Ethenphon-Induced Gummosis in Sour Cherry (Prunus cerasus L.)

II. FLOW CHARACTERISTICS OF GUM SOLUTIONS

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Received for publication August 28, 1981 and in revised form March 25, 1982

ABSTRACT

Flow of sour cherry (Prunus cerasus L. cv. Montmorency) gum solutions through a glass capillary was Newtonian for pressure gradients from 0 to 1.8 megapascals per meter, and hydraulic conductance was inversely proportional to solution viscosity in this range. However, flow became plastic at pressure gradients above 1.8 megapascals per meter, resulting in a decrease in solution viscosity. The magnitude of this effect diminished as gum concentration increased. Flow of water, a solution of the component sugar monomers of sour cherry gum, and sucrose solutions remained Newtonian over the entire pressure gradient range examined (0-4 megapascals per meter). Plastic flow of gum solutions in the vessels of intact sour cherry shoots is possible under pressure gradients induced by transpiration when high resistance to flow occurs over short distances.

Sour cherry gum is a high mol wt, hydrophilic, weakly acidic arabinogalactan polysaccharide (19). Gum synthesis and accumulation in Prunus is promoted by stress and wounding (2, 3, 6, 7) or more directly by ethylene (1, 10). The gum formed can enter the xylem vessels and interfere with flow through the vessels both by increasing vessel sap viscosity and by occlusion of vessels (14). Laminar flow through capillaries is described by the Hagen-Poiseuille equation (15, 17):

\[ Q = \frac{\pi r^4}{8 \eta} \frac{\delta P}{\delta L} \]

where \( Q \) is volume rate of flow (m³ s⁻¹), \( r \) is capillary radius (m), \( \eta \) is solution viscosity (1 Pa s = 10 poise), \( P \) is pressure (Pa), and \( L \) is capillary length (m). The assumption that flow is laminar and not turbulent is based on calculation of Reynolds number (16). Laminar flow can be assumed when this unitless parameter has a value less than 2,000. The ability of a capillary or the xylem vessels of a shoot to conduct fluid is expressed as hydraulic conductance (\( k \)), defined here as the ratio of volume rate of flow and the pressure gradient driving the solution:

\[ k = \frac{Q}{\delta P/\delta L} \]

with units of m⁴ s⁻¹ Pa⁻¹.

The presence of even dilute concentrations of gum in the vessels of sour cherry shoots would decrease shoot \( k \). Viscosity of a 1.90% (w/v) gum solution was 15 times greater than H₂O at 25°C (14).

Flow rate is directly proportional to pressure gradient, and solution viscosity remains constant as the pressure gradient increases. However, flow of polymer solutions is often non-Newtonian due to the large size of the polymer (4, 18, 19) and the tendency for such molecules to interact with each other (5, 9, 18). Several types of deviation from Newtonian behavior are possible (5, 8, 11, 16, 17) and a summary is provided in Figure 1. The objective of this study was to establish the effect of gum concentration and applied pressure gradient on the flow characteristics of aqueous sour cherry gum solutions, and to relate these effects to conduction of sap through xylem vessels of sour cherry shoots.

MATERIALS AND METHODS

Test Solutions. Clear, nonpigmented gum exudates were collected from branches of mature sour cherry Prunus cerasus L. cv. Montmorency) trees and stored frozen until needed. Gum exudation was induced by a foliar spray of ethephon, (2-chloro-ethyl)phosphonic acid, at concentrations up to 69.2 µm. Gum solutions of 1.90% and 3.81% (w/v) were prepared by dissolving gum in warm, deionized, distilled H₂O. The solutions were then centrifuged to remove debris and stored at 4°C. Gum concentration was determined from the residue dry weight of a 2-ml aliquot of solution. Gum solutions of 1.09% and 1.91% were prepared by dilution of the 3.81% solution. Solution density was determined at 25°C with a glass pycnometer (25 ml) and kinematic viscosity with an Ostwald viscometer at the same temperature. Kinematic viscosity was multiplied by solution density to obtain solution viscosity. Deionized, distilled H₂O, solutions of 44% and 66% (w/v) sucrose, and a solution of the component sugar monomers of sour cherry gum at concentrations equivalent to a gum solution of 1.90% were also prepared for comparison with gum solutions. The composition of the solution of gum monomers was based on previous gas-liquid chromatographic assay (13) of the monomer composition of exuded 'Montmorency' sour cherry gum. The gum contains 55.0% (w/w) L-Ara, 32% D-Gal, 6.3% D-Man, 6.1% D-Xyl, and 0.6% D-Glu. Concentrations, densities, and viscosities were determined as described above (Table I).

Flow Experiments. Volume rate of flow through a glass capillary (4.0 cm x 0.1 mm i.d.) of the test solutions was measured under pressure gradients from 0 to 0.15 MPa m⁻¹. Pressure gradients were applied by adjusting the head height of a solution reservoir. Higher pressure gradients were attained by use of a pressure chamber and micropump (Technicon AutoAnalyzer Hi-Pressure Micropump; Technicon Chromatography Corp., Ardsley, NY). The test solution was placed in the pressure chamber ahead of a lubricated steel piston fitted with an O-ring. H₂O was pumped through the micropump, driving the piston forward to provide the required pressure. As the test solutions were forced through the capillary, flow rates were measured by timing the rate of meniscus advance in a 0.1-ml pipet calibrated in 0.01-ml divisions. The frictional resistance of the pressure chamber piston was determined from the relation of applied pressure and flow rate for H₂O

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FLOW OF SOUR CHERRY GUM SOLUTIONS

![Diagram of flow dynamics](image)

**Fig. 1.** Possible types of flow dynamics, modified from Dinsdale and Moore (4). In considering laminar flow through a capillary, the driving stress is \( Pr/2L \) where \( P \) is the hydraulic pressure applied and \( r \) and \( L \) are the capillary radius and length. Shear rate is the change in flow velocity per change in radius: \( dv/dr \). Plotted in this way, the slope is the viscosity coefficient of the fluid. Line NF represents Newtonian flow as described by the Hagen-Poiseuille equation where change in shear rate is directly proportional to change in driving stress (viscosity is constant). Line BPF represents Bingham plastic flow with a yield (threshold) value of Y. Line PPF represents pseudoplastic flow with an extrapolated yield value of EY. Line DF represents dilatent flow.

<p>| Table I. Concentration, Density, and Viscosity of Sugar and Sour Cherry Gum Solutions |
|---------------------------------|------------------|------------|-----------|</p>
<table>
<thead>
<tr>
<th>Solution</th>
<th>Concentration, %, w/v</th>
<th>Density, g cm(^{-3})</th>
<th>Viscosity, cp</th>
</tr>
</thead>
<tbody>
<tr>
<td>H(_2)O</td>
<td>767</td>
<td>2.930</td>
<td></td>
</tr>
<tr>
<td>Sugar monomers</td>
<td>1.90</td>
<td>1062</td>
<td>2.464</td>
</tr>
<tr>
<td>Sucrose</td>
<td>44</td>
<td>682</td>
<td>0.536</td>
</tr>
<tr>
<td>Gum</td>
<td>66</td>
<td>2</td>
<td>0.204</td>
</tr>
<tr>
<td>Gum</td>
<td>1.90</td>
<td>14</td>
<td>0.260</td>
</tr>
<tr>
<td>Gum</td>
<td>1.91</td>
<td>18</td>
<td>0.212</td>
</tr>
<tr>
<td>Gum</td>
<td>3.81</td>
<td>2</td>
<td>0.086</td>
</tr>
</tbody>
</table>

Density and viscosity were determined at 25°C. Values for H\(_2\)O were taken from the Handbook of Chemistry and Physics, Chemical Rubber Publishing Co., Cleveland, OH.

Hydraulic conductance \( (k) \) was measured as the solutions were forced through a glass capillary (4.0 cm \( \times \) 0.1 mm i.d.) over a range of pressure gradients from 0 to 4.0 MPa m\(^{-1}\). Values of \( k \) presented here are restricted to pressure gradients for which flow was Newtonian (0-4.0 MPa m\(^{-1}\) for H\(_2\)O, monomer, and sucrose solutions and 0-1.8 MPa m\(^{-1}\) for gum solutions). Reynolds numbers were calculated for maximum flow rates obtained. Flow through capillaries can be assumed to be laminar since the unitless Reynolds numbers are less than 2,000.

**Table II. Effect of Sugar and Gum Concentration on Hydraulic Conductance and Reynolds Number**

<table>
<thead>
<tr>
<th>Solution</th>
<th>Concentration, %, w/v</th>
<th>Reynolds Number</th>
<th>Mean Measured k, ((m^{3} s^{-1} MPa^{-1}) \times 10^{9})</th>
</tr>
</thead>
<tbody>
<tr>
<td>H(_2)O</td>
<td>767</td>
<td>2.930</td>
<td></td>
</tr>
<tr>
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<td>44</td>
<td>682</td>
<td>0.536</td>
</tr>
<tr>
<td>Gum</td>
<td>66</td>
<td>2</td>
<td>0.204</td>
</tr>
<tr>
<td>Gum</td>
<td>1.09</td>
<td>53</td>
<td>0.937</td>
</tr>
<tr>
<td>Gum</td>
<td>1.90</td>
<td>14</td>
<td>0.260</td>
</tr>
<tr>
<td>Gum</td>
<td>1.91</td>
<td>18</td>
<td>0.212</td>
</tr>
<tr>
<td>Gum</td>
<td>3.81</td>
<td>2</td>
<td>0.086</td>
</tr>
</tbody>
</table>

Pressure was applied by solution head height.

**RESULTS**

**Reynolds Number.** Calculated values of Reynolds numbers were less than 2,000 for all experiments (Table II). Thus, the assumption of laminar flow could be made in all cases.

**Hydraulic Conductance.** Flow rates of all solutions were directly proportional to the applied pressure gradient between 0 and 0.15 MPa m\(^{-1}\) (Fig. 2). There was no inherent threshold pressure gradient (yield value) to overcome before flow occurred for any of the solutions.

Reynolds numbers were calculated for maximum flow rates achieved to determine whether the assumption of laminar flow, inherent in the Hagen-Poiseuille equation, could be made for the experimental conditions employed.

\[
predicted k = \frac{\pi r^4}{8 \eta}
\]

Reynolds numbers were calculated for maximum flow rates achieved to determine whether the assumption of laminar flow, inherent in the Hagen-Poiseuille equation, could be made for the experimental conditions employed.
FIG. 3. Effect of pressure gradient on flow rate through a glass capillary of water and solutions of sucrose, sour cherry gum, and the component sugar monomers of sour cherry gum at concentrations equivalent to a 1.90% (w/v) gum solution. Pressure was applied by a micropump. Capillary dimensions were 4.0 cm x 0.1 mm i.d. Data for line W were obtained for H2O without the piston in the pressure chamber while data for line A through G were obtained with the piston in the pressure chamber.

FIG. 4. Relationship between hydraulic conductance and viscosity for flow through a glass capillary (4.0 cm x 0.1 mm i.d.) under conditions of Newtonian flow. Solutions tested were water, sucrose, and a solution of the component sugar monomers of sour cherry gum (O, ●) and solutions of sour cherry gum (△, △). (○, △) represent data for pressure gradients obtained with a micropump; (●, △) represent data for pressure gradients obtained by solution head height.

FIG. 5. Effect of pressure gradient on flow of sour cherry gum solutions in a glass capillary (4.0 cm x 0.1 mm i.d.). Pressure gradients were applied with a micropump and were not adjusted for resistance of the pressure chamber piston. Slope is inversely proportional to solution viscosity. Decrease in viscosity with the shift from Newtonian (flow directly proportional to pressure) to plastic flow diminished as gum concentration increased. The transition from Newtonian to plastic flow occurred at a mean pressure gradient (corrected for piston resistance) of 1.78 ± 0.30 MPa m⁻¹.

Table III. Effect of Sour Cherry Gum Concentration on the Increase in Slope of Pressure Gradient versus Flow Rate for Plastic Flow Relative to Newtonian Flow

<table>
<thead>
<tr>
<th>Gum Concentration, %, w/v</th>
<th>Plastic Flow Relative to Newtonian Flow, ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.09</td>
<td>2.549</td>
</tr>
<tr>
<td>1.90</td>
<td>2.158</td>
</tr>
<tr>
<td>1.91</td>
<td>2.071</td>
</tr>
<tr>
<td>3.81</td>
<td>2.000</td>
</tr>
</tbody>
</table>

the test solutions. Thus, all solutions exhibited Newtonian flow in this pressure gradient range and hydraulic conductance was constant for each solution. Data for the gum monomer solution were essentially identical to those for water, while the flow rates for the sucrose and gum solutions were markedly lower, as expected from the solution viscosities.

Flow characteristics of H2O, gum monomer, and sucrose solutions, but not gum solutions, remained Newtonian over the pressure gradient range from 0 to 4.0 MPa m⁻¹ (corrected for piston resistance) (Fig. 3). Mean measured k for conditions giving Newtonian flow, obtained with both pressure systems, is presented for all solutions in Table II.

Measured k for all solutions was proportional to the inverse of viscosity over the region of Newtonian flow (Fig. 4), consistent with the Hagen-Poiseuille equation. The correlation coefficient (r = 0.989) was significant at p = 0.01. The mean of the ratio of measured to predicted k over the pressure gradient range giving Newtonian flow was close to unity, 1.16 ± 0.21, indicating good agreement between observed and predicted k.

Plastic Flow of Gum Solutions. An apparent decrease in the viscosity of gum solutions, especially when dilute, occurred at pressure gradients greater than 2 MPa m⁻¹ (Fig. 3). This indicated a deviation from Newtonian to plastic flow. This deviation was not an artifact of the experimental system because flow remained Newtonian for the other solutions over the entire pressure gradient range examined. Flow rate of the gum solutions was apparently again linearly related to applied pressure above the transition to
plastic flow (correlation coefficient from 0.995 to 0.999) (Fig. 5). Separate linear regressions for data collected at pressure gradients above and below 2 MPa m⁻¹ allowed calculation of the pressure gradient where the deviation from Newtonian flow occurred for each gum solution. The transition point was similar for all gum concentrations, with a mean of 1.78 ± 0.30 MPa m⁻¹.

The deviation from Newtonian to plastic flow, however, diminished with increasing gum concentration. Not only did the magnitude of the deviation decrease, but there was also a decreasing trend in the ratio of the pressure-flow slopes above and below the transition pressure gradient with increasing gum concentration (Table III). The ratio of these slopes declined from 2.5 for a 1.09% gum solution to 2.0 for the 3.81% gum solution. Increase in slope is inversely proportional to the change in solution viscosity. The correlation coefficient between the ratio of pressure-flow slopes and gum concentration was −0.778, but was not significant at p = 0.05. The correlation between slope ratio and the inverse of solution viscosity (determined under conditions of Newtonian flow) was 0.952, which was significant at p = 0.05.

**DISCUSSION**

Pressure gradients in the xylem of trees at maximum rates of transpiration have been estimated to be between 0.02 and 0.05 MPa m⁻¹ (12, 13, 20). These values are, however, averaged over the height of the tree. While flow of gum solutions is Newtonian in this pressure gradient range, gradients sufficient to cause plastic flow might occur over short distances of high resistance to flow in the xylem, as would be caused by the occlusion of a proportion of the vessels by gum or by other factors. When corrections are made for differences in the capillary radius and the sum of xylem vessel radii (14), both to the 4th power, a 10-fold increase in the pressure gradient would be required for plastic flow to occur in 1-year-old untreated sour cherry shoots.

The effect of gum on vessel sap viscosity is a function of both gum concentration and the pressure gradient driving the solution. The occurrence of plastic flow at high pressure gradients would to some extent compensate for the presence of gum in the vessel as solution viscosity decreases. The decrease in viscosity could result from the breaking of weak intermolecular bonds between gum polymers, as in thixotrophy, and also from a more streamlined orientation of the gum molecules in the vessels, resulting in less internal resistance to flow in the solution (9, 11). However, deviation from Newtonian to plastic flow diminished as gum concentration increased and, thus, the compensating effect of viscosity becomes negligible at gum concentrations above 4% (w/v).

Previously (14), we found that small increases in the concentration of sour cherry gum greatly increased solution viscosity, and thus decreased hydraulic conductance. There is probably a distribution of gum concentrations within and among xylem vessels. When ethylene induces an increase in gum synthesis and accumulation, more gum enters the vessels, increasing sap viscosity and, at high enough concentrations, occluding vessels entirely. Both the increase in sap viscosity and decrease in number of functional vessels reduce flow of fluid in the xylem. Decrease in water potential and even tissue death can occur when the reduction in shoot hydraulic conductance is severe.

Acknowledgment—The hydraulic pressure chamber used in these studies was designed by Dr. C. R. Olien, United States Department of Agriculture—Science and Education Administration, and Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI.

**LITERATURE CITED**