

# Diurnal Variation in Water Potential Components and Stomatal Resistance of Irrigated Peach Seedlings<sup>1</sup>

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**Abstract.** Peach [*Prunus persica*, (L.) Batsch] seedling growing in irrigated soil showed strong diurnal variations in total water potential, turgor potential, and stomatal resistance. A significant positive correlation existed between turgor potential and total water potential while osmotic potential remained fairly constant. There appeared to be no rapid, diurnal osmotic adjustment to maintain constant turgor, although there may have been some slight, long-term osmotic adjustment over the 2-week experimental period. When turgor approached zero, a depression of osmotic potential due to water loss through transpiration maintained turgor above zero. Stomatal resistance remained low throughout the day, even though total water potential dropped below -16 bars and turgor potential was below 2 bars. Stomatal resistance was negatively correlated with irradiance level but not with turgor potential.

Diurnal and seasonal variations in total water potential with changing environmental conditions have been studied recently in peach (7, 12) and cherry (9). However, variations in the components of total water potential were not investigated. Total leaf water potential may be partitioned into the following components:

$$\psi_w = \psi_p + \psi_s + \psi_m$$

where  $\psi_w$  is the total water potential of the leaf tissue,  $\psi_p$  the turgor potential,  $\psi_s$  the solute or osmotic potential, and  $\psi_m$  the matric potential. Matric potential has been considered negligible in most herbaceous plant tissue (6, 11). Thus the turgor and osmotic potential components contribute most significantly to total water potential.

Because water stress directly reduces plant growth through a reduction in turgor potential (6), it is important to know the relative contributions of the turgor and osmotic components. Active osmotic adjustment to maintain turgor potential during water stress has been reported in apple trees by Davies and Lakso (4), but has not been investigated in peach. Also, the relationship between turgor potential and stomatal resistance in peach is unknown. Xiloyannis and Martin (12) reported high stomatal conductance at peach leaf water potentials above -18 bars and low conductance at potentials below -26 bars, but turgor potential was not measured. Davies and Lakso (4) found that stomatal conductance was poorly correlated with turgor potential in apple seedlings, but did decrease along with turgor potential at total potentials below -15 bars.

The objectives of this study were to explore the diurnal changes in total water potential, the osmotic and turgor potential components, and to determine the relationship of turgor potential with stomatal resistance in irrigated peach seedlings. We also attempted to determine if diurnal osmotic adjustments exist to maintain constant turgor.

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## Materials and Methods

Open-pollinated 'Halford' peach seeds were sown in a greenhouse bed in August, 1979 and allowed to grow for 3 months under an 18-hr photoperiod using Cool White fluorescent bulbs as supplemental light until the seedlings were about 1 m tall. Seedlings were watered and fertilized regularly throughout the study period. Seedlings were transferred to natural photoperiod on November 30, 1979, and measurements were taken on 3 nonconsecutive days in early December. Each set of measurements was taken within a 0.5 hr period at 2-hr intervals, 7 times daily, beginning before sunrise at 0530 hr and ending after sunset at 1730 hr. Five fully expanded, nonsenescent leaves were selected randomly from the seedlings for each set of measurements.

Stomatal resistance was determined *in situ* using a Licor LI-65 diffusion porometer (3). The leaf was then detached and total leaf water potential was measured by the pressure bomb technique of Scholander et al. (8). The leaf was then sealed in a plastic bag (excluding air as much as possible), immediately frozen on dry ice, and transferred to a freezer at -85°C for subsequent osmotic potential determinations. Throughout the diurnal sampling period for each day: air temperature was 22 ± 1.5°, leaf temperature was 21 ± 1.0°, and relative humidity was 45 ± 10%. Irradiance was measured using a Wescor integrating quantum meter which accumulated  $\mu\text{Em}^{-2} \text{sec}^{-1}$  at canopy level. Soil moisture was maintained above field capacity throughout the study period.

Osmotic potential was measured by 2 methods on each frozen leaf. Each leaf was removed from the freezer, and fresh weight was taken as the leaf thawed. A 2-cm<sup>2</sup> piece was then cut from the leaf blade and immediately placed in a Wescor leaf chamber, and the osmotic potential was read by the psychrometric method after the chamber had reached equilibrium. The remainder of the leaf was placed in a Scholander pressure bomb, and 50  $\mu\text{l}$  sap was expressed by increasing the pressure to about 35 bars. The expressed sap was diluted to 300  $\mu\text{l}$ , and the osmotic potential was measured in an Osmette Automatic osmometer by the freezing point depression technique. Both pieces of the leaf were then dried at 75°C for 72 hr, and dry weight was determined.

Cellular disruption, due to exposure of plant tissue to a lethal freeze-thaw cycle, results in complete loss of turgor. Components of total water potential are then only osmotic and matric potentials (1, 2, 5). The matric component is no longer negligible due to the perfusion of large amounts of water into intracellular spaces. Therefore, measurements of water potential on cryogenically killed tissue will yield an artificially low osmotic potential be-

cause of the presence of water bound to the cell walls (11). The proportion of this bound water can be estimated by a technique described by Weatherley (11), whereby the water content and water potential of a cryogenically killed leaf are determined periodically as the leaf loses water. The amount of bound water per unit dry weight is determined at varying water contents by the following formula:

$$m = \frac{\pi_2 M_2 - \pi_1 M_1}{(\pi_2 - \pi_1)D}$$

where  $m$  is the amount of bound water per unit dry weight,  $M_1$  is the initial water content,  $\pi_1$  the initial potential,  $M_2$  is the water content after some loss,  $\pi_2$  is the potential at  $M_2$ , and  $D$  is the dry weight. Once  $m$  is determined then the original osmotic potential of a frozen and thawed leaf can be corrected by the following formula:

$$\psi_s = \frac{\pi M}{Dm + M}$$

where  $\psi_s$  is the corrected osmotic potential,  $\pi$  is the uncorrect osmotic potential, and  $M$  is the leaf water content by weight.

In order to test this method of determining osmotic potential, the osmotic potentials of a series of peach leaves at various total water potentials were determined using the procedure described above. At the same time, the osmotic potentials of another series of leaves, within 0.5 bars of the same total water potentials, were measured using the pressure bomb method described by Scholander (8) and Tyree et al. (10). Osmotic potentials determined

from pressure-volume curves were within 1 bar of the corrected potentials obtained by the method described above.

## Results and Discussion

The amount of bound water per unit dry weight in cryogenically killed peach leaves ranged from 0.83–0.90 g/g and appeared to be independent of the total water potential of the unfrozen leaves over the range tested. Therefore, the mean value of 0.86 g/g was used in subsequent analyses. This value represents 44% of the total water content of these cryogenically killed leaves, which is within the range measured for leaf tissues of other species (11).

Comparison of the 2 techniques used to measure  $\psi_s$  revealed that the method utilizing sap exuded by a pressure bomb and analyzed with an osmometer generally yielded  $\psi_s$  values 1.8  $\pm$  0.8 bars higher than the psychrometric method. It is difficult to explain this discrepancy, since both techniques involve frozen and thawed leaves — a process which mixes cellular and intercellular components. The osmometer method did, however, show a higher degree of variability within replicated samples and between leaves sampled at the same time. This variability may be inherent in the technique and may have been magnified by the dilution factor involved in the samples. For these reasons, only  $\psi_s$  determined by the psychrometric method will be reported here.

Total leaf potentials varied from –4 to –5 bars before sunrise to –12 to –16 bars at midday, then recovered to –6 to –8 bars just after sunset (Fig. 1). Osmotic potentials remained fairly constant throughout the day with only a slight downward trend of 1 or 2 bars. However, during mid-morning of day 2,  $\psi_w$  decreased rapidly to almost equal  $\psi_s$  at 0930 hr. At this point,  $\psi_s$  began to decrease at the same rate as  $\psi_w$  then recovered between 1330 and

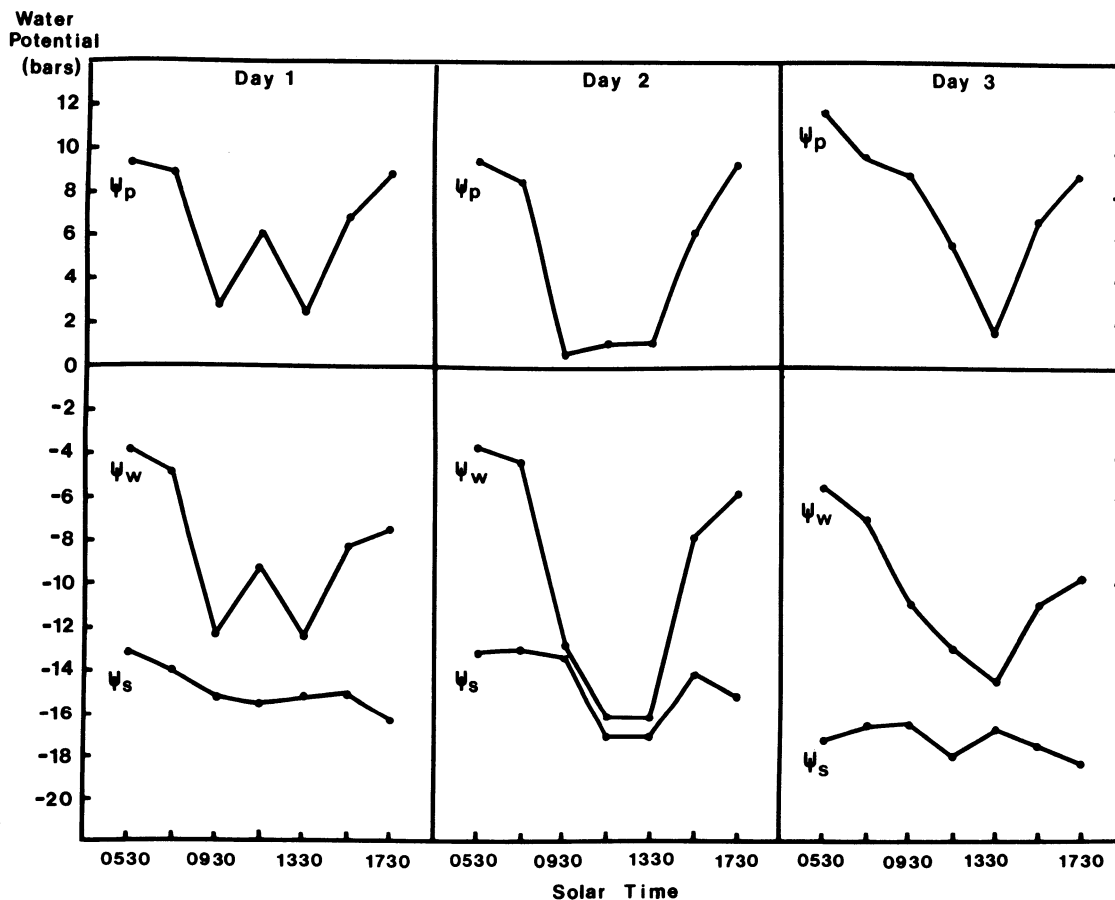


Fig. 1. Diurnal variations in total water potential ( $\psi_w$ ), osmotic potential ( $\psi_s$ ), and turgor potential ( $\psi_p$ ) in irrigated peach seedlings on 3 days in December. Tukey's Least Significant Range, 5% level, for Day 1 = 1.6 bars, Day 2 = 1.8 bars, and Day 3 = 2.1 bars.

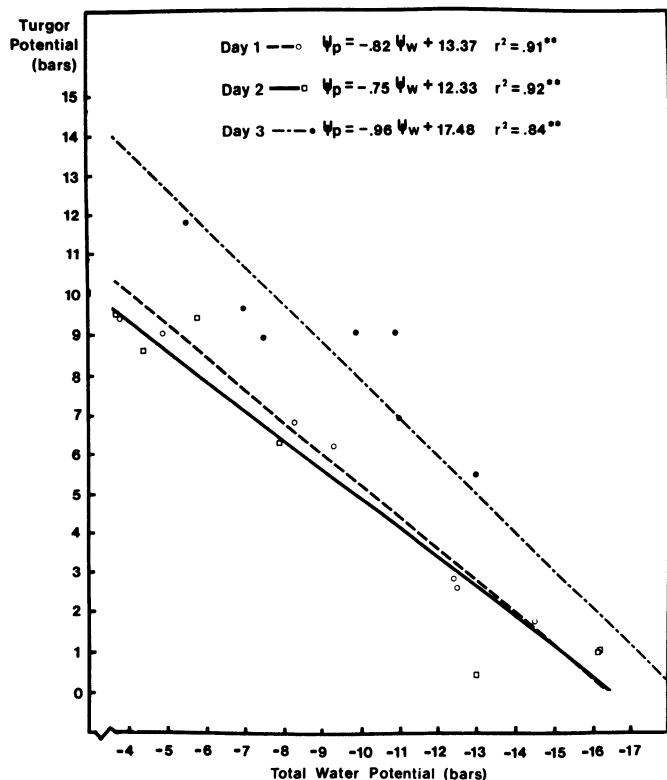


Fig. 2. Relationship between turgor potential ( $\psi_p$ ) and total water potential ( $\psi_w$ ) in irrigated peach seedlings on 3 days in December. Each point is mean of 5 separate samples. Asterisks indicate significance at the 1% level.

1530 hr as  $\psi_w$  increased. Using a variation of Vant Hoff's Equation,  $\psi_s \pm RTM$ , where  $R$  = gas constant,  $T$  = temperature in  $^{\circ}\text{K}$ , and  $M$  = osmolality of the intracellular solution, a loss of 17% of the intracellular water could account for the  $-3.5$  bars depression in  $\psi_s$  observed at 0930 hr. This much water loss would not be unusual under mid-morning conditions with low stomatal resistance. The turgor potential remained above zero throughout each day (Fig. 1) and paralleled  $\psi_w$ , except between 0930 and 1130 hr of day 2. During this time,  $\psi_p$  remained above zero only because  $\psi_s$  decreased.

Turgor potential was significantly correlated with  $\psi_w$  and with  $r^2$  values of 0.91, 0.92, and 0.84 for days 1, 2, and 3 respectively (Fig. 2). Because  $\psi_s$  did not decrease to maintain  $\psi_p$  at a constant level, peach seedlings apparently lack the ability to undergo rapid, diurnal osmotic adjustment. However, the fact that  $\psi_p$  was lower, at a given  $\psi_w$ , on day 3 than on either of the other days (significant at the 98% level according to the nonparametric sign test) suggests that a slight increase in  $\psi_s$  had occurred. Whether this indicates a slight osmotic adjustment over the entire study period or simply natural variation cannot be determined from this study.

Stomatal diffusive resistance decreased rapidly with an increase in irradiance, remained low until the irradiance level began to decrease after 1530 hr (Fig. 3), and was not correlated with any other environmental parameter measured. Stomata apparently remained fully open through midday even though  $\psi_w$  was below  $-16$  bars and  $\psi_p$  decreased to below 1 bar. This agrees with results reported by Xiloyannis et al. (12), who found that peach stomata were open at midday  $\psi_w$  of  $-18$  bars and did not begin closing until  $\psi_w$  dropped below  $-26$  bars. Stomatal opening was significantly correlated with the increase in irradiance from 1530 to 0930 hr

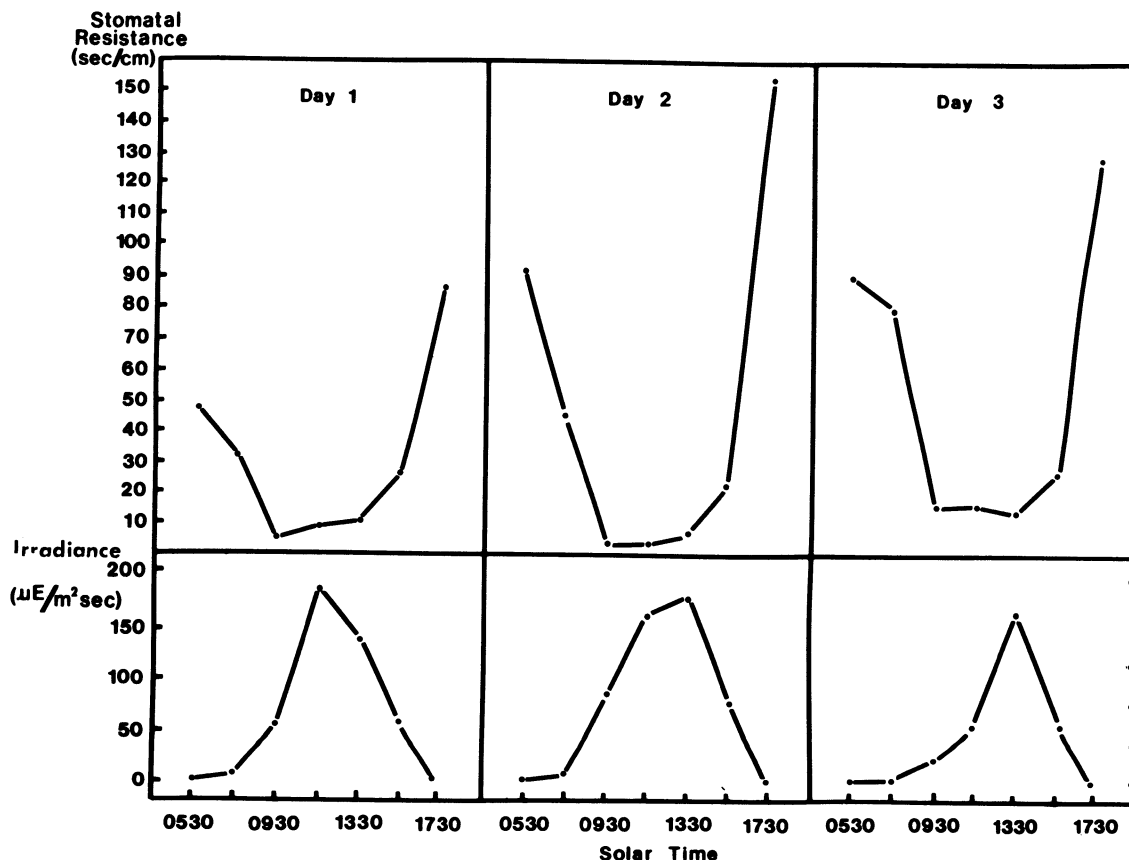


Fig. 3. Diurnal variations in stomatal resistance of irrigated peach seedlings and irradiance levels on 3 days in December. For stomatal resistance, Tukey's Least Significant Range, 5% level, for Day 1 = 5.6 sec/cm, Day 2 = 10.8 sec/cm, and Day 3 = 13.9 sec/cm.

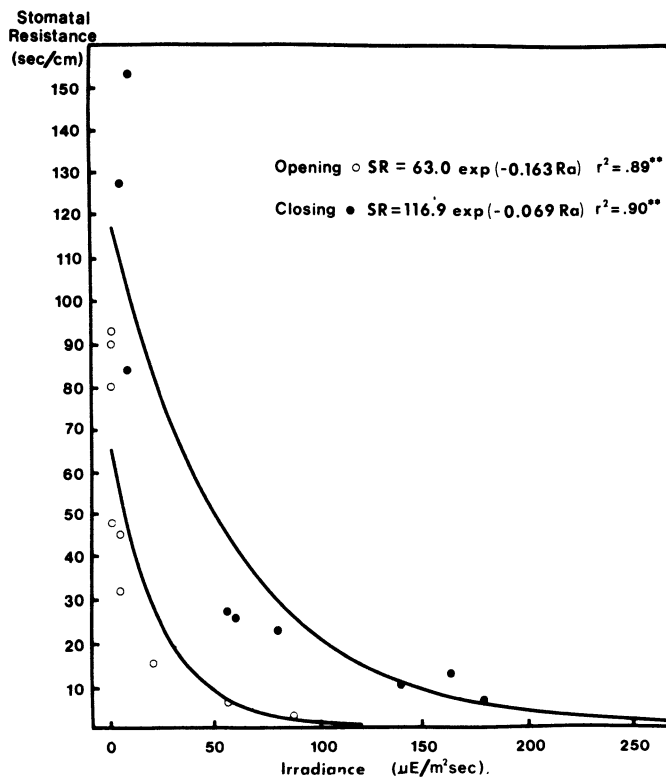


Fig. 4. Relationship between stomatal resistance and irradiance during stomatal opening and closing in irrigated peach seedlings. Data represents combination of measurements on 3 days in December. Each point is mean of 5 separate samples.

( $r^2 = 0.89$ ) (Fig. 4). Stomatal closing was significantly correlated with the decrease in irradiance from 1330 to 1730 hr ( $r^2 = 0.90$ ) (Fig. 4). Stomatal opening and closing were not significantly correlated with  $\psi_p$  ( $r^2 = 0.41$  and  $0.46$ , respectively). Stomatal resistance was higher after sunset than before sunrise on each day (Fig. 3), which may indicate a slightly stressed condition at sunset that was apparently relieved overnight. Whether this brief but re-

petitive stress induced the increased  $\psi_s$  observed at day 3 (Fig. 1) cannot be presently ascertained.

Peach seedlings in irrigated soil showed an apparent lack of diurnal osmotic adjustment to maintain turgor. Rather,  $\psi_p$  varied with  $\psi_w$ . In spite of reduced  $\psi_p$ , stomatal resistance was not affected by low turgor, but was strongly related to irradiance level. Apparently,  $\psi_p$  must fall almost to zero before turgor-induced stomatal closure occurs.

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