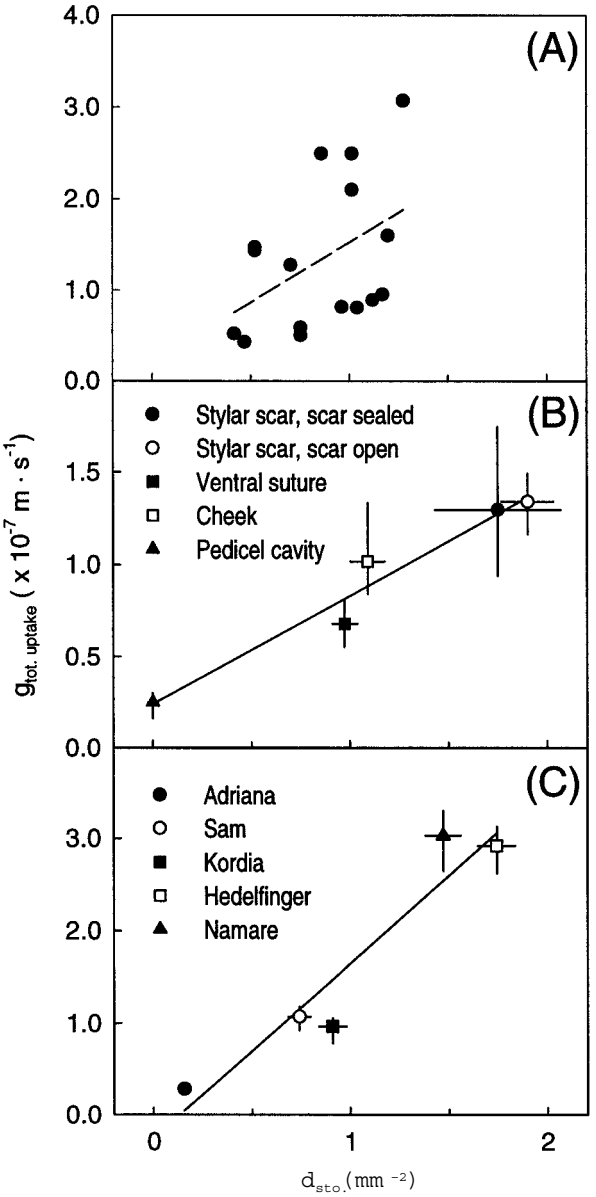


Fig. 4. Relationship between conductance for water uptake ($g_{tot. uptake}$) and stomatal density ($d_{sto.}$) of exocarp segments of sweet cherry fruit. (**A**) Individual cheek segments of 'Sam'. (**B**) Segments from cheek, suture, pedicel cavity, and stylar scar regions of 'Sam'. The regression equation was $g_{tot. uptake}$ (m·s^{-1}) = 5.90 (±0.74) × 10^{-8} × $d_{sto.}$ (mm^{-2}) + 2.41 (±0.98) × 10^{-8}, $r^2 = 0.96^{***}$. (C) Cheek segments from 'Adriana', 'Hedelfinger', 'Kordia', and 'Sam'. The regression equation was $g_{tot. uptake}$ (m·s^{-1}) = 19.03 (±3.53) × 10^{-8} × $d_{sto.}$ (mm^{-2}) – 2.57 (±4.05) × 10^{-8}, $r^2 = 0.91^{*}$. Symbols and vertical bars in **B** and **C** represent means ± SE values of log transformed conductance data following back transformation, horizontal bars in **B** and **C** SE values of stomatal densities. Number of observations were 11 and 13 to 25 in **B** and **C**, respectively.

Table 2. Conductance for water uptake ($g_{tot.\ uptake}$) and stomatal density ($d_{sto.}$) ± SE of exocarp segments excised from the cheek of fruit of selected sweet cherry cultivars.

Cultivar	$g_{tot.\ uptake}$ ($\times 10^{-7}$ m·s^{-1})[z]	$d_{sto.}$ (mm^{-2})
Adriana	0.33 a[y] (± 0.02)	0.16 a (± 0.02)
Hedelfinger	2.81 c (± 0.26)	1.74 c (± 0.09)
Kordia	0.96 b (± 0.14)	0.74 b (± 0.06)
Namare	2.68 c (± 0.26)	1.47 c (± 0.09)
Sam	0.87 b (± 0.15)	0.90 b (± 0.08)

[z]Data log-transformed before ANOVA.
[y]Mean separation (n = 13 to 25) within columns by Tukey's studentized range test, $P < 0.05$.

The data generated in our experiments are in general agreement with the arguments presented above. First, varying $A_{segment}$ altered F, but had no significant effect on $g_{tot.\ uptake}$. Second, F was positively related to the osmolality of the receiver solution and except for PEG at 300 mmol·kg^{-1}, there was no effect on $g_{tot.\ uptake}$. Third, replacing the osmoticum PEG by sucrose at constant osmolality had no significant effect on $g_{tot.\ uptake}$. In addition, the $g_{tot.\ uptake}$ determined using diffusion cells was in general agreement with the $g_{tot.\ uptake}$ calculated from the rate of water absorption of detached sweet cherry fruit. When incubating 'Sam' sweet cherry fruit (pedicel/fruit juncture and pedicel end sealed) in deionized water at 20 °C an F_{fruit} of 1.47×10^{-6} g·s^{-1} per fruit was obtained (Beyer et al., 2002). Assuming a spherical shape of the fruit as a first approximation ($A_{fruit} = 1.84 \times 10^{-3}$ m^2 per fruit), a J of 7.99×10^{-4} g·s^{-1}·m^{-2} was calculated. Dividing J by the gradient in water potential ($\Delta Y = -2.18 \pm 0.03$ MPa by pressure bomb; M. Hinz, unpublished data) yielded a $g_{tot.\ uptake}$ of 0.49×10^{-7} m·s^{-1} on a whole fruit basis. This value is well within the range of the $g_{tot.\ uptake}$ determined using diffusion cells, PEG as a receiver solution, and exocarp segments excised from different regions of 'Sam' sweet cherry fruit (range of $g_{tot.\ uptake}$ 0.19×10^{-7} m·s^{-1} to 1.26×10^{-7} m·s^{-1} for pedicel cavity to stylar scar region; data from Table 1 recalculated for 20 °C using the relationship depicted in Fig. 5). Thus, the $g_{tot.\ uptake}$ established in our in vitro system adequately reflected the $g_{tot.\ uptake}$ of the fruit surface in vivo.

Pathways for water uptake. Water uptake into sweet cherry fruit may have occurred via several parallel pathways, i.e., cracks, stomata, and the CM. First, microscopic cracks that occurred at high frequency in the stylar region of the fruit in this and our earlier studies (Knoche et al., 2000, 2001) significantly increased $g_{tot.\ uptake}$ from 0.74×10^{-7} m·s^{-1} to 1.57×10^{-7} m·s^{-1} (estimated from regression lines fitted through plots of $g_{tot.\ uptake}$ vs. $d_{sto.}$ at $d_{sto.} = 1.09$ mm^{-2}, for segments of all regions with and without cracks, respectively). Cracks represent openings in the CM, which formed the primary barrier also to water uptake in sweet cherry fruit. This conclusion is based on 1) the observation of increased water uptake into fruit having the CM damaged by treatment with carborund powder (S. Peschel and M. Knoche, unpublished data) and 2) the absence of an effect of thickness of the tissue adhering to the CM in exocarp segments.

Second, we obtained positive relationships between $d_{sto.}$ and $g_{tot.\ uptake}$, suggesting a direct or indirect role of stomata in water uptake. At present, the mechanism of this penetration is not clear. Theoretically, open stomata may be penetrated (e.g., Poiseuille flow through pores; Nobel, 1991). However, Schönherr and Bukovac (1972) concluded that the high surface tension of water, the wetting characteristics of the CM, and geometrical constrains of the stomatal pore prevent aqueous solutions from infiltrating stomata in the absence of surfactants and/or externally applied pressure. For sweet cherry fruit, the critical surface tension was 25 mN·m^{-1} (Peschel et al., 2001) which is well below the surface tension of the PEG receiver (57.4 ± 0.3 mN·m^{-1}; M. Harz, unpublished data) or the water donor solution (71.5 ± 0.2 mN·m^{-1}; M. Harz, unpublished data). Furthermore, unpublished data obtained in our laboratory indicated that gravimetrically detectable flow of water through stomata on the sweet cherry fruit surface required hydrostatic pressures above 4.6 kPa (S. Peschel and M. Knoche, unpublished data). Also, when dipping sweet cherry fruit for 1 min in aqueous solutions containing the fluorescent tracer acridine orange or $AgNO_3$ (surface tension 71 mN·m^{-1}), we did not observe any infiltration of stomata in the absence of surfactants, while a large portion of stomata appeared infiltrated in the presence of a surfactant (Silwet L-77, 21 mN·m^{-1}; Peschel et al., 2001). These arguments make a direct flow of water through open stomata (Poiseuille flow; Nobel, 1991) unlikely.

Interestingly, Eichert et al. (1998) hypothesized that uranine, a large molecule carrying a negative charge, penetrated stomata in a water film that formed on the wall of the stomatal pore under a drying droplet of an aqueous treatment solution applied to *Allium porrum* L. (synonym *A. ampeloprasum*; leek) leaves. If such films formed on the pore wall of stomata in sweet cherry fruit, water uptake could proceed via these films and hence, would be related to $d_{sto.}$ (Fig. 4). However, direct evidence is lacking.

Alternatively, stomata may be involved indirectly in penetration. Water uptake may have occurred through structures and pathways that are related to stomata. For example, the CM above guard and accessory cells has been reported to be more permeable, possibly as a result of a higher density of polar pathways (Franke, 1964; Jyung et al., 1965; Schönherr and Bukovac, 1970). If such pathways were associated with the stomatal apparatus of the sweet cherry fruit, a positive relationship between $g_{tot.\ uptake}$ and stomatal density would be obtained although penetration of the stomatal pore was not necessarily involved. Little is known about such pathways and their relative contribution to water uptake.

The third pathway that contributed to $g_{tot.\ uptake}$ was penetration through the CM between stomata. Extracting total wax by dipping fruit in chloroform/methanol increased conductance in water uptake 2.2-fold. This effect is small compared to effects of wax

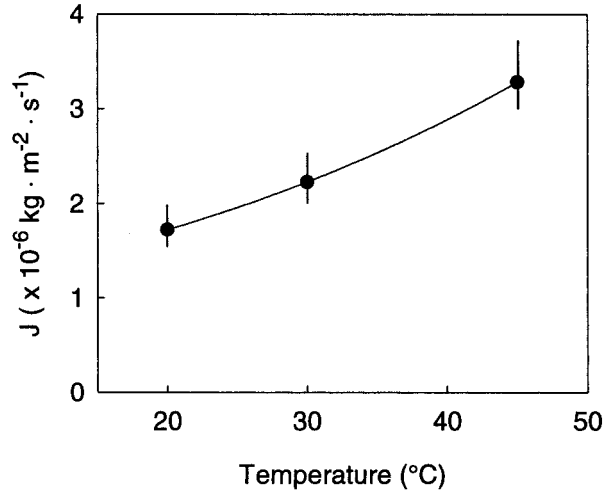


Fig. 5. Effect of temperature on water flux (J) through segments excised from the cheek of mature 'Sam' sweet cherry fruit. Vertical bars = SE (n = 25). The regression equation fitted through back transformed means of log transformed flux data was $J\ (\times 10^{-6}\ kg \cdot m^{-2} \cdot s^{-1}) = 0.05 + 0.99 \times e^{(0.05 \times T\ (°C))}$, $r^2 = 1.0^{***}$.

extraction on penetration of larger and more lipophilic molecules in a liquid/cuticle/liquid system, which can yield up to 9200-fold increase upon dewaxing (2,4 dichlorophenoxyacetic acid, MW = 221.04; Schönherr and Riederer, 1989). However, small polar ions such as $^{45}Ca^{2+}$ experienced only a 1.8 to 2.9-fold increase upon dewaxing (Schönherr, 2000), which is of comparable magnitude as the effect on water uptake obtained in sweet cherry fruit.

Comparing conductance for uptake and transpiration. Water uptake through excised exocarp segments was similar qualitatively to transpiration in many aspects (Knoche et al., 2000). First, time courses of water uptake and transpiration were linear over extended periods of time (up to 12 h in water uptake and up to 48 h in transpiration, respectively; Knoche et al., 2000) indicating that driving force and conductance remained constant during these periods. Second, $g_{tot.\ uptake}$ and $g_{tot.\ transp.}$ were characterized by log-normal distributions (Knoche et al., 2000). A log-normal distribution is characteristic for CM permeability in many plant species (Baur, 1997). Third, NaN_3, a potent inhibitor of metabolism, had no effect on $g_{tot.\ uptake}$ (the present investigation) and $g_{tot.\ transp.}$ (Knoche et al., 2000). Fourth, holding fruit at storage for extended time periods had no effect on $g_{tot.\ uptake}$ and only a small effect on $g_{tot.\ transp.}$ (Knoche et al., 2000). Fifth, there was no effect of thickness of exocarp segments on $g_{tot.\ uptake}$ (the present investigation) and $g_{tot.\ transp.}$ (Knoche et al., 2000). Sixth, $g_{tot.\ uptake}$ and $g_{tot.\ transp.}$ were related positively with stomatal density (Knoche et al., 2000, 2001). In addition, extracting wax with chloroform/methanol or increasing temperature increased $g_{tot.\ uptake}$ (the present investigation) and $g_{tot.\ transp.}$ (Knoche et al., 2000). These arguments suggested that 1) water uptake and transpiration were similar qualitatively, 2) water transport through the sweet cherry fruit surface was a physical process where the CM represented the primary barrier, and 3) stomata played a direct or indirect role in water transport. However, a quantitative comparison of conductance for water uptake and transpiration revealed a striking difference. The median conductance for water uptake was 0.97×10^{-7} m·s^{-1} which is 43 times larger than the median conductance for transpiration expressed on a water density basis (water density basis $g_{tot.transp.} = 2.24 \times 10^{-9}$ m·s^{-1}; water vapor concentration basis $g_{tot.transp.} = 1.15 \times 10^{-4}$ m·s^{-1}) reported by Knoche et al. (2000) for the same cultivar and the same region of the fruit surface ($P \leq 0.0001$) and a similar temperature (22 °C in the transpiration studies of Knoche et al., 2000 vs. 25 °C in the uptake study). Presently, we do not know the reason for this discrepancy, but several factors may be involved.

First, the mechanism of transport may have differed between water uptake and transpiration, since driving forces and hence conductance for the two processes differed. Transpiration is driven by a gradient in water vapor concentration. Since there is no evidence for transpiration through any polar pathways through the CM, transport occurs by diffusion (Kerstiens, 1996). Thus, the $g_{tot.\ transp.}$ represented a diffusional conductance (Kerstiens, 1996). In contrast, $g_{tot.\ uptake}$ is an osmotic conductance that, in addition to diffusion, may comprise a viscous flow component driven by a pressure gradient (here osmotic pressure) provided that a liquid continuum existed across the CM (Schönherr, 1982). Depending on the number and cross sectional area of these pathways, viscous flow may be rapid compared to diffusion. It has long been argued that polar pathways may exist in plant CM (Franke, 1967; Schönherr and Bukovac, 1970) and recently, Schönherr (2000) reported that $^{45}Ca(Cl)_2$ penetrated CM via aqueous pathways. If such polar pathways also existed in sweet cherry fruit CM, viscous flow may have contributed to water uptake in our system, while transpiration occurred by diffusion only. A significant contribution of viscous flow to $g_{tot.uptake}$ would also account for the small effect of temperature on water uptake ($Q_{10} = 1.3$ for 20 to 45 °C). Further, the small effect of wax extraction on $g_{tot.\ uptake}$ as compared to $g_{tot.\ transp.}$ (2.2-fold increase vs. 48.6-fold increase in water uptake vs. transpiration, respectively; Knoche et al., 2000) would support the concept of an additional polar pathway for penetration of free water into the fruit.

Second, it may be argued that the difference between conductance for water uptake and transpiration was an artifact caused by growing conditions that differed between the years the water uptake and transpiration experiments were conducted. For example, $d_{sto.}$ averaged 0.49 mm^{-2} in 1998, but 1.14 mm^{-2} in 2000 (data for cheek region of mature 'Sam' fruit; Table 1). However, when recalculating $g_{tot.uptake}$ for $d_{sto.} = 0.49$ mm^{-2} thereby accounting for the difference in stomatal density between 1998 and 2000, $g_{tot.uptake}$ averaged 0.53×10^{-7} m·s^{-1} which still is 24-fold higher than the $g_{tot.transp.}$ on a density basis reported by Knoche et al. (2000). Also, Riederer and Schneider (1990) studying the effect of climatic factors on CM permeability (in transpiration) concluded that there was no relationship between water conductance through *Citrus aurantium* L. (synonym *C. aurantiacum*; bitter orange) leaf CM and growing conditions of leaves used as a source of CM. Thus, growing conditions are unlikely to be a factor.

Third, the direction of transport differed between water uptake and transpiration. If conductance depended on the direction of transport, conductance in uptake and transpiration would differ. However, this was unlikely to be a factor in sweet cherry fruit. The $g_{tot.\ uptake}$ obtained when reversing the direction of transport did not differ significantly from the $g_{tot.\ uptake}$ in the normal direction of transport.

Fourth, CM hydration and hence swelling, may have differed between water uptake and transpiration experiments. In water uptake, the CM would be fully hydrated, while in transpiration, hydration may be less, since the CM is exposed to a marked gradient in water vapor concentration. If conductance was related positively to swelling of the CM, this effect may contribute to the higher conductance in water uptake. To our knowledge the effect of hydration on conductance of the sweet cherry fruit exocarp has not been studied. For other species, CM permeability in transpiration was reported to increase up to 3-fold as RH increased from 2% to 100% (Schönherr and Schmidt, 1979; Schreiber et al., 2001). It may be speculated that the higher conductance at an osmolality of the receiver solution of 300 mmol·kg^{-1} was related partly to increased hydration, since decreasing osmolality in the receiver would increase water activity and hence hydration. However, an alternative explanation for the latter phenomenon might also be decreased sensitivity of our water uptake test at small fluxes caused by low driving forces (Fig. 3B, osmolality ≤300 mmol·kg^{-1}) or small surface areas (Fig. 2B; <10 mm^2), but direct evidence is lacking. These arguments demonstrate that the hypothetical swelling effect associated with exposure of the CM in a water/CM/water system on water conductance would be too low to account for the magnitude of the observed difference between $g_{tot.\ uptake}$ (the present investigation) and $g_{tot.\ transp.}$ (Knoche et al., 2000). Last, flow, that may occur through a water film formed on outer and inner surfaces of the stomatal apparatus by a yet unknown mechanism (Eichert et al., 1998), would also contribute to the higher conductance in water uptake than in transpiration.

In conclusion, our experimental system allowed a reproduc-

ible determination of conductance in water uptake of sweet cherry fruit under highly controlled conditions. The data generated using this system suggested that water uptake was a physical process and the CM represented the primary barrier to penetration. Water uptake was similar qualitatively to transpiration, but different quantitatively, the most striking difference being a 43-fold higher conductance in water uptake. This and other observations support the hypothesis that different pathways and mechanisms may be involved in water uptake and transpiration through the sweet cherry fruit exocarp. This subject merits further study. Experiments in which conductance in water uptake and transpiration is established on an individual segment basis would be useful. Also, data on exocarp conductance for labeled water, i.e., tritiated or deuterated water, in the absence of a water potential gradient and on the effect of water vapor activity on conductance would be helpful to assess whether viscous flow contributed to water uptake (Schönherr, 1976; Solomon, 1968). Such information may now be generated using the system described herein.

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