

Diurnal and Seasonal Effects of Environment on Plant Water Relations and Fruit Diameter of Citrus¹

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Abstract. Leaf water potential of 'Valencia' orange trees was influenced by soil water availability, soil temp, and vapor pressure deficit (VPD) of the atmosphere. Low soil water availability prevented full nighttime recovery from water stress. Soil temp below 15°C decreased root permeability for water absorption and contributed to low daytime water potentials (high water stress), but at night when transpiration was minimal, complete recovery occurred. VPD effects on leaf water potential were also most noticeable during the day. Stage II fruits exhibited a recurring diurnal size change during daylight hr. This reversible shrinkage was correlated with simultaneous changes in fruit and leaf water potential and fruit diffusion resistance. However, the irreversible nighttime growth rate could not be correlated with day or night water potentials or air temp, or with night VPD. While differences between fruit and leaf water potentials occurred, no evidence presented here or elsewhere permits an unequivocal statement that transpiring fruits can behave as a midday reservoir of water for leaves.

Considerable evidence suggests that climatic and local environmental conditions affect enlargement of fruits (4, 6, 8, 9, 11, 18). In a recent review, Kaufmann (15) collected information demonstrating that reproductive growth at all stages can be affected by the water relations of plants. It is a reasonable hypothesis that much of the impact of environmental conditions on fruit growth is attributable to environmental influences on plant water relations and to temp.

To test this hypothesis, a complex field experiment using 'Valencia' oranges was designed, with several specific objectives. First, information was required which would determine the relationship between plant water relations and plant environment. This was accomplished by making several types of plant water relations measurements on plants exposed to widely contrasting environmental conditions. Measurements were made throughout diurnal cycles to understand the dynamic relationship among plant and environment factors. Secondly, simultaneous measurements were made of fruit diam to determine whether or not short-term diam changes could be correlated with changes in plant water relations or environmental conditions. Such a correlation was found in pears by Klepper (16).

Methods

Experiments were performed on 10- to 12-year-old 'Valencia' orange trees [*Citrus sinensis* (L.) Osbeck] on 'Troyer' citrange rootstocks (*Poncirus trifoliata* x *C. sinensis*). Trees were growing in 3 widely different climatic situations in southern California, varying from a cool, humid coastal environment near San Juan Capistrano through an intermediate inland valley environment at Riverside to the lower Colorado Desert environment at Mecca near the Salton Sea in the Coachella Valley. Data were collected for selected 24- or 48-hr periods between August, 1970 and August, 1971. A mobile research laboratory, equipped with

generators, housed precision equipment and provided a base for experimentation. During each data-collection period, a uniform set of measurements was collected at various times of the day or night. All measurements were made 1 to 2 meters above ground on the north side of trees where direct solar radiation would not interfere with interpretation of data.

Three plant measurements were made. First, plant water stress was determined by pressure chamber measurements on branch tips and conversion of these values to leaf water potential with a calibration equation (13). Leaf water potential is a negative value, given in bars, representing the reduction in energy status of water in the leaves compared with the energy status of pure, free water at the same temp. It is equal to diffusion pressure deficit but opposite in sign, so that as water stress increases leaf water potential decreases (becomes more negative). Secondly, stomatal activity of leaves was evaluated by measuring leaf diffusion resistance with a porometer (20). When stomata open, the resistance of the leaf to loss of water vapor during transpiration is decreased. Therefore leaf diffusion resistance is inversely correlated with transpiration. Considerable effort was made to assure that the calibration of the porometer remained accurate under field conditions. Porometer calibration is described in another paper⁴. Leaf water potential and leaf diffusion resistance were measured on 10 trees at each sampling time. Standard error of the mean leaf water potential was never greater than ± 1.0 bar and generally was less than ± 0.5 bar. All measurements were completed in about 45 minutes. Measurements were collected at least 3 times during a diurnal cycle, and in some experiments measurements were collected at 2-hr intervals. The third plant measurement was a continuous record of fruit diam. Measurements were made with linear variable displacement transducers (19) using representative fruits 1 to 2 m above the ground. From 1 to 3 fruits were measured on the north side of trees, and an occasional fruit on the south side was measured, with the sensor and fruit shaded from direct radiation.

Simultaneously, measurements were made to characterize the soil and atmospheric environments around the plants. Soil water status was evaluated with tensiometers, and soil temp was measured at a depth of 15 cm. Tensiometers were stationed inside the drip line on the north side of trees at depths of 46, 61, and 91 cm. Soil temp was also measured inside the drip line on the north side. Air temp and relative humidity were measured with a wet and dry-bulb psychrometer. Vapor pressure deficit (VPD) of the atmosphere was calculated from the psychrometer data to provide an estimate of evaporative demand. VPD is directly correlated with transpiration, and relative

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⁵Reuther, W. 1972. Climate and citrus behavior. The citrus industry, (W. Reuther, ed.) Vol. 3. Univ. of Calif., Div. of Agric. Sci., Berkeley. In Press.

⁶Kaufmann, M. R., and D. C. Elfving. 1972. Evaluation of tensiometers for estimating plant water stress in citrus. In preparation.

transpirational flux of water through the plant can be approximated with VPD and leaf diffusion resistance data⁴.

Results

The 3 environmental factors most likely to affect water stress in citrus leaves are soil water availability, soil temp, and VPD of the atmosphere. Nighttime data indicated that as soil water became limiting (more negative tensiometer readings) nighttime leaf water potential decreased (Fig. 1). The effect of soil water

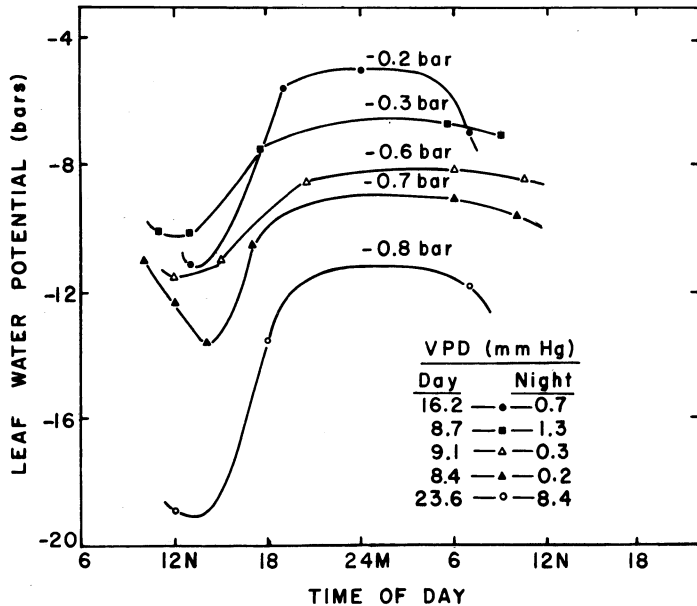


Fig. 1. Effect of soil water availability on diurnal changes in leaf water potential. The diurnal max and min VPD's indicate evaporative demand of the atmosphere. Data from several irrigation cycles in a cool, coastal environment at San Juan Capistrano when soil temp were above 15°C. Tensiometer values are averages of readings at 3 depths.

stress on plant water potential was not independent of VPD, however. When the VPD was high (high gradient for transpiration) leaf water potentials were more negative than at low VPD's. For example, daytime leaf water potential was -11.1 bars when the VPD was 16.2 mm Hg and tensiometers indicated -0.2 bar. Water potential was -10.1 bars when the VPD was 8.7 mm Hg even though the soil was slightly drier (-0.3 bar).

The soil temp at a depth of 15 cm was selected to represent the temp of the roots from 10 to 120 cm deep. Soil temp profiles observed by us and by Reuther⁵ indicated that vertical temp gradients in this zone were always less than 5°C, and diurnal temp variations at 15 cm were less than 2.5°C. Although the curves are drawn with no data shown during the middle of the night, measurements made during other diurnal cycles indicate clearly that sunrise values of water potential are very near those taken at midnight. Night levels of leaf water potential were unaffected by soil temp (Fig. 2). During the daytime, however, a soil temp of 7.5°C sharply reduced leaf water potential even though VPD was much lower than at the other soil temp. The effect of low soil temp on leaf water potential is probably caused by increased resistance to flow of water in the root system⁴. This effect is observed near 15°C rather than at 10°C as suggested by the transpiration data of Cameron (3).

The effects of VPD on leaf water potential shown in Fig. 1 indicated that higher VPD's resulted in more negative leaf water potentials. The influence of VPD is shown more clearly in Fig. 3 and 4 (center graph of leaf water potential and numbers indicating VPD). When the daily maximum VPD changed from 3.1 to 11.4 mm Hg (Fig. 3) daytime leaf water potential decreased from -7.5 to -10.3 bars while leaf diffusion resistance (lower graph) remained the same. At a VPD of 38.7 mm Hg (Fig. 4) leaf water potential decreased to -16.0 bars, even

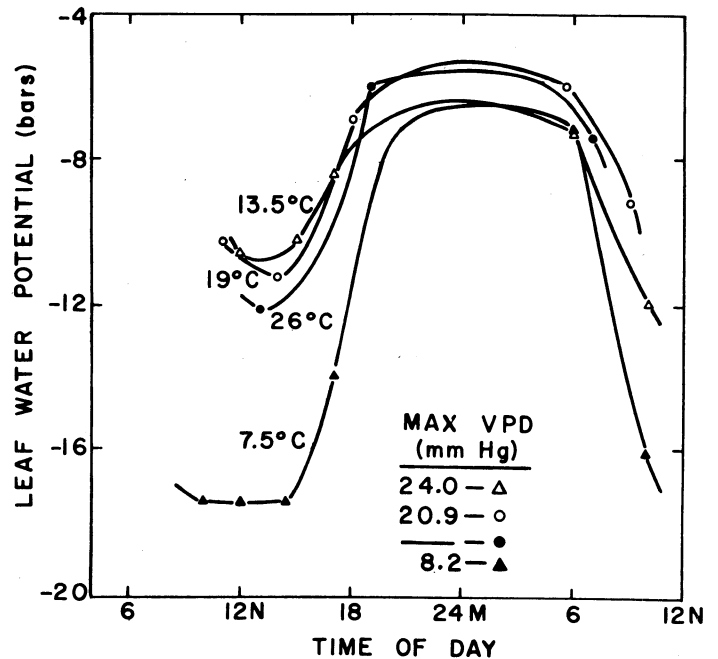


Fig. 2. Effect of soil temp on diurnal changes in leaf water potential. The daytime max VPD's indicate evaporative demand of the atmosphere. Data collected in the lower Colorado Desert environment at Mecca when soil water availability was adequate.

though the leaf resistance was slightly higher. The relationship between leaf water potential and VPD must be treated cautiously, however. Elfving et al.⁴ found a fair correlation between potential and VPD only when soil water and temp did

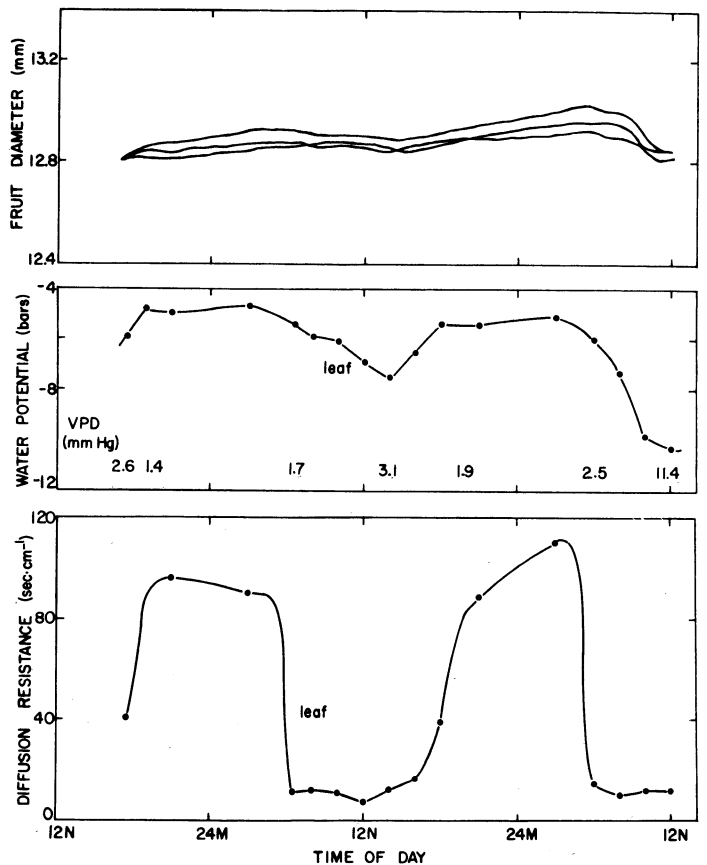


Fig. 3. Diurnal changes in fruit diam, leaf water potential, leaf diffusion resistance, and VPD during mid-June. Diameter changes were plotted from a base of 12.8 mm, the average diam of the 3 fruits measured.

not impose restrictions on water supply to the leaf, and leaf diffusion resistance also affected the reliability of the correlation. They found that daytime leaf water potential was curvilinearly related to the ratio of VPD and leaf resistance under specific non-limiting environmental conditions. However, when soil water became limiting or soil temp was below 15°C, water potential became more negative than predicted by the ratio of VPD and leaf resistance, largely because of altered

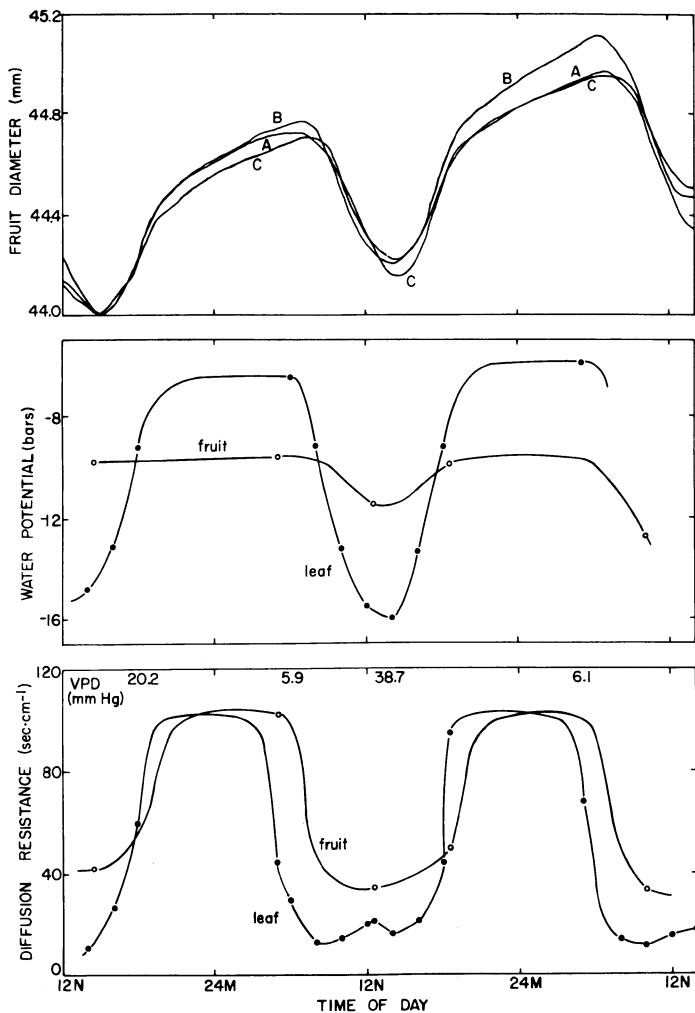


Fig. 4. Diurnal changes in fruit diam, fruit and leaf water potential, fruit and leaf diffusion resistance, and VPD late in August. Diameter changes were plotted from a base of 44.0 mm, the average diam of the 3 fruits measured.

gradients and resistances to water movement. At night VPD had a very small effect on citrus leaf water potential because leaf diffusion resistance was high and transpiration was minimal. Night leaf water potentials are influenced primarily by soil water status⁶. The data presented here leave no doubt that plant water stress is closely linked with conditions in the plant environment and with leaf resistance.

Simultaneous changes in fruit diam, fruit and leaf water potentials, and fruit and leaf resistances were examined. The diam of small fruits (late Stage I, ref. 1) increased at night (Fig. 3). During the first complete day of measurement, fruits remained nearly constant in diam when leaf water potential decreased only slightly (cool, humid conditions). On the second day, however, fruit diam and leaf water potential both decreased significantly. Leaf resistance followed the same pattern on both days. During conditions of high daily VPD (Fig. 4), Stage II fruits increased in size at night but reversibly decreased in size during the day. Diameter changes were very

similar for the 3 fruits measured. Limitations in the number of thermocouple psychrometers available and in the time required to complete psychrometer measurements prevented more frequent determinations of fruit water potential. The striking similarity of fruit diam and leaf water potential and diffusion resistance on successive days support the procedure of using several days of fruit data to determine curve shape for fruit water potential or diffusion resistance during a single diurnal cycle. Fruit and leaf water potentials were higher at night and lower during the day, but the diurnal fluctuation in leaf water potential was about 10 bars compared with only about 2 bars in fruit pericarp tissue. Larger diurnal changes in fruit water potential were observed in another study (14), probably because water potential reached a higher value at night than in this experiment. While nighttime leaf and fruit resistances were roughly equal, daytime fruit resistances were 30 to 40 sec·cm⁻¹ compared with 10 to 20 sec·cm⁻¹ for leaves. A considerable diurnal change in fruit diffusion resistance occurred, however, indicating that fruit stomata were highly active at this stage of development.

The diurnal pattern of change in fruit diam shown in Fig. 4 occurred commonly in Stage II fruits in August and September. An important feature of the fruit growth pattern during this period was the completely reversible shrinkage and expansion during the daylight hr. To determine the correlation between fruit diam changes and leaf water potentials between sunrise and sunset, comparisons were made of all data available during these months (Fig. 5). The data were collected when soil water tensions were 0.3 bar or less and soil temp in the root zone was above 15°C. Apparently a linear relationship existed between

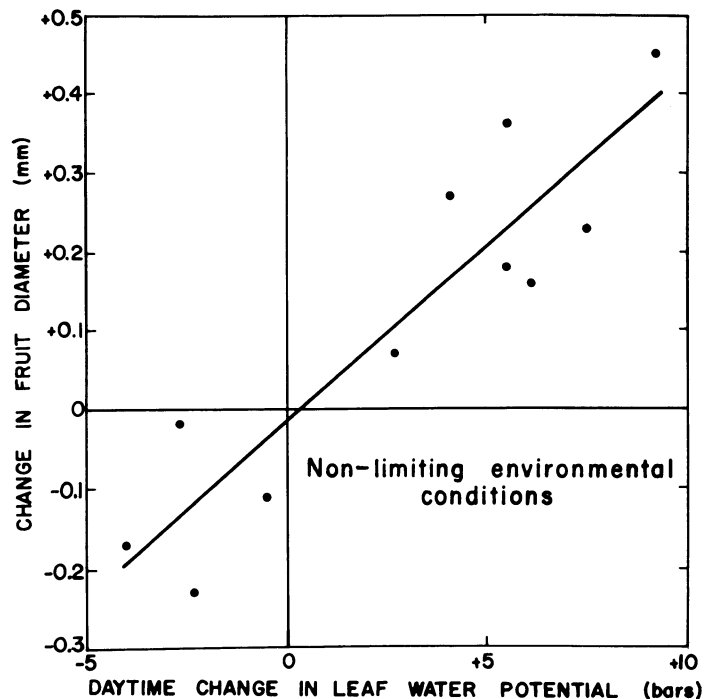


Fig. 5. Relation between changes in fruit diam and leaf water potential during daylight hr. Measurements were collected during August and September when reversible daytime shrinkage and expansion in diam occurred. Fruit diam changes were determined for the period during which the water potential change occurred. The correlation coefficient is 0.91.

fruit diam and leaf water potential changes. Such a relationship was not found for older fruits, however, because beginning in October (30 to 35 weeks after anthesis) morning decreases and afternoon increases in diam became much more erratic. By late November fruits sometimes showed a net decrease in diam during a 24-hr period. No consistent difference was found

Table 1. Comparisons of nighttime fruit growth rates over an 8-hr period with day or night extremes of leaf water potential, air temp, or VPD. Data are ranked in decreasing order of fruit diam growth rate, for measurements made in August or September.

Growth rate (mm/hr)	Location ^z	Time after anthesis (weeks)	Leaf water potential (bars)		Air temp (°C)		Min. night VPD (mmHg)
			Night Max.	Day Min.	Night Min.	Day Max.	
.026 ^y	Riv.	20	-5.9	-16.0	19	36.5	6
.025 ^y	Riv.	20	-6.5	-14.8	18	35	5.5
.025	Riv.	25	-7.2	-12.8	17	32.5	12
.020	SJC	18	-5.0	-11.1	17	30	0.7
.016	Mecca	25	-5.7	-12.1	22	37	4
.015	Riv.	19	-6.0	-16.3	22	38	7
.015	Mecca	21	5.6	-14.3	31	—	—

^zRiv., Riverside; SJC, San Juan Capistrano.

^yMean of 3 fruits. All other growth rates are for single fruits.

between fruits on the north and south side of the tree.

Because diurnal changes in fruit diam during August and September followed the same pattern, it is appropriate to try to determine what plant and environmental factors may be associated with rate of change of diam. Attempts were made to correlate factors with the nighttime rate of fruit growth, since diam increased linearly during most of the night (Fig. 4). Night growth rates were compared with leaf water potential and air temp during the day and night and with night VPD. These factors were selected because they are likely to influence fruit growth in some way (5, 9). Temperature may affect physiological growth processes, and leaf water potential and night gradients for fruit transpiration provide some information about supply and loss of water for the fruit. Although the rate of fruit growth varied from 0.015 to 0.026 mm/hr, no correlation among growth rate and any factor measured could be found (Table 1).

Short-term changes in fruit diam cannot be analyzed simply, although certain correlations are apparent. Our data indicate that daytime changes in fruit size and in leaf water potential occur almost simultaneously. They may not be perfectly in phase with each other, however. Fruit resistance changes lagged behind leaf resistance changes (Fig. 4), and fruit temp changes may lag behind and be considerably different from air temp changes (W. Reuther, personal communication), resulting in differences in transpirational gradients for leaves and fruits. Greater losses of water can be sustained by the fruit relative to the leaves for a comparable decrease in water potential because of their different mass. In contrast, the rate of fruit enlargement at night (Table 1) shows no apparent correlation with night-time leaf water potential, nor with minimum night temp or VPD. Similarly, attempts to correlate changes in fruit diam with leaf water potential or atmospheric conditions of the previous day were unsuccessful.

Discussion

Based on the data presented here, we conclude that continuous changes in the diam of growing citrus fruits result from a complex interaction of a number of environmental and physiological factors. We also conclude that the dependence of fruit water balance on leaf water balance may be more apparent than real. These conclusions can be supported by considering the various factors which must influence the water balance and the physiology of fruit enlargement. It is likely that changes in fruit diam are both reversible and irreversible, although when soil water uptake is limited, net shrinkage of fruits may occur (7, 11). Reversible changes in fruit diam undoubtedly are caused by changes in water content, primarily in the pericarp tissue. Our measurements of water potential of pericarp and those of Kaufmann (14) indicated that water potential decreases during the morning when fruit size decreases, and both increase in the afternoon. Fruit water balance depends upon supply of water to

the fruit and upon water loss from the fruit. Water transport into the fruit depends upon gradients for water flow and upon any resistances to flow. Since the only significant source of water is the soil, any environmental or plant factors affecting water transport to leaves such as soil water availability or soil temp will also affect water transport to the fruit. Water loss from the fruit may occur by fruit transpiration or perhaps by reversed water flow through the stem toward the leaves. Fruit temp and vapor pressure of water in the atmosphere are important because they define the vapor pressure gradient for evaporation, and fruit diffusional resistance estimates the barrier to water vapor movement from fruit to air. Therefore, transpirational loss of water from fruits is influenced by the same environmental and plant factors that affect leaf transpiration.

Many investigators, beginning with Hodgson (12) and Bartholomew (2), have contended that water may move from citrus fruits to leaves during the day when leaf water content is reduced. The experiments which led to this conclusion were done with fruited branches detached from trees. Under these conditions the development of unnatural water potential gradients may have induced water movement from fruit to leaf. Under normal field conditions such water potential gradients may occur only rarely if at all. No investigation has yet been made of the development of water potential gradients in detached branches. On the surface, some of our data supports the possibility for water movement from fruit to leaf, since during midday the fruit water potential was less negative than leaf water potential. Our data are not conclusive, however. For water flow from fruit to leaf to occur, there must be an uninterrupted gradient for movement between the 2. Therefore, water potential would need to decrease beginning from the pericarp to the pedicel, then to the point of attachment to the stem, along the stem to the leaf petiole, then to the leaf blade. Normal water flow, when both fruit and leaf are losing water by transpiration, involves movement along a single pipeline, the trunk and branch, which divides into 2 separate pipelines, 1 leading to the fruit and 1 to the leaf. The only way water could move from the fruit to the leaf would be if a water potential gradient existed from the fruit to its point of attachment to the normal transpiration stream to the leaves. No information is available here or in the literature which supports or disproves the existence of uninterrupted water potential gradients from fruits to leaves. Therefore, with attached fruits it is not yet possible to state unequivocally that an orange or any other transpiring fruit can behave as a midday reservoir of water for leaves. Diurnal diam changes in non-transpiring fruits may, however, be related to reversed flow of water from fruit to leaves (16, 17).

Irreversible increases in fruit size which occur at night presumably represent growth, and therefore are the result largely of physiological processes such as carbohydrate transport

to the fruit, cell enlargement, and internal conversion and redistribution of cell constituents. These processes are likely to be influenced by a number of factors, including the level of net photosynthesis, size of the fruit crop, temp, water balance, and others (6, 8, 11). The difficulty in finding correlations of nighttime increases in fruit size with the plant and environmental factors examined is probably explained by the fact that individual factors may affect both reversible and irreversible diam changes, but in different ways and at different times. For example, air temp might be expected to influence various physiological processes associated with tissue growth, but it also may influence fruit water balance by affecting stomate activity and vapor pressure gradients for transpiration.

The conclusion that the fruit may be rather independent of the leaves is also supported by the response of fruit size, leaf water potential, and fruit and leaf diffusion resistances. Leaf resistance was low by 6 AM, and by 8 AM leaf water potential had decreased significantly. However, fruit resistance decreased a few hr later, followed by a decrease in fruit size beginning about 8 AM. At 6:30 PM (1830 hr), leaf resistance had increased to the normal nighttime level, but fruit resistance increased later. It appears from these and other data that diffusional resistances and water potentials of fruits and leaves may not cycle perfectly in phase with each other, suggesting that each type of organ behaves independently.

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