DIFFERENCES AMONG SEEDLING PEACH CLONES IN STOMATAL RESPONSE UNDER GREENHOUSE CONDITIONS

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Abstract
Twenty three local clones of seedling peach were included to determine the variation among clones in stomatal response to air temperature (T), air vapor pressure deficit (VPD) and soil moisture (PW). Differences in isozyme banding among clones were also studied. Temperature was the variable best related to stomatal conductance in well-watered plants but there were differences in stomatal response. Vapor pressure deficit was significantly related to stomatal conductance in some of the included clones but it was not determinant in others. Under drought cycles, peach stomata did not longer respond to T or VPD but it was related to PW. Stomata of seedling peach clones also responded diversely to drought cycles, varying their rates of stomatal closure. Stomata partially closed at temperatures above 30°C and vapor pressure deficits above 2.84 Kpa. Slight differences among clones in isozyme patterns for malate dehydrogenase (MDH) were recorded.

1. Introduction
Stomata clearly respond to changes in air temperature, light intensity, and air humidity. The combined effects of temperature and light intensity on stomatal behaviour of peach have been reported (Tan and Butter, 1986). Water stress effects on stomatal movements have been described in peach (Hand et al., 1982). These aclimation responses of stomata are obviously important in yield potential and general behaviour of trees (Tan and Butter, 1986), and become particularly important for the peach growing area of Zacatecas Mexico, with 20 000 ha of unirrigated orchards.

Although stomatal responses of peach to environment have been published, there are no reports on the variation of these responses among cultivars or clones. The objective of this study was to determine whether there were differences among seedling peach clones in the stomatal response to fluctuations in T, VPD, and in PW. In addition, isozyme analysis were carried out to find out differences in isozyme banding patterns.

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2. Materials and methods

Vigorous and healthy seedling peaches were selected at commercial orchards in Zacatecas Mexico, at the driest season of the year (April and May). Selected trees were propagated by hardwood cuttings. Rooted cuttings were then transferred to 10 lt plastic plots with sterile sand. Pots were irrigated every other day, and once a week a mineral solution was used instead of water.

Two experiments were established in a greenhouse under natural radiation. Two irrigation regimes were used: 1) irrigation every other day to replenish consumed water, and 2) ten day drought cycles. Stomatal conductance (SC) was measured daily at 9:00, 12:00 and 15:00 hours, in both regimes. An automatic diffusion porometer (Delta T), calibrated daily, was used to estimate stomatal conductance on two different leaves of each plant. Air temperature (T) and relative humidity, calculated as vapor pressure deficit (VPD), were taken at the same times with a higrothermograph. Pot weight, to calculate soil moisture content (PW), was recorded every morning. Multiple regression analysis relating SC to T, VPD and PW was carried out using a stepwise program. Two replicates, each with one seedling, were used.

Three isozyme systems were analyzed: malate dehydrogenase (MDH), leucine aminopeptidase (LAP) and phosphoglucomutase (PGM), using the procedures described by Arulasekar and Parfitt (1986).

3. Results

A general model fitted for stomatal behaviour of well-watered plants of seedling peach as their leaf SC (cm s⁻¹), based on daily fluctuations of T (°C), VPD (kPa) and PW (%), was:

\[ SC = B_1 \text{VPD} - B_2 \text{VPD}^2 + B_3 T^2 - B_4 T + B_5 PW + C \]

where \( B_1, B_2, B_3, B_4, B_5 \) were coefficients for the included variables and C was a constant term in the model.

Considering data of all clones in a single analysis, this model was significant (P=0.01) for seedling peach in general, with a multiple regression coefficient \( r^2 \) of 0.45 (table 1). However, on individual basis \( r^2 \) ranged from 0.36 to 0.90, thus from a total of 23 clones included, the above-mentioned model was highly significant (P=0.01) for two clones and significant (P=0.05) for another 10 clones, while other 11 clones had non-significant coefficients. In general, as shown by partial \( r^2 \) and the order of entry into the model of data for all clones, T was the most important variable related to SC, although there were dissimilarities among peach clones. The next related variable was \( T^2 \), but again differences were noted between clones, accounting for 35% in clone 3 and for only 1% in clone 23. On the other hand, vapor pressure deficit, as VPD or VPD², was the least related environmental variable to SC when considering data
for all clones in a single analysis. However, taking into consideration response of individual clones, VPD was a more important factor than \( T^2 \) in clone 23, only with a \( r^2 \) lower than \( T \). Under well-watered conditions PW tended not to be related to SC in seedling peach (table 1).

Regression analysis of data for plants under drought cycles (table 2) indicated that the model and responses of SC to T, VPD and PW were not the same as those of well-irrigated trees. Stomata of peach did not longer respond to T or VPD under limited irrigation. Under this condition, soil moisture content (PW) became an important variable related to SC, giving a linear relation between SC and PW, therefore as soil got drier, stomatal conductance decreased. As for well-watered plants, variation among clones were observed in \( r^2 \), coefficients for PW (β) and intercept terms in the model (α). The relation between PW and SC in drought-cycled plants was not significant (P=0.05) for 11 clones, was significant (P=0.05) for 7 clones, and was highly significant (P=0.01) for 5 clones.

Substituting values of T and VPD, over the ranges found in the field, an optimum of T and VPD for stomata of seedling peach was obtained, according to equations derived. Optimum values of the two variables were 21°C C and 1.28 KPa for T and VPD, respectively (figure 1).

Migration patterns for LAP and PGM did not differ among clones, while malate dehydrogenase (MDH) showed slight differences (figure 2). Selected seedling peaches had a MDH with shorter migration patterns in starch gels than those of control trees. Clone 16, with sensitive stomata to drought cycles (table 2), migrated longer than a relatively unsensitive control. Control trees had also a more pronounced enzyme activity, based on darker staining colors.

4. Discussion

Differences among peach clones indicate that stomata of trees of about half of the clones clearly responded to environmental conditions, while others seemed not to do so. Moreover, the equations derived for different clones, accounted for as low as 36% and for as high as 90% of the variation of SC. These data indicate that sensitivity of stomata to environment may be different for each clone.

Temperature relations to SC suggested that stomata respond primarily to air temperature, as reported by others (Schulze et al., 1974; Osonubi and Davies, 1980). However, this variable accounted for 62% of the variation observed in SC of clone 10 and for only 36% of clone 3. This suggests that although T is related to stomata, fluctuations in T would account for high or low proportions of changes in SC, depending on the peach clone.

It has been shown that stomata of peach, besides temperature, may also respond to vapor pressure deficit, although relations are not clear (Tan and Buttery, 1986). Our data indicate that, at least for some clones of seedling peach, fluctuations of relative humidity or VPD also
contribute to a variation in SC.

Variation in coefficients (β) for variables in derived equations, also supported that there were dissimilarities among clones in stomatal response to environment. Equation coefficients for T varied from as high as 1.82 to as low as 0.40; therefore, stomata would respond to a similar change of air temperature in different magnitude, according to the clone. As observed in T, coefficients for $T^2$, VPD, VPD$^2$, PW, and C in the model also differed between clones of seedling peach.

It is known that stomata of peach decreases stomatal conductance or increases stomatal resistance under drought (Hand et al., 1982). Despite of similar drying rates of soil and soil moisture content values, stomata of drought-cycled peach was not equally related to PW in all clones. Under our experimental conditions, stomata of 11 clones remained relatively open during the drought cycles, compared to those of the other 12 clones. This also suggests that stomata may close during drought more rapidly in one clone than others. According to equations derived for clone 1 and 6, both with significant (P=0.01) regression coefficients, and a reduction in PW from 20% to 15%; SC would be similar under high (20%) soil moisture levels, with 0.37 and 0.39 cm.s$^{-1}$ of SC for clone 6 and 1, respectively. However, the estimated values of SC under a lower soil moisture content (15%) are 0.22 cm.s$^{-1}$ for clone 6 and 0.14 cm.s$^{-1}$ for clone 1. Therefore clone 1, with higher values in the equation, will close stomata faster than clone 6. Although stomatal response to soil drying in clones of seedling peach varied, at present we do not know whether these differences in closure rate may contribute to a better adaptation of plants under limited moisture conditions.

Optimum values of T and VPD for SC of peach stomata in this work, were the same as those reported by Tan and Butterly (1986) under 144 μmol.s$^{-1}$.m$^{-1}$ of photosynthetically active radiation. A temperature above 30° C and a vapor pressure deficit above 2.84 KPa will partially close stomata. Values of T and VPD of this magnitude are definitely observed in this peach growing area, resulting in reduction of SC of peach stomata from about 12 to 17 hours, at the highest atmospheric water demand during daily cycle and despite of soil moisture content. This decrease in turn may affect tree performance, particularly in unirrigated orchards (20 000 has).

Isozymes are useful to differentiate among deciduous fruit trees; differences among known peach cultivars have been reported for malate dehydrogenase (Arulsekar and Parfitt, 1986), as reported here for seedling peaches. Nevertheless, the significance of this finding in future selection and breeding programs of these clones remains to be studied.

In summary, stomata of seedling peach primarily responded to changes in T, VPD seems to be an important variable for certain clones, while PW was not related to SC under well-watered conditions but it was important in drought-cycled plants. Our data have also shown that there
are differences among seedling peach clones in stomatal closure rate under drought, since some closed stomata faster than others. Therefore, future research with this type of peaches, on the relations of stomata to environment or drought, needs to consider these findings. Several unresolved questions remain with regards to their significance in drought tolerance, tree yield potential, and differences with seed propagated plants and among known peach cultivars. Isozyme analysis, particularly malate dehydrogenase, may be useful to separate clones in seedling peach but more research is needed to find a relationship with the different stomatal responses reported.

Acknowledgments
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References
Table 1.- Partial regression coefficients ($r^2$) and equation coefficients ($\beta$) for temperature ($T$ °C), vapor pressure deficit (VPD KPa), and soil moisture content (PW %) in their relation to stomatal conductance of seedling peach clones under well-irrigated conditions. Number in bracket shows order of entry into the model.

<table>
<thead>
<tr>
<th>CLONES</th>
<th>VA-</th>
<th>RIA</th>
<th>BLE</th>
<th>$r^2$</th>
<th>$\beta$</th>
<th>$r^2$</th>
<th>$\beta$</th>
<th>$r^2$</th>
<th>$\beta$</th>
<th>$r^2$</th>
<th>$\beta$</th>
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<tbody>
<tr>
<td>3</td>
<td>0.36(1)</td>
<td>1.82</td>
<td>0.62(1)</td>
<td>0.75</td>
<td>0.52(1)</td>
<td>0.40</td>
<td>0.27(1)</td>
<td>0.35</td>
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<td></td>
</tr>
<tr>
<td>10</td>
<td>0.35(4)</td>
<td>0.37</td>
<td>0.21(2)</td>
<td>0.16</td>
<td>0.01(2)</td>
<td>0.08</td>
<td>0.06(2)</td>
<td>0.07</td>
<td></td>
<td></td>
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<tr>
<td>23</td>
<td>0.13(2)</td>
<td>5.79</td>
<td>0.02(4)</td>
<td>1.90</td>
<td>0.19(4)</td>
<td>1.26</td>
<td>0.03(5)</td>
<td>0.59</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ALL</td>
<td>0.04(3)</td>
<td>1.61</td>
<td>0.02(3)</td>
<td>0.55</td>
<td>0.02(3)</td>
<td>0.35</td>
<td>0.02(4)</td>
<td>0.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.02(5)</td>
<td>0.04</td>
<td>0.01(5)</td>
<td>0.05</td>
<td>0.09(5)</td>
<td>0.08</td>
<td>0.07(3)</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>0.90</td>
<td>0.88</td>
<td>0.83</td>
<td>0.45</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

Table 2.- Linear regression equations for the relation between stomatal conductance (SC) and soil water content (PW) in seedling peach clones under drought cycles. The equation is SC=$\beta$*PW + $\alpha$. NS, *, ** denote non-significant, significant at P=0.05 or P=0.01, respectively.

<table>
<thead>
<tr>
<th>CLONE</th>
<th>$r^2$</th>
<th>$\beta$</th>
<th>$\alpha$</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>0.86 **</td>
<td>0.051</td>
<td>-0.63</td>
</tr>
<tr>
<td>6</td>
<td>0.64 **</td>
<td>0.031</td>
<td>-0.25</td>
</tr>
<tr>
<td>16</td>
<td>0.38 *</td>
<td>0.025</td>
<td>-0.30</td>
</tr>
<tr>
<td>5</td>
<td>0.29 *</td>
<td>0.012</td>
<td>-0.04</td>
</tr>
<tr>
<td>23</td>
<td>0.20 NS</td>
<td>0.014</td>
<td>+0.05</td>
</tr>
<tr>
<td>8</td>
<td>0.18 NS</td>
<td>0.006</td>
<td>+0.24</td>
</tr>
<tr>
<td>3</td>
<td>0.04 NS</td>
<td>0.008</td>
<td>-0.02</td>
</tr>
</tbody>
</table>

Figure 1. Stomatal conductance of seedling peach at various air temperatures (TEMP, °C) and vapor pressure deficits (VPD, KPa), as estimated by equations derived for the relation between stomata and environment.

Figure 2. Migration patterns of malate dehydrogenase (MDH) for several peach clones.