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Internal and External Factors Affecting Stomatal Movement in 'Montmorency' Sour Cherry (Prunus cerasus L.)

presented by

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has been accepted towards fulfillment of the requirements for

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#### INTERNAL AND EXTERNAL FACTORS AFFECTING STOMATAL MOVEMENT IN 'MONTMORENCY' SOUR CHERRY (Prunus cerasus L.)

BY

Lynnell Elise Teichman

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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#### ABSTRACT

#### INTERNAL AND EXTERNAL FACTORS AFFECTING STOMATAL MOVEMENT IN 'MONTMORENCY' SOUR CHERRY (Prunus cerasus L.)

BY

#### Lynnell Elise Teichman

Stomatal responses of 'Montmorency' sour cherry leaves to various internal and external factors were characterized, and a simple model to predict transpiration developed and analized. Differences in leaf age appeared to affect stomatal conductance and transpiration; as individual leaves matured, stomatal conductance increased, remained level for a period, then decreased. Transpiration is consistent for a period, then Leaf or shoot type did not appear to affect stomatal declined. conductance or transpiraton of leaves 3-5 nodes from the shoot base. A diurnal pattern in all parameters measured was detected. Peak conductance appeared to occur about 10:00 under conditions of a clear Oscillation of stomata occurred as evidenced by stomatal skv. conductance and transpiration. Fruit appeared to influence stomatal conductance and transpiration since fruited branches had lower conductances than defruited branches during both slow and rapid fruit development. The day of the year was more significant in the prediction of transpiration than were all combinations of environmental parameters photosynthetically active radiation, temperature and air vapor pressure.

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LITERATURE REVIEW

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#### Literature Review

Michigan has nearly thirty thousand acres of sour cherries (Prunus cerasus L.) representing 78 percent of total production in the U.S. (Anon. 1986). Many of these orchards are planted in sandy soils with low water-holding capacity. Although annual Michigan rainfall is 60 to 90 cm (Sommers, 1977), moisture deficiencies often occur for a period of 30 or more days during the growing period (Kenworthy, 1979). Whereas peach (Lister, 1974; Smith and Kenworthy, 1979) and pear (Riley, 1974) fruit size and/or yield have been shown to increase under trickle (drip) irrigation, Smith and Kenworthy (1979) saw no increase in either fruit size or yield of sour cherry with trickle irrigation. Nutrient composition of leaves increased with trickle irrigation; trickle irrigation may have allowed for increased soil ion content and element mobility (Smith and Kenworthy, 1979). Under drought conditions, trickle irrigation on cherry results in an increase in tree vigor and tree survival rate (Riley, 1974). To retain and even enhance the state's competitive position in the cherry industry, improvements in cultural practices such as irrigation are essential.

Trickle irrigation is a preventative approach to plant water stress (Kenworthy, 1972; Elfving, 1982), in contrast to sprinkler irrigation which is best adapted to the correction of water stress conditions. According to Kenworthy (1972) "25% of the root system can supply enough water to prevent moisture stress of fruit trees." Therefore, if 25% of the root system is supplied with water daily, moisture stress can be prevented (Kenworthy, 1972). Also, a reduction in water usage is often possible with trickle irrigation (Elfving, 1982; Howell <u>et. al.</u>, 1981; Goldberg et. al., 1976). While trickle irrigation provides consistency

in water application and conservation of water, the maintenance approach presents new problems in scheduling; i.e. how much water to apply, when, and how often (Kenworthy, 1972; Proebsting <u>et. al.</u>, 1981). Sound irrigation management depends upon an understanding of, and predictive means for estimating crop water consumption.

Methods to determine when irrigation is necessary include: 1) a critical point of soil water depletion, 2) soil water potential, 3) leaf water potential, 4) growth and, 5) evapotranspiration (soil evaporation and plant transpiration) deficits (Stegman <u>et. al.</u>, 1981). They may be catagorized as: soil or plant parameters; water balance models; and pan evaporation (Stegman <u>et. al.</u>, 1981).

Soil based methods include soil appearance and "feel" (dampness), gravimetric sampling (Goldberg <u>et. al.</u>, 1976), measurements of electrical resistance with porous blocks and soil matric potential with a tensiometer (Stegman <u>et. al.</u>, 1981; Kidder and Schleusener, 1952; Haise and Hagan, 1967). Such methods assume uniform soil wettness, a condition which does not exist under trickle irrigation (Goldberg <u>et.</u> <u>al.</u>, 1976; Kenworthy, 1972; Proebsting <u>et. al.</u>, 1981). Soil based techniques do not give representative soil moisture measurements of the whole root system (Verner <u>et. al.</u>, 1962). The question that arises is, where does one sample? Soil moisture measurements used alone are, therefore, inadequate indices for irrigaton scheduling requirements (Kenworthy, 1972).

Plant based methods to measure plant water status, such as thermocouple psychrometers or pressure chamber measurements of leaf water and xylem potential, diffusion porometers for stomatal conductance or non-contacting thermometers for leaf temperature measurements (Stegman <u>et. al.</u>, 1981; see Haise and Hagan, 1967), can best serve as research tools to characterize water status. Lysimetery, a direct approach to determine plant water usage, is difficult to use with large plants such as fruit trees (Howell <u>et. al.</u>, 1981), and is very expensive. Lysimetry is more adapted to model development than model usage (see Worthington <u>et. al.</u>, 1984).

Plant parameters such as shoot length, leaf emergence and leaf growth (Houle, 1984), trunk growth (Houle, 1984; Verner <u>et. al.</u>, 1962), and shoot diameter growth rate (Flore and Bralts, 1984), etc., however, may be useful as indicators of plant water status. Such plant indicators tend to incorporate water loss due to atmospheric conditions and uptake due to soil moisture supply (Verner <u>et. al.</u>, 1962). Used in combination with soil or evaporative factors, plant parameters can be very useful and accurate. Tree age, along with an estimated volume of water necessary per tree year, is another plant based method used to predict water requirements (Burgess <u>et. al.</u>, 1984). While the tree age method has been successfully used, over-irrigation can occur due to the omission of a natural precipitation component (Burgess <u>et. al.</u>, 1984).

Water balance models estimate root zone water content as affected by transpiration, soil evaporation, irrigation, precipitation, infiltration, runoff, deep percolation, capillary rise, etc. (Stegman <u>et. al.</u>, 1981). Although water balance models are fairly comprehensive in projecting plant water use (Stegman <u>et. al.</u>, 1981) and include evapotranspiration (ET), they ususally have soil evaporation as a major, inseparatable compoment (Doorenbos and Pruitt, 1977). While separate estimates of transpiration and soil evaporation are possible, direct measurement of plant transpiration to establish specific crop

coefficients (K factors) for trickle irrigated plantings have not been done (Ritchie, 1974). Additional information on plant water use would be helpful (Proebsting <u>et. al.</u>, 1981).

Evaporation from a pan of free water, porous bulb or porous plate are other devices for irrigation scheduling (Stegman et. al., 1981). Pan evaporation, using a U.S. Weather Bureau Class "A" pan in combination with a crop coefficient integrates climactic effects on evaporation to predict evapotranspiration (ET) (Doorenbos and Pruitt, 1977). It provides a simple, yet useful method to predict plant-soil water status (Elfving, 1982), and thus a way of scheduling irrigation based on the replacement of evaporated water. As with other water balance models, few crop coefficients have been determined. In general, a K factor of 0.75 has been recommended for Michigan fruit crops (Kenworthy, 1972). Worthington et. al. (1984) has determined weekly crop coefficients for well watered peach using weighing lysimeters and Class A pan evaporation. The seasonal average k factor was 0.712, but the weekly coefficients ranged from 0.982 early in the season to 0.399 late in the season, despite increasing foliage (Worthington et. al., 1984).

Evaporative water loss, which causes water deficiencies in the soil and/or leaf, is the main factor in determining irrigation requirements (Chalmers <u>et. al.</u>, 1983). Water in the soil, generally supplied by irrigation and precipitation, provides the tree with water for use in metabolic processes, turgor, etc. Much of the water, however, is transpired into the atmosphere (Goldberg <u>et. al.</u>, 1976).

#### Transpiration

Transpiration occurs when internal cell water is vaporized during evaporation and then diffused, via the stomata, from the saturated (assumed) environment of the leaf to the atmosphere. Stomatal opening and closing in response to increases and decreases in guard cell turgor, (respectively), partially regulate vapor movement.

Transpiration (TR) and evaporation are similiar processes since both encounter pathway resistances to water vapor diffusion into the atmosphere. Transpiration includes resistances due to both the leaf and air (or boundary layer), while evaporation encounters resistances due to the air. Thus, transpiration is a function of energy for the vaporization of water, vapor concentration or pressure difference to drive the vapor flow, and resistances to vapor diffusion along the pathway (Slayter, 1967). Simply stated,

$$TR = \frac{Cleaf - Cair}{rleaf + rair} \text{ or } \frac{Eleaf - Eair}{rleaf + rair},$$

where C, E, and r are water vapor concentration, water vapor pressure and resistance, respectively, due to either the leaf or air as indicated (Kramer and Kozlowski, 1979). Interdependent in nature, a change in one does not proportionately change the others (Slayter, 1967).

Stone and pome fruit leaves transpire water and assimilate  $CO_2$  through stomata located on the abaxial (lower) leaf surfaces; the adaxial surfaces contribute little to gas exchange (Chalmers <u>et. al.</u>, 1983). For example, Chalmers <u>et. al.</u> (1983) reported maximum stomatal conductance from the upper tree canopy from 0.29 - 0.49 cm s<sup>-1</sup> for the abaxial leaf surface of peach, whereas cuticular conductance on the adaxial surface was approximately 0.01 cm s<sup>-1</sup>.

#### Resistance/Conductance

Leaf resistance to vapor flow,  $(r_1)$ , consists of two parallel resistances, cuticular,  $(r_c)$ , and stomatal resistance,  $(r_s)$  (Kramer, 1983; Slavik, 1974). Stomatal resistance includes resistances due to both the pore and intercellular spaces (Kramer, 1983). Cuticular resistance contributes very little to water vapor loss when stomata are open, and is therefore disregarded (Kramer, 1983). Conductance, the inverse of resistance, is a more appropriate expression when concerned with functional relationships of stomata (Burrows and Milthorpe, 1976); a linear and more interpretable relationship exists between stomatal conductance and pore opening, while the relationship with resistance forms an hyperbola (Burrows and Milthorpe, 1976; Kramer, 1983).

#### Porometry

Porometry is a convenient method for determining stomatal resistance or conductance of intact plants in the field. In principle, transpiration rate is controlled by changes in the stomatal aperature (Slavik, 1974). Therefore, transpiration resistance is commonly used to measure stomatal resistance (Slavik, 1974).

Brown and Rosenburg (1970) found diffusion porometer  $r_s$  and stomatal impression  $r_s$  in good agreement. Steady state porometry, as opposed to non steady state porometry, (see Beardsell <u>et. al.</u>, 1972) is the more commonly accepted method. The principle of porometry is to determine resistance (r; s cm<sup>-1</sup>) by the flux of water transpired per unit leaf area, (q, g cm<sup>-2</sup> s<sup>-1</sup>), where:

$$q = \frac{C_s(T_1)-C_a}{r};$$

 $C_S$  is the concentration of water vapor inside the leaf at saturation; T<sub>1</sub>

is the temperature of the leaf; and  $C_a$  is the mean concentration of water vapor on the outside of the leaf, or at the sensor (Jarvis, 1971).

The theory behind steady state diffusion porometry is to maintain ambient conditions about the leaf in the chamber for the duration of the measurement. Ambient humidity ( $C_a$ , g cm<sup>-3</sup>) is maintained around the leaf by a flow of dry air through the ventilated chamber in compensation for the flux of transpired water. The inflow of dry air is adjusted to maintain a balance between the flux of transpired water (q) and the outflow of moist air (f, cm<sup>3</sup> s<sup>-1</sup>). In short,

$$q = \frac{fC_a}{A} (g cm^{-2} s^{-1}),$$

and

$$r = \frac{C_{s}T_{1}}{C_{a}} - 1 \frac{A}{f} (s \ cm^{-1})$$

where A is the leaf area subject to measurement (Beardsell <u>et.</u> <u>al.</u>, 1972).

Under constant conditions, the vapor concentration of the air does not change and may be expressed relative to an assumed vapor saturated atmosphere within the leaf, or

$$r = \frac{100}{RH} - 1 \frac{A}{f} (s cm^{-1})$$

(Beardsell <u>et. al.</u>, 1972). Then, since relative humidity, RH, and leaf area, A, are known and constant, resistance can be measured by direct calibration of the flow meter (Beardsell <u>et.</u> <u>al.</u>, 1972). Boundary layer and porometer chamber resistances are minimized by stirring the porometer chamber air. Boundary layer resistance becomes small, constant and reproducible. Porometer chamber resistances are eliminated

#### (Beardsell <u>et.</u> <u>al.</u>, 1972).

#### Inputs

To develop an irrigation model for sour cherry based on a tree's water loss, inputs are required for 1) soil moisture, 2) vegetative and reproductive bud development, 3) total leaf area, and stomatal responses to 4) external and 5) "internal" factors.

#### Soil Moisture

Flore and Bralts (1984) showed that stomatal conductance and soil moisture of sour cherry are not strongly correlated until soil water content drops to about 15%. Water potential and soil water content on the other hand, have a stronger and positive correlative response at all levels. While water potential may better indicate a condition for the onset of stress, other plant factors such as leaf emergence, leaf growth, shoot growth and trunk growth are more sensitive to moisture stress (Houle, 1984). Stomatal response to soil moisture may be an inadequate indicator by which to schedule irrigation (Houle, 1984), but it provides useful information in the development of a predictive model for plant water loss.

#### Bud Development in Sour Cherry

Buds of Montmorency sour cherry originate from the leaf axils of the previous year's growth. Reproductive growth occurs only from buds lateral to the shoot (Kenworthy, 1974). Lateral flower buds average two or three flowers per bud, but may contain one to five flowers per bud. Tukey (1934) reported three growth stages of sour cherry fruit development after the pre-bloom period, Stage I, II and III. Stage I begins after fertilization and lasts about 22 days. During this time, cell number and size increase in both the stony and fleshy pericarps.

Cells of the stony pericarp thicken and eventually begin to harden towards the end of the stage. During Stage II, approximately 12 days in length, hardening of the stony pericarp is completed while development of the fleshy pericarp is minimal. Stage III is most characterized by increased cell size in the fleshy pericarp, or the "final swell". The period lasts about 23 days and ends at fruit ripening (Tukey, 1934).

Vegetative growth can occur from the buds either terminal or lateral on a shoot, while reproductive growth occurs only from lateral buds (Kenworthy, 1974). Lateral buds which produce vegetative growth a) less than five centimeters in length are characterized as spurs; and b) greater than five centimeters as lateral shoots. Regardless of length, the growth of a ternminal bud is characterized as a terminal shoot. Eisensmith et. al. (1980) found that leaf number per terminal shoot or spur is linearly related to degree-day accumulation (base  $4^{\circ}$ C), and that leaf emergence per individual tree is not completely synchronous. Spur leaf emergence, a period of about 21 days, ends as Stage II fruit growth commences. However, terminal shoot leaf emergence continues until late Stage III aand lasts about 60 days. As degree-days and number of leaves increases, average area per leaf increases until the final leaf has fully expanded (Eisensmith et. al., 1980). Eisensmith et. al. (1982) also reported that average area per leaf varies with year, although proportinate-wise, the change is minimal (Kvet and Marshall, 1971).

#### Leaf Area

Kvet and Marshall (1971) discuss several techniques for calculating individual leaf areas. One of the easiest field methods for elliptictype leaves is leaf length and maximum breadth measurements multiplied by a crop coefficient (Kvet and Marshall, 1971). For sour cherry (ovate

to obovate leaves), a coefficient of 0.67 has been reported (Kvet and Marshall, 1971 after Rubin and Danilevskaya, 1957), and is a useful guide (Kvet and Marshall, 1971). However, it is beneficial to compute coefficients on a local level, as variations can occur due to environmental factors (Kvet and Marshall, 1971). For East Lansing, Michigan, USA, a coefficient of 0.65 has been computed (Kappes, 1985) The coefficients are generally constant for a given fruit cultivar (Kvet and Marshall, 1971 after Rubin and Danilevskaya, 1957).

Total leaf area in apple has been estimated from trunk and branch girths, or branch girths for an entire tree (Holland, 1968; Barlow, 1969; Landsberg, 1979), or branch (Byass, 1968), respectively. Leaf area, LA, fits the relationship,

# $LA=kG^{b}(m^{2}),$

where G is the girth (cm), and k and b are constants for the given set of cultural, genetic, seasonal, etc. conditions (Barlow, 1967; Holland, 1968; Landsberg, 1979). This relationship has been successfully used for total leaf area measurements of a sour cherry scaffold or whole canopy (Flore, unpublished data).

Eisensmith <u>et. al.</u> developed prediction models for 'Montmorency' sour cherry leaf emergence (1980) and leaf expansion (1982). Final leaf area of spur leaves is less than that of terminal shoot leaves (Eisensmith <u>et. al.</u>, 1982), but both followed an asymptotic pattern in develpoment. During the first three weeks of growth, leaf area increased linearly with time. Overall, Eisensmith <u>et. al.</u> (1982) found that reasonable predictions for average spur and terminal-shoot leaf area from one year can be derived from field observations from another year, although the model does not include factors such as tree age, vigor, pruning practices, crop load, etc.

#### Stomatal Response

Since plant water loss, or transpiration, is primarily controlled by stomata, a knowledge or understanding of the external and internal factors that affect stomatal aperature is essential for the prediction of plant water loss. Changes within the plant and the plant's environment affect stomatal movement and thus, transpiration (Raschke, 1979). External, or environmental, factors include vapor pressure deficit (VPD) or humidity, temperature,  $CO_2$ , and light. Some internal factors include nutrient status, internal water status, growth substances, morphological and physiological leaf age effects, fruit effects, seasonal, diurnal and time course effects.

#### External Factors

<u>VPD</u> and <u>Temperature</u>. Flore <u>et. al.</u> (1984) reported that increasing VPD from 1.0 to 2.0 kPa resulted in decreased stomatal conductance ( $g_s$ ), photosynthesis (Pn) and water use efficiency (WUE) of well watered cherry trees. Response of stressed trees was similiar except for higher WUE and a more moderate decrease of  $g_s$ . In a study by Sams and Flore (1982) on 'Montmorency' cherry leaves, photosynthesis increased with increasing temperature to some optimum from which it then declined. Since VPD was not held constant, the direct effect of temperature on Pn was not determined. Optimum ranges varied with PAR and VPD from 12 - 25° at 300 µmol·m<sup>-2</sup>·s<sup>-1</sup> and 0.4 - 6.6 kPa, to 18-24° at 2000 µmol·m<sup>-2</sup> s<sup>-1</sup> and 0.4 - 6.6 kPa.

<u>CO2.</u> In apple, increased external CO2 results in decreased  $g_s$ , but increased photosynthesis (Flore <u>et. al.</u>, 1984). High CO<sub>2</sub> concentrations affect water-stressed and non-stressed trees differently; stressed trees

have lower  $g_s$  and Pn values than nonstressed, but WUE is greater (Flore <u>et. al.</u>, 1984). In cotton, stomatal opening was induced by  $CO_2$  free air (Jarvis and Slayter, 1970). In 'Montmorency' sour cherry, Pn rate increases as  $CO_2$  concentration is increased from 0 to 600 ppm (Sams and Flore, 1982). Sour cherry has a predicted  $CO_2$  compensation point of 80 ppm (Sams and Flore, 1982). Transpiration is indirectly affected by  $CO_2$  through  $g_s$  (Jarvis and Morison, 1981).

<u>Photosynthetically Active Radiation (PAR).</u> Stomata are affected by the quantity of radient energy up to an optimum level; as PAR increases,  $G_s$ , TR and Pn increase up to that optimum, and then plateau. Sams and Flore (1982) found hyperbolic increases in the Pn rate of 'Montmorency' sour cherry with increased PAR. Optimal PAR was between 800 and 1200  $\mu$ mol·m<sup>-2</sup>·s<sup>-1</sup> at all tested temperature and VPD levels, and maximum Pn was within the range of 30 to 38 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>. Optimal PAR for sour cherry stomatal opening was not investigated.

#### Internal Factors

Internal Water Status and Growth Regulators. Growth regulators, especially abscisic acid (ABA), appear to affect stomatal behavior (Kramer and Kozlowski, 1979). Increased ABA typically causes the stomata to close. Studies by Flore <u>et. al.</u> (1985) on apple and cherry in whole plant chambers suggested a relationship between the degree of previous stress and stomatal response to  $CO_2$ . Dubbe <u>et. al.</u> (1978) found that both transpiration and  $CO_2$  assimilation were reduced in various C<sub>3</sub> and C<sub>4</sub> species by ABA (applied) induced stomatal closure. However, transpiration was reduced by a greater percentage than  $CO_2$ assimilation (Dubbe <u>et. al.</u>, 1978). Flore <u>et.</u> al. (1985) hypothesize that a water stress or a high VPD situation may induce an internal ABA build-up which lowers initial  $g_s$  and increases sensitivity to CO<sub>2</sub>.

Houle (1984) found lower  $g_s$  and TR values for peach trees under water stress at least one week. Late morning and afternoon values were lower for stressed trees from the onset of the stress (Houle, 1984). After the stress was removed, all trees responded similiarly (Houle, 1984).

Lakso (1979) found a good correlation between  $g_s$  and Pn of both field and potted apple trees under various water stress treatments. Therefore, Pn appears to be limited primarily by  $g_s$  (Lakso, 1979).

Leaf Age. Stomatal conductance (or diffusive resistance), transpiration and/or Pn have been shown to differ between leaves of different ages (Sato et. al., 1984; Liu et. al., 1978). Although maximum conductances generally increase with leaf expansion, much variation exists in regards to the length of time before values begin to decrease (Burrows and Milthorpe, 1976). During early stages of leaf development in apple, TR and rs decreased as leaves aged, while Pn increased (Kennedy and Johnson, 1981). During later stages, these factors were fairly consistent (Kennedy and Johnson, 1981). Sams and Flore (1982) reported that maximum Pn in 'Montmorency' cherry shoot leaves occurred between nodes nine and thirteen from the shoot base. Pn was lowest in older (nodes one through nine) and younger (nodes greater than thirteen) leaves. Leaf Pn increased with leaf expansion up to 80 percent or more of full expansion when Pn leveled off for two to four weeks, and then declined (Sams and Flore, 1982).

<u>Fruit Effect.</u> It has been well documented for peach (Crews <u>et.</u> <u>al.</u>, 1975; Chalmers <u>et. al.</u> 1983) and apple (Kazaryan <u>et. al.</u>, 1965 (Pn); Tunsuwan and Buenemann, 1973; Hansen, 1971; also see review by

Barden, 1978), that gas exchange functions -- stomatal opening, transpiration, and photosynthesis -- are greatest in leaves closest to fruits. In peach, Crews <u>et. al.</u> (1975) measured the highest rates of Pn on leaves closest to fruits. Chalmers <u>et. al.</u> (1983) found that leaves of defruited peach trees transpired at rates lower than those of fruited trees, especially during periods of rapid fruit growth. However, defruited tree transpiration did exceed fruited tree transpiration during the stage of slow fruit growth, (Chalmers <u>et. al.</u>, 1983). Defruited tree transpiration rates were highest early in the growing season, but low during the slow stage of fruit growth. Transpiration of fruited tree leaves increased during the stage of slow fruit growth (Chalmers <u>et. al.</u> 1983).

In a study by Hansen (1971) on apple, fruited tree leaves transpired more than in non-fruited tree leaves; water consumption and stomatal diameters also appeared to be greater in the prescence of fruit (Hansen, 1971). Kazaryan <u>et. al.</u> (1965) found decreased Pn on fruited apple branches as distance between leaves and fruit increased. Tunsuwan and Buenemann (1973) observed greater stomatal opening in spur leaves of apple trees fruited than of trees defruited. If the fruit was removed shortly before the normal harvest date, stomatal opening decreased (Tunsuwan and Buenemann, 1973).

In sour cherry, Sams and Flore (1983) compared photosynthetic rates of fruited and non-fruited 'Montmorency' shoots. Results for the two years of experiments varied. During Stage II and III of fruit development, in the first year of measurement, Pn was greatest in leaves of fruited shoots. Post harvest Pn rates were not significantly different. In the second season, Pn tended to be higher with the presence of fruit during Stages I and III, but lower than non-fruited shoot leaves in Stage II and after harvest, although differences were not significant and seasonal averages were similiar (Sams and Flore, 1983).

<u>Seasonal.</u> It has been demonstrated on red oak and red maple that seasonal changes in diffusive resistance occur (Turner and Heichel, 1977). Daily water use for non-fruited peach trees generally decreased over the season from July through October (Worthington <u>et. al.</u>, 1984).

Seasonal Pn trends of field grown 'Montmorency' sour cherry were monitered for two seasons by Sams and Flore (1983) using individual leaves from excised fruited shoots. Trends varied between seasons; early in the first season, the Pn rate was 1.14 mg  $CO_2$  m<sup>-2</sup> s<sup>-1</sup>, but declined and plateaued at about 0.50 - 0.55 mg  $CO_2$  m<sup>-2</sup> s<sup>-1</sup> during Stage III of fruit development before a further decline late in the season. During the second season, however, the initial Pn rate of 0.75 - 0.83 mg  $CO_2$  m<sup>-2</sup> s<sup>-1</sup> was consistent for 8-10 weeks before decreasing (Sams and Flore, 1983). Seasonal comparison measurements between spur and terminal shoot leaves of similiar physiological ages during the second season reveled no significant differences in Pn trends.

<u>Diurnal.</u> Time of day may also have a significant affect on stomatal conductance. Chalmers <u>et. al.</u> (1983) found that in the uppermost canopy layers of peach, maximum stomatal conductances occurred before 10:00 am and then steadily decreased. Maximum  $g_s$  for lower layers was obtained later in the morning (Chalmers <u>et. al.</u>, 1983). Houle (1984) reported daily fluctuations of  $g_s$  in both peach and cherry. Sams and Flore (1983) monitered diurnal Pn patterns on 'Montmorency' sour cherry using non-fruited potted plants. Whole trees under natural

daylight and constant temperature were found to have a strong diurnal pattern whereas that of individual leaves under constant radiation, temperature, and relative humidity did not. A peak in Pn occurred prior to solar noon, plateaued for a few hours, then declined.

Oscillation. While stomatal behavior is most often characterized by response over longer time spans, i.e. every few hours of days, weeks, etc, measurements over short spans frequently exhibit stomatal oscillations, or cycling. Evidence exists for many species, patterns, frequencies, and magnitudes (Hopmans, 1971; see review by Barrs, 1971; and for examples: Barrs and Klepper, 1968; and Levy and Kaufmann, 1976), although little is documented for temperate fruits. Oscillations may occur by induction or spontaneously (Barrs and Klepper, 1968; Hopmans, 1971) in either stable or unstable environments (Hopmans, 1971).

Levy and Kaufman (1976) found evidence of oscillatory behavior in <u>Citrus</u> both in the field and greenhouse. Two years of dendrograph data showed cycling of trunk diameters over one hour periods, while one year leaf conductance and photosynthesis measurements showed cycling for periods of less than one hour (Levy and Kaufmann, 1976). Both  $g_s$  and Pn measurements were taken on clear days. While day to day variations occurred, they were most commonly due to the time of morning at which oscillation began (Levy and Kaufmann, 1976). Cycling of greenhouse trees varied with root temperature, with greater conductances occuring earlier and decreasing later in the day than trees with higher root temperatures (Levy and Kaufmann, 1976). Kerr <u>et. al.</u> (1985) observed individually distinct rhythymic behaviors in sucrose phosphate synthase activily, carbon dioxide exchange rate and stomatal resistance

under constant environmental conditions.

# INTERNAL AND EXTERNAL FACTORS AFFECTING STOMATAL MOVEMENT IN 'MONTMORENCY' SOUR CHERRY (Prunus cerasus L.)

#### INTERNAL AND EXTERNAL FACTORS AFFECTING STOMATAL MOVEMENT IN 'MONTMORENCY' SOUR CHERRY (Prunus cerasus L.)

#### Introduction

Michigan rainfall is often inadequate during summer months for high maximum fruit production; irrigation is often a necessity. As trickle irrigation systems have replaced conventional sprinkler systems, a water maintenence approach to scheduling has replaced the water replenishment approach. Scheduling methods have been developed to help facilitate water maintenance, but none adequately considers plant water loss. To develop an irrigation model for sour cherry based on a tree's water loss, it is necessary to characterize stomatal response to both external and "internal" plant factors.

The objectives of the following research were as follows:

#### I. Leaf age and seasonal trend experiments.

A. Selected leaves: to characterize differences in stomatal conductance  $(g_S)$  and transpiration (TR) of leaves of differing positions on terminal and lateral shoots (current season): a) for a particular day, and b) throughout the season.

B. Shoots: to characterize differences in  $g_s$ , TR, and leaf areas of all leaves on a shoot (current season) both before and after terminal bud set.

As shown by Sato <u>et. al.</u> (1984) and Liu <u>et. al.</u> (1978), stomatal conductance (or diffusive resistance), transpiration and/or photosynthesis have been shown to differ between leaves of different ages. Sams and Flore (1982) reported differences in photosynthesis between leaves at different nodes in sour cherry.

As a shoot extends, new leaves are continually emerging; each leaf on the shoot is at a different stage of development which may affect transpiration (TR) and stomatal conductance  $(g_s)$  on any particular day. Seasonal changes in  $g_s$  and TR may be influenced by fruit and vegetative development (fruit ripening, terminal bud set, senescence, etc.) and/or environmental changes, and were therefore, characterized throughout the season.

II. <u>Leaf type experiment</u>: to characterize differences in stomatal conductance and transpiration between spur leaves and shoot leaves.

Terminals, laterals, and spurs, while appearing similiar in morphology may have very dissimiliar microclimates, e.g. laterals and especially spurs are usually more shaded than terminals. Characterizing differences would help determine future sampling techniques.

III. <u>Diurnal trends</u>: to characterize diurnal trends in  $g_s$  and TR for a) terminal shoot, lateral shoot and spur leaves, and b) within different quadrants of the tree.

Diurnal patterns in plants mechanisms are common. Houle (1984) reported daily fluctuations of  $g_s$  in both peach and cherry. Sams and Flore (1983) found diurnal photosythesis (Pn) patterns in cherry. Whole trees under natural daylight and constant temperature were found to have a strong diurnal pattern whereas that of individual leaves under constant radiation, temperature, and relative humidity did not. Pn peaked prior to solar noon, plateaued for a few hours, and then declined. Work done by Chalmers <u>et. al.</u> (1983) in the southern hemisphere showed that the time of maximum  $g_s$  varied with the canopy layer measured; higher layers had peak  $g_s$  earlier than lower layers.

Since the position of the earth in relation to the sun changes diurnally, leaf exposure to the sun may be affected by both leaf canopy depth and compass direction. To some degree, shoot or leaf type determines leaf position within the canopy. To predict water loss, it is important observe diurnal differences between plant parameters in relation to sun exposure. Therefore, both leaf type and compass direction were investigated.

IV. <u>Short-term</u> oscillation: to observe possible oscillatory behavior of stomata through short term, continuous  $g_s$  and TR measurements.

Studies in a variety of plants indicate that oscillatory behavior of stomata is common. Whether or not oscillation occurs in sour cherry may be of interest in the development of a water loss model.

V. <u>Fruit effect:</u> to characterize differences in SC and TR between: a) terminal spurs with and without fruit, and b) spurs close and distant to fruit.

Gas exchange functions, such as stomatal opening, transpiration and photosynthesis tend to be greatest in leaves closest to peach fruits (Crews <u>et. al.</u>, 1975; Chalmers <u>et. al.</u>, 1983). In sour cherry, Sams and Flore (1983) found inconsistent results in photosynthesis (Pn) of fruited and non-fruited shoot leaves. During Stage II and III of fruit development in the first year of measurement, Pn was greatest in leaves of fruited shoots. Post harvest Pn rates were not significantly different. In the second season, Pn tended to be higher with the presence of fruit during Stages I and III, but lower than non-fruited shoot leaves in Stage II and after harvest. However, differences were not significant and seasonal averages were similiar (Sams and Flore, 1983).

VI. <u>Prediction</u>: to develop a simple equation for the prediction of transpiration from external (PAR, temperature, vapor pressure difference (VPD) or air vapor pressure) and internal (seasonal effect) factors influencing stomatal movement and evaporation from the previous characterizations.

Evaporative water loss is the main factor in determining irrigation requirements (Chalmers <u>et. al.</u>, 1983). Although soil water evaporation and pan evaporation have been used to determine plant water loss, plant
evaporation, or transpiration, itself may be a more accurate method to predict plant irrigation requirements. Factors both 1) internal to the plant (seasonal, daily, hourly,etc.) due to reproductive and vegetative development of the plant, and 2) external to the plant (PAR, temperature, vapor pressure), may affect the transpiration process. If the combinaion of such factors in a prediction equation would account for a major portion of the variability in transpiration, the model developed could be a useful tool in the determination of irrigation requirements.

## Materials and Methods

#### General

Experiments were conducted between June and September of 1983 and in June and July of 1984 at the Michigan State University Horticultural Research Center, East Lansing. All experiments, except for the shortterm oscillation study, were on field grown sour cherry trees (<u>Prunus</u> <u>cerasus</u> cv. 'Montmorency' on 'Maheleb' rootstock) randomly selected for use from an orchard planted in 1979. Trees were representative of a young newly bearing orchard with shoots more dominant than spurs. Tree vigor ranged from medium to high (shoot lengths from 20 to 40 cm and node number per shoot from 12 to 22) with some vigor differences evident between trees. Soil type was a Miami loam. Orchard management was performed by the farm staff and included: clean cultivation of the orchard floor, recommended fertilizer application, and commercial pest control. No supplimental irrigation was used. Shading due to other trees was negligible. Unless otherwise indicated, measurements were taken between 13:00 and 16:30 (Daylight Savings Time). Sample size was limited by time.

Diffusive resistance  $(r_s)$ , transpiration (TR), relative humidity (RH), photosynthetically active radiation (PAR) and leaf temperature (T) were measured with a LiCor Steady State 1600 model porometer with a broadleaf (2 cm) leaf chamber and direct-read tape recorder attachment. All measurements were taken from the widest portion of the leaf on either side of the mid-vein. Dessicant was replaced and battery recharged prior to each use. A calibration check was performed by LiCor in December of 1982. Data on the cassette were transfered to a mainframe (Cyber 750) system via a Datapod Cassette Reader interface. Stomatal conductance ( $g_s$ ) values were calculated as the inverse of  $r_s$ . Vapor pressure deficits (VPD) were calculated according to the following equations adapted from a BASIC computer program for calculating photosynthetic rates (Moon, 1985):

VPD = LEAFVP \* ((100 - RH) / 1000)

where LEAFVP = 10\*\*(PART7 + PART8 + PART9),

and PART7 = -7.90298 (R3 - 1) + 5.02808 (LOG (R3)) PART8 = -1.3816 (10\*\*-7) (10\*\*(11.344 (1 - T3 / TS) - 1)) PART9 = 8.1328 (10\*\*-8) (10\*\*(-3.49149 (TS / (T3 - 1))) - 1) + (LOG (1013.246)),

and T3 = LEAF TEMPERATURE ( $^{\circ}$ C) + 273, TS = 373.16, and R3 = TS / T3. (LEAFVP abbreviates leaf vapor pressure, and double asterisks (\*\*) denote exponatation.)

Diffusive resistance values were transformed to stomatal conductance. Analyses were performed using the <u>Genstat</u> statistical program (Rothamsted Experimental Station, 1980), and graphics were done by the Plotit plotting program (Eisensmith, 1984).

Phenology was observed at the same site on five randomly selected

trees; branches were randomly selected on the day of measurement. Fruits were randomly harvested from trees throughout the whole orchard, and then average weights taken for fresh weight growth estimates. Rainfall data were obtained from daily weather records taken at the research station.

#### Leaf age, Leaf Type and Seasonal Trend Experiments

Selected leaves on shoots and spurs: Four 'Montmorency' cherry trees were randomly selected and used for measurements. Porometer data were taken from designated spur and shoot leaves throughout the 1983 season (from the 164th to 272nd day of the year, or 6/13 to 9/29/83). Readings were taken from all four trees on all dates except days 171, 236 and 272 (6/20, 8/24, 9/29/83). Lateral buds that developed into shoots 1) less than 5 cm long were designated spurs, 2) greater than 5 cm were considered lateral shoots. Terminal buds that developed into shoots were designated terminal shoots. Two leaves on both terminal and lateral shoots were selected the first day (day 164, 6/13) based on physiological leaf age and monitered throughout the season, the same leaves each measurement. The first leaf, designated as "A" and located 3-5 nodes from the shoot base, was initially the most recently matured leaf (youngest unfolded and expanded leaf; full green color) and was about 2 weeks "old" on the first day of measurement. Leaf "B", 5-7 nodes from the shoot base, was initially the terminal, most recently unfolded leaf (90° angle between blade halves; yellow-green to green in color), or 0-3 days old. Since shoots continued to elongate, a third leaf ("C"), the new terminal, most recently unfolded leaf, was measured on experimental dates subsequent to day 164 (6/13), 1983. Leaf "C" was a leaf 0-3 days old on the day of measurement, up until full shoot expansion. After shoot expansion was complete, leaf "C" was located between nodes 12 and 19. (On day 164 (6/13), leaf "C" was also leaf "B", located 5-7 nodes from the shoot base. Therafter, the "C" leaf went from one node above "B" on the second experimental date to 14 above on the last day.) Spurs were represented by one leaf per spur, three spurs per tree. The selected spur leaves, ca. 4-5 leaves from the base in the whorl sequence, were of the same physiological age as the "A"designated shoot leaves.

<u>All leaves on shoot (age and season experiments)</u>: Experiments were conducted on three shoots (1 shoot per tree) in 1983 and on two shoots per tree for four trees in 1984. Stomatal conductance for each leaf was measured in sequence from the basal leaf to the terminal leaf. The experiment was repeated twice each season: in 1983, on days 187 and 216 (7/6 and 8/4/83), and in 1984, on days 164 and 201 (6/12 and 7/19/84). Leaf area and stomatal conductance were regressed with one another. **Diurnal** 

Data from three trees of the leaf age experiment were collected on day 207 and 222 (7/26 and 8/10/83). Trees were sectioned by quadrant: north (N), east (E), south (S) and west (W). One spur leaf, two terminal and two lateral shoot leaves per quadrant were selected and tagged (a total of 20 leaves per tree) for monitering. All leaves were within 1-2 meters from the ground. Shoot leaves were five to eight nodes from shoot base and well exposed to the overhead sun. Spur leaves were located one to two nodes from the base in the whorl sequence. Since spur leaves were of different physiological ages than the terminal and lateral shoot leaves, analyses were done separately.

Data were taken on days 207 and 222 (7/26 and 8/10/83), starting at

8:00, 10:00, 12:00 and 14:00 on both dates, and also at 16:00 on day 207. Measurements began with the northern quadrant of each tree and progressed in a clockwise pattern around the tree (N,E,S,W) with Tree "I" first and Tree "III" last. The time to complete the sequence was about one hour.

Experimental design for the terminal and lateral shoot experiment was a randomized complete block, three-factor factorial split-split plot. Time was the main plot, direction the subplot and leaf type the sub-subplot. A randomized complete block, two-factor factorial split plot design was used for the spur leaf analyses.

Weather conditions were as follows: 1) Day 207 (7/26): clear, blue sky throughout the day, 2) Day 222 (8/10): a) 8:00 — white, cumulus clouds, b) 10:00 -- overcast, a few sprinkles, c) 12:00 -- clear southern sky, but hazy, becoming overcast overhead, d) 14:00 -overcast, period ending with sprinkles.

## Short-term Oscillation

The short-term oscillation experiment was conducted in 1983 using one-year-old potted sour cherry trees (<u>Prunus cerasus</u> cv. 'Montmorency' on "Maheleb" rootstock). Trees were grown in a loam:sand (1:1) mix in black plastic pots outside under natural conditions. Pesticides (Sevin, Plictran, Karathane), fertilizer (Peter's 20-20-20) and water were applied as needed.

Stomatal conductance and transpiration for two shoot leaves on each of two potted trees were monitered using a LiCor 1600 Steady State Porometer under natural conditions. Measurements were made on day 214 (8/2/83) between 14:00 and 18:30 at 30 second intervals for a period of ca. 45 minutes for 2 of the shoots, and for a period less than 20 minutes for the other two shoots. Leaf "A" was about 4 weeks old (from date of unfolding), and Leaf "B" about 2 weeks old. A ring stand and clamps supported the porometer so that the monitered leaf remained in the chamber for the duration of the experiment.

#### Fruit Effect

<u>Selected leaves:</u> Five 'Montmorency' cherry trees were chosen, and two major limbs were selected per tree for the experiment (1983). One limb per tree was defruited on day 161 (6/10) about two weeks after fruit set (early Stage II). Data from designated terminal shoot and spur leaves, 3 leaves per leaf type on 5 trees, were recorded. Both shoot and spur leaves had been fully expanded about 2 weeks, and were located about 3-5 nodes from the shoot or spur base in the whorl sequence. Spur leaves were selected a) within 2.5 centimeters of fruit and b) five or more centimeters from fruit. Readings were first taken on day 165 (6/14/83), and then about once a week through day 201 (7/20); measurements were then on days 220 (8/8) and 235 (8/23). All 5 trees were used on each day of the experiment, except on day 179 when 4 trees were used. (Area around 5th tree was flooded.) Fruits were harvested on day 196 (7/15) in 1983.

## **Prediction Equations**

Data for leaf age "A", 3-5 nodes from the shoot base of both terminal and lateral shoots (collected from the leaf age experiment) were used to develop prediction equations for transpiration. Leaf age "B" data were also used through the initial regression in the model development process. In the initial step, tree data were regressed singularly, and together. Variables inluded PAR, temperature, air vapor pressure and a time (date) component calculated as the day of the year.

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Regressions were done with and without the log of the time parameter. (The day of year time component was used since no physiologically based time component was easily available. Day of the year does not directly transfer to other locations, crops or even seasons, but was useful as a simple tool to determine the value of a simple model.) To allow for the inclusion of possible interactions between variables, and linear or quadratic responses, a response surface equation of the general form,

 $Y = a + bX_1 + cX_2 + dX_1^2 + dX_2^2 + eX_1X_2$ 

where Y is transpiration (TR),  $X_{1,2...}$  are terms and a,b... are constants, was chosen (Little and Hills, 1978). Terms considered were 1) first ( $X_n$ ) and second ( $X_n^2$ ) degree terms of PAR, temperature, air vapor pressure and date, 2) all possible interactive terms ( $X_nX_{n'}$ ), 3) a third degree time component ( $X_n^3$ ), and 4) log terms (ln  $X_n$ ) of PAR, air vapor pressure and date were considered. Each term was initially regressed alone (one component of the equation) with transpiration. For model development, data from all trees for leaf age group "A" were used. The equation for the term ("A" age group) with the highest R<sup>2</sup> was increased by each of the other terms and then again tested by R<sup>2</sup>. The process was repeated until there was no significant difference (F test, 5%) between the last two models due to the addition of another term.

#### Results

#### **General**

In 1983, spur leaves were fully unfolded by day 150 (5/30) (Figure 1a). Terminal and lateral shoot extension ended as the fruit began to color, about day 181 (6/30) (Figure 1). By day 193 (7/12), most leaves were fully unfolded, terminal buds were set and the fruit was ready for

Figure 1. 'Montmorency' sour cherry phenology, 1983. A) Vegetative development by number of leaves unfolded. (\*) marks completion of shoot expansion, i.e. total number of leaves may be visible, but are not yet unfolded. (Laterals and spurs were not distinguishable prior to day 150 (5/30/83). B) Reproductive development by average weight per fruit on day of observation. (+) designates beginning of change in fruit color from green to red.



harvest (Figure 1). Fruit was harvested from trees of the fruit effect experiment on day 196 (7/15), and the leaf age experiment on day 200 (7/19), by which time birds had already consumed much of the crop.

Growth and ripening occurred about two weeks earlier in 1984 than in 1983. Terminal buds on spurs set about day 146 (5/25), 1984 (Figure 2a). Shoots reached full extension, terminal buds set, and fruit coloration began about day 170 (6/18) (Figure 2b). Fruits were mature by day 184 (7/2).

Precipitation for the months of May, June, July, August and September of 1983 was or 12.1, 10.9, 6.7, 5.5, 10.1 cm, respectively (Figure 3), for a period total of 33.2 cm. Between day 152 and 156 (6/1 and 6/5), 1.4 cm fell. From day 156 to day 167 (6/5 to 6/16), 0.2 cm of rain were recorded. The rainfall on day 167 (0.6 cm) was followed by a ten day period without rain. From day 178 through day 180 (6/27-29), 8.2 cm of rain fell. Another drought period occurred during the first 17 days of July (days 181-198). Between days 201 and 273 (7/20-9/30), precipitation of over 2.5 cm occurred on days 203, 223, and 262 (7/22, 8/11 and 9/19). Relative humidity and temperature values for all experiments other than diurnal studies are shown in Table 1. Relative humidity means and full sun measurements for the diurnal experiments are listed in Table 2 and 3. Sunrise times are given in Table 4.

# Trends between leaves of different ages.

<u>Selected leaves on a shoot.</u> Selected leaves of different physiological ages on a shoot generally exhibited different  $g_s$  and TR throughout much of the season (Figure 4). Four to six weeks after harvest, no differences in  $g_s$  or TR (LSD, 5%) occurred between leaves (Tables A1 and A2). "A" leaves (nodes 3-5) initially had higher  $g_s$  than

Figure 2. 'Montmorency' sour cherry phenology, 1984. A) Vegetative development by number of leaves unfolded. B) Reproductive development by average weight per fruit on day of observation.



Figure 3. Rainfall in centimeters, 1983 growing season, MSU Horticulture Research Center.



Day of Year	Date	Mean Leaf Temp OC	Mean R.H.' (%)
1983         164         165         167         171         172         175         179         180         187         193         195         201         210         214         226         220         214         235         236         272	6/13 6/14 6/16 6/20 6/21 6/24 6/28 6/29 7/05 7/06 <sup>a</sup> 7/06 <sup>b</sup> 7/12 7/14 7/20 7/12 7/14 7/20 7/21 7/29 8/02 8/04 8/08 8/12 8/23 8/24 9/29	31.7 30.4 28.9 30.9 31.3 30.9 18.5 26.8 18.5 22.8 24.3 31.0 33.5 30.8 35.1 31.3 29.9 29.9 33.7 25.8 26.0 30.5 26.4	31.5 42.0 34.8 35.1 30.1 32.8 78.3 45.1 44.6 28.2 32.4 37.1 52.2 43.3 45.8 43.0 44.3 67.5 37.3 40.8 44.0 30.2 45.7
1984 164 201	6/12 7/19	32.0 32.7	45.3 28.0
*insi	de porom	eter cu	vette
<sup>a</sup> leaf	age and	type e	xpt.

Table 1. Mean leaf temperature and cuvette relative humidity on experimental dates.

<sup>b</sup>shoot expt.

Table	2.	Mean	relative	humidity	for	shoot	and	spur	leaves	of
'Montmo	orenc	y <b>',</b> diu	urnal expe	riment.						

Relative	Humid	ity (%)
Day	of Yea	ar
Time	207 <b>a</b>	222b
8:00	58.8	65.3
10:00	42.1	51.3
12:00	36.9	43.3
14:00	34.5	53.8
16:00	33.6	
<del>°</del> 7/26/83		

b8/10/83

	1 PAR (umo	m <sup>-2</sup> s <sup>-1</sup> )
Time	Day 207	Day 222
9:00	*	410
11:00	1790	620 450
16:00 18:00	1770	219

Table 3. Full sun PAR on dates of diurnal experiments, 1983.

Table 4. Monthly sunrise and sunset times for Lansing, Michigan, May 31 - Sept. 30, 1983 (The Old Farmer's Almanac, 1983).

1983	Sunrise	Sunset
5/31 6/31 7/31 8/31 9/30	5:04 5:03 5:38 6:01 6:33	20:08 20:20 20:00 19:15 18:23

.

Figure 4. Stomatal conductance and transpiration of shoot leaves, average of terminals and laterals. Physiolgical age groups: "A" - 3-5 nodes from base and 12-15 days unfolded (90° angle between blade halves); "B" - 5-7 nodes from base and 0-3 days unfolded; "C" - leaf most recently unfolded on day of experiment, nodes 5-19. Same leaf monitered throughout season for groups A and B, and C after terminal bud set. Standard error bars included.



"B" leaves (nodes 5-7 from shoot base) but the trend began to reverse by day 171 (6/20), or at the beginning of Stage II fruit growth (Figure 4). From day 180 through 202 (6/29 - 7/21),  $g_s$  of "B" leaves was higher than  $g_s$  of "A" leaves. "A" and "B" leaves were similiar for most of the remaining season.

"B" leaf  $g_s$  was greater than "C" (terminal) leaf  $g_s$  from day 167 through day 224 (6/16 - 8/12), about 4 weeks after harvest (Figure 4). Before terminal bud set and fruit maturation (Figure 1), "C" leaves generally had lower conductances than "A" leaves (Figure 4). After leaf expansion had ceased and terminal bud set had occurred (Figure 1),  $g_s$  values of the terminal leaves were somewhat higher (although not significantally different, LSD  $_{5\%}$ ) than those of the most mature leaves (Figure 4). As the season progressed,  $g_s$  values of all leaves converged (Figure 4).

Trends in transpiration rates of differently aged leaves were similiar to that of stomatal conductance: 1) "A" leaf transpiration was initially greater than "B" leaf transpiration, but for the remainder of the season prior to fruit harvest, "B" leaves transpired at higher rates than "A" leaves (Figure 4). 2) Transpiration of "B" leaves was greater than "C" leaves for most of the season. TR of the older "A" leaves was generally greater than TR of the most terminal leaves ("C") up until fruit maturation and terminal bud set when the trend began to reverse (Figures 1 and 4). No differences occurred between leaf ages measured after day 202 (7/21) (Figure 4).

Although subject to much variation on days of heavy rainfall,  $g_s$  of leaves mid to apical on the shoot tended to increase, remain high for a short period, and then decrease (see leaf age "B" and "C" after day 187

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(7/6), Figures 3 and 4). Transpiration in "B" leaves was relatively consistent until after harvest (leaves about 6 weeks old) when it declined (Figures 1 and 4). TR of the younger, most terminal leaf ("C") decreased as the shoot expanded (Figures 1 and 4); after shoot expansion (Figure 1), and as the final terminal leaf matured, TR increased, and then decreased as TR of the older leaves decreased (Figure 4). Except during certain periods of heavy rainfall (days 167, 180, and 224; 6/16, 6/29, 8/12, 1983) (Figure 3) when  $g_s$  peaked, TR and  $g_s$  of "A" leaves (2 weeks old when the experiment was initiated) gradually declined for 4-5 weeks and then remained constant for at least 2 weeks before again declining (Figures 1 and 4).

<u>Whole shoot study.</u> Prior to completed terminal leaf opening and expansion, g<sub>S</sub> was low for basal shoot leaves, increased to a high in mid-shoot leaves, and then dropped off again for newer, more recently expanded leaves (Figures 5a and 6a, representative).

 $g_{\rm S}$  and TR trends between the 3 shoots were not consistent on day 216 (8/4/83). (Mite damage to two of the three shoots may have been the cause; therefore the undamaged shoot is presented for both days.)  $g_{\rm S}$  and TR trends for the undamaged shoot were similiar to trends on day 187 (7/6/83) with values increasing with node number, plateauing and then decreasing Figure 5). All leaves on each of the damaged shoots exhibited similiar leaf areas,  $g_{\rm S}$  and TR values to one another (Table B1b).

On day 201 (7/19), 1984, and after full shoot expansion, leaf area and  $g_S$  values of the leaves at the terminal end of the shoot more closely resembled leaf areas and  $g_S$  of leaves located in the central part of the shoot (Figure 6b). Transpiration increased as leaf node Figure 5. Stomatal conductance, leaf area and transpiration for all leaves on a shoot, a) apical leaves expanding (day 187, 7/6/83), b) all leaves expanded (day 216, 8/4/83). Leaves from base to apex on shoot in whorl sequence. (Rep. 1-3).



Figure 6. Stomatal conductance, leaf area and transpiration for all leaves on a shoot, a) apicalleaves expanding (day 164, 6/12/84), b) all leaves expanded (day 201, 7/19/84). Leaves from base to apex on shoot in whorl sequence. (Rep. 3-1)



number increased up to the mid portion of the shoot, and then remained fairly consistent between mid leaves and terminal leaves. Data for all shoots and leaves on all dates are presented in Appendix B.

The regression of leaf area with  $g_s$  resulted in a range of  $R^2$  values from 0.0004 to 0.742 (Table 5).  $R^2$  values were higher, in general, for the first measurement of the season which was prior to terminal bud set. However, after leaf emergence was complete,  $R^2$  values of  $g_s$  and leaf area were very low (0.018 to 0.243 cm s<sup>-1</sup> in 1983, and 0.006 to 0.350 cms<sup>-1</sup> in 1984) (Table 5).

#### Leaf type experiment: spurs, shoots (terminal and lateral)

Except for the first and last day of measurement (days 164 and 272; 6/13 and 9/29/83), there were no significant differences in  $g_{\rm S}$  or TR between similiarly aged "A" terminal and lateral shoot leaves (Tables C1 and C2).  $g_{\rm S}$  and TR rates of spur leaves were lower than terminal or lateral shoot leaves on the first and last day of measurement (days 164 and 172) (Figure 7). Selected spur leaves were of a similiar age to selected shoot leaves, all having emerged about the same time. Although no other statistically significant differences occurred, TR and  $g_{\rm S}$  values tended to be lowest in spur leaves and highest in terminal shoot leaves.

Stomatal conductance was fairly constant prior to terminal bud set and fruit harvest, but declined thereafter (Figures 1 and 7). Transpiration in both spur and shoot leaves tended to decrease over the season except in post-rain conditions (Figures 3 and 7b).

### Diurnal

Under clear conditions, shoot  $g_s$  values varied depending on quadrants (Table 6) and leaf type (Table 7).  $g_s$  peaked highest at 10:00

Day of Year	Date	Code	R2	Y	df	F,5%
187	1983 7/06	all 1-1 1-2 1-3	.489 .166 .490 .649	-0.159 + 0.023X 0.186 + 0.009X 0.029 + 0.014X -0.321 + 0.031X	41 16 14 17	* n.s *
21ó	8/04	all 1-1 1-2 1-3	.200 .040 .018 .243	0.024 + 0.045X 1.222 - 0.012X 0.940 + 0.008X 0.802 + 0.038X	42 15 15 18	* n.s n.s *
164	1984 6/12	$ \begin{array}{r} 1-1 \\ 4-2 \\ 1-1 \\ 5-2 \\ 1-1 \\ 2-2 \\ 3-1 \\ 3-2 \\ 4-1 \\ 4-2 \\ 5-1 \\ 5-2 \\ \end{array} $	.280 .300 .012 .000 .214 .528 .581 .432 .400 .596 .742 .260	0.349 + 0.014X 0.339 + 0.015X 0.739 + 0.004X 0.525 + 0.001X 0.234 + 0.015X 0.178 + 0.015X 0.241 + 0.015X 0.112 + 0.026X 0.259 + 0.012X 0.132 + 0.020X 0.051 + 0.032X 0.398 + 0.013X	42 81 5 6 7 6 5 7 9 8	* n.s n.s n.s n.s * n.s
201	7/19	1-1 · 4-2 1-1 2-1 2-2 3-1 3-2 4-1 4-2	.021 .227 .253 .005 .113 .357 .077 .026 .060	0.332 + 0.002X 0.382 + 0.005X 0.147 + 0.019X 0.437 - 0.002X 0.159 + 0.006X 0.753 - 0.012X 0.663 - 0.003X 0.168 + 0.002X 0.218 + 0.003X	98 13 9 10 13 13 13 8	n.s n.s n.s n.s n.s n.s

Table 5. Coefficients of determination  $(R^2)$  from the regression of leaf area (X) and stomatal conductance (Y) measurements of each leaf on the shoot.

Figure 7. A) Stomatal conductance and B) transpiration on terminal, lateral, and spur leaves of a similiar physiological age (age group "A", 3-5 nodes from base and 12-15 days unfolded on day 164, 6/13/83). Terminal buds set and fruit ready for harvest by day 193 (7/12/83); fruit harvested day 200 (7/19/83). Standard error bars included.



Table 6. Stomatal conductance  $(g_s)$  (cm s<sup>-1</sup>), transpiration (TR) (µg cm<sup>-2</sup> s<sup>-1</sup>), photosynthetically active radiation (PAR) (µmol m<sup>-2</sup> s<sup>-1</sup>) and temperature (T) (°C) means and standard deviation (means of terminal and lateral shoots) on day 207 (7/26/83).

				COM	PASS D	IRECTIO	N				
		NOR	TH	EAS	T	SOUT	Ή	WES	T	ME	AN
	TIME	X	S.E.	X	S.E.	X	S.E.	X	S.E.	X	S.E.
9s	8:00 10:00 12:00 14:00 16:00	0.47 0.74 0.49 0.45 0.39	0.03 0.11 0.11 0.09 0.08	0.51 0.84 0.49 0.44 0.32	0.05 0.16 0.11 0.09 0.06	0.58 0.86 0.63 0.46 0.54	0.05 0.14 0.14 0.16 0.15	0.52 0.80 0.74 0.52 0.46	0.04 0.13 0.21 0.19 0.18	0.52 0.81 0.59 0.47 0.43	0.02 0.06 0.07 0.07 0.06
	MEAN	0.51		0.52		0.62		0.61		0.56	
TR	8:00 10:00 12:00 14:00 16:00	5.5 15.4 13.6 15.7 13.6	0.38 1.51 2.22 2.85 2.27	6.2 17.0 15.1 14.9 10.9	0.7 1.8 2.4 2.7 1.7	6.8 17.2 17.7 14.7 15.3	0.5 1.5 2.6 4.0 3.8	6.1 15.8 17.6 15.8 14.8	0.4 1.3 3.2 4.6 3.9	6.1 16.4 16.0 15.3 13.6	0.3 0.7 1.3 1.7 1.5
	MEAN	12.7		12.8		14.3		14.0		13.5	
PAR	8:00 10:00 12:00 14:00 16:00	421 890 1325 1138 1072	46 91 178 241 98	548 1232 1678 1440 542	41 63 15 119 70	407 1085 1637 1578 1333	82 127 36 125 20	106 389 1547 1746 1420	18 82 37 159 59	371 899 1547 1475 1092	42 79 52 83 78
	MEAN	969		1088		1208		1042		1077	
т	8:00 10:00 12:00 14:00 16:00	20.4 25.4 28.0 30.1 30.1	0.2 0.1 0.4 0.4 0.2	20.6 25.4 30.0 29.9 29.5	0.2 0.3 0.2 0.2 0.1	20.4 25.4 28.9 30.3 30.0	0.2 0.3 0.2 0.3 0.2	20.3 24.9 28.0 30.4 30.3	0.3 0.3 0.4 0.2	20.4 25.3 28.4 30.2 30.0	0.1 0.1 0.2 0.2 0.1
	MEAN	26.8	· · · · · · · · · · · · · · · · · · ·	26.9		27.0		26.8		26.9	
g <sub>s</sub>	LSD,	5%: di	rectio	n, 0.08	6 cm <sup>-2</sup>	•s-1					<u> </u>
PAR	LSD, for	5%: same t	time, imes,	128; d then 26	lirecti 8 µmol	on, 120 •m <sup>-2</sup> •s <sup>-</sup>	; time	x dire	ection,	265 e	xcept

T LSD, 5%: time, 0.4; direction x type, 0.6°C except for same direction, then 0.5.

Table 7. Mean diurnal transpiration rates ( $\mu$ g m<sup>-2</sup> s<sup>-1</sup>) of terminal and lateral shoot leaves at 4 different directions on day 207 (7/26/83) (2 samples, 3 trees), 'Montmorency'.

Time	Туре	North	East	South	West
8:00	terminal lateral	<b>5.</b> 88	6.23 6.00	7.39 6.15	6.15 5.98
10:00	terminal	16.47	17.04	18.28	16.27 15.28
12:00	terminal	14.40	15.51	18.96	19.42
14:00	terminal	17.98	16.09	14.85	17.07
16:00	terminal lateral	15.57 11.56	11.66 10.06	19.12 11.46	14.12 15.57
LSD, 5 differ	%, between ent direc	time m	eans fo d type	r the s means:	ame or 5.74
µg m-2 same t	s <sup>-1</sup> ; betw ime and sa	veen dir ume or d	ection lifferen	means f t type:	or the 3.82
ug m <sup>-</sup> same o µg m <sup>-2</sup>	2 s-1; be r differen s-1.	e <b>tween l</b> It time	eaf typ and dir	e mean ection:	s for 2.80

and lowest at 16:00, but differences were not significant (LSD, 5%) (Figure 8). In the morning, southern, western and eastern shoot leaves tended to have higher  $g_S$  than northern shoot leaves; however, by 12:00, eastern shoot leaves were more similiar to northern leaves (Table 6). Terminal shoot  $g_S$  (0.601 cms<sup>-1</sup>) was significantly higher (F,5%) than lateral shoot  $g_S$  (0.524 cms<sup>-1</sup>).

Transpiration rates were significantly higher (F, 5%) for terminals  $(14.43 \ \mu g \ cm^{-2}s^{-1})$  than for lateral shoot leaves  $(12.52 \ \mu g \ cm^{-2}s^{-1})$ . Significance also occurred between the interaction of time, leaf type and compass direction (Table 7). Although not significantly different (LSD, 5%), some additional trends were evident. Transpiration at 8:00 was much lower than transpiration at all other times (Figure 8, Table 6). TR rates in the afternoon decreased (Figure 8, Table 6). While northern and eastern quadrants, and southern and western quadrants had similiar rates, rates of the former two quadrants appeared to be lower than the latter (Table 6).

Measurements on spur leaves on day 207 showed statistical differences between time means for  $g_S$  and TR (Table 8), direction means for transpiration (Table 9), and time x direction means for T (not shown). TR rates in northern spur leaves were significantly less than eastern, southern or western shoot leaves (Table 9).

PAR received by shoot leaves varied with time, direction and between time and direction (Table 6), over type, and between direction and shoot type (Table 10). PAR increased until 12:00 (Figure 8, Table 6), and was highest in the eastern quadrants in the morning and at noon, and in the western quadrants in the afternoon (Table 7). Terminal shoots received significantly more PAR than lateral shoots (Table 10).

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Figure 8. Diurnal characterization of stomatal conductance, transpiration, PAR, and vapor pressure difference on day 207 (7/26/83) for shoot leaves (located 5-8 nodes from shoot base, two leaves per quadrant on both lateral and terminal shoots) and spur leaves (1-2 nodes from base in whorl sequence, 1 leaf per quadrant). (Clear sky). Standard error bars included. (

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Table 8. Stomatal conductance (cm s<sup>-1</sup>), transpiration ( $\mu$ g cm<sup>-2</sup> s<sup>-1</sup>), photosynthetically active radiation ( $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>), temperature (°C) and vapor pressure deficit (kPa) for 'Montmorency' spur leaves, diurnal reading on day 207 (7/26/83).

	g <sub>s</sub> 1		TR2		PA	R	TE	мрЗ	VP	D4
TIME	X	S.E.	X	S.E.	X	S.E.	X	S.E.	X	S.E.
8:00 10:00 12:00 14:00 16:00	0.288 0.454 0.279 0.252 0.205	0.023 0.048 0.023 0.018 0.016	4.03 10.18 8.75 9.05 7.66	0.27 0.67 0.58 0.57 0.49	169 322 471 646 495	34 78 108 114 104	20.8 25.0 27.9 29.7 30.1	0.1 0.1 0.2 0.1	1.08 1.91 2.46 2.79 2.88	0.01 0.04 0.03 0.03 0.03
Mean	0.295		7.93		421		26.7			
<sup>1</sup> LSD, s	5%: 0.10	)3								
2 <sub>LSD</sub> ,	5%: 2.05	5								
<sup>3</sup> LSD,	5%: 0.60	)								
4LSD.	5%: 0.2									

Table 9.	Spur	leaf tra	anspirati	on (TR)	(µg d	cm-2 s-1),	photos	ynthetica	11y
active ra	diatio	n (PAR)	(µmol m-	<sup>-2</sup> s <sup>-1</sup> ),	and t	temperature	e (°C)	averaged	Ьy
direction	over	time on	ɗay 207	(7/26/83	3).				

Direction	TR	PAR	TEMP
	<del></del>		
North	6.50	299	26.6
South	a 10	525 478	20.7
West	8.00	381	26.8
TR: LSD, S	5%: 1.34		
PAR: n.s.			
TEMP: n.s.			

Table 10. Photosynthetically active radiation ( $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>) by direction and leaf type for diurnal measurements on day 207 (7/26/83).

Direction	Terminal	Lateral
North	1117	822
East South	1092	1084 1149
West	1087	998
Means	1140	1013
	100	

LSD, 5%, 156  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, except for same direction, then 155  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>.

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While no significant PAR differences occurred for spur leaves, values increased steadily until 14:00 and then dropped off at 16:00 (Table 8). Mean PAR received by the spur the leaves was greatest in the southern and eastern quadrants (Table 9).

Temperature and VPD both increased with time until 14:00 for shoot (Table 6) and spur (Table 8) leaves. Significant interactions also occurred between time x direction (Table 6) and time x leaf type (Table 11).

Diurnal trends on day 222 (8/10) were somewhat different than on day 207 (7/26/83) (Figures 8 and 9). Although  $g_S$  of shoot leaves appeared to be higher at 8:00 than at any other time, the differences were not significant (LSD, 5%) (Figure 9). Terminal shoot leaves in the eastern quadrant had lower  $g_S$  than respective lateral shoot leaves (Table 12). Highest  $g_S$  and TR of terminal shoot leaves occurred in the N, while lowest occurred in the S and E (Table 12).  $g_S$  of lateral shoot leaves was highest in the E quadrant, and lowest in the N and S quadrants (Table 12).

Transpiration for shoots on day 222 (8/10/83) was very low, but increased from 8:00 to 12:00, and then decreased at 14:00 (Figure 9); No differences in TR occurred between compass directions, nor shoot types. Mean spur leaf  $g_s$  and TR on day 222 (8/10/83) were significantly lower in the W than in the N, E or S (Table 13). TR significantly increased from 8:00 to 12:00 (Figure 9).

PAR was consistently low throughout the day (Figure 9). Spur leaves in the W quadrant received the least PAR, while those in the N and S quadrants received the most (Table 13). Temperature for both shoots and spurs were similiar, although shoot temperatures peaked

	Leaf Temperature								
Time	Terminal Shoot	Lateral Shoot	Mean Shoot						
8:00 10:00 12:00 14:00 16:00	20.3 25.1 28.4 30.4 29.9	20.6 25.5 28.4 30.0 30.0	0.98 1.87 2.45 2.82 2.82						
Temp: 1	Temp: LSD, 5%= 0.3, all comparisons								
VPD: LS	SD, 5%= 0.1								
1) Mea shoots	an of term	inal and	lateral						

•

Table 11. Diurnal temperature (°C) and vapor pressure difference (VPD) (kPa) for terminal and lateral shoot leaves on day 207 (7/26/83).

Figure 9. Diurnal characterization of stomatal conductance, transpiration, PAR and vapor pressure difference on day 222 (8/10/83) for shoot leaves (located 5-8 nodes from shoot base, two leaves per quadrant on both lateral and terminal shoots) and spur leaves (1-2 nodes from base in whorl sequence, 1 leaf per quadrant). Standard error bars included. (Overcast sky).



Parameter			Dire	ction	
	Туре	North	East	South	West
gs <sup>1</sup>	terminal	0.751	0.548	0.556	0.641
	lateral	0.630	0.855	0.655	0.683
TR <sup>2</sup>	terminal	5.35	4.14	4.14	4.52
	lateral	4.26	5.70	4.58	4.87

Table 12. Stomatal conductance  $(g_s, cm s^{-1})$  and transpiration (TR,  $\mu g cm^{-2} s^{-1})$  averaged over time for terminal and lateral shoots located in 4 different compass directons on day 222 (8/10/83).

 $^{1}LSD$ , 5% = 0.173 except for comparisons within same direction, then 0.177.

 $^2 \rm LSD$ , 5% = 1.18 except for comparisons within same direction, then 0.93.

Parameter	North	East	South	West	Mean	LSD 5%
gs TR PAR	0.774b 5.16b 250c	0.721b 4.89b 190b	0.615b 4.25b 226bc	0.333a 2.48a 107a	0.611 4.20 193	0.175 1.16 50

Table 13. Stomatal conductance  $(g_s)(cm s^{-1})$ , transpiration  $(TR)(\mu g cm^{-2} s^{-1})$  and photosynthetically active radiation (PAR) ( $\mu mol m^{-2} s^{-1}$ ) of spur leaves averaged over time on day 222 (8/10/83).

Mean separation by LSD, 5%.

earlier (Table 14). Mean temperature for terminal shoot leaves at 20.0°C was significantly greater than the temperature for lateral shoot leaves at 19.8°C (LSD, 5% = 0.17). VPD also increased over time with the highest deficit at 12:00, and lowest at 8:00 (LSD, 5% = 0.21) (Figure 9).

In summary, on day 207 (7/26/83), a clear day,  $g_s$  of shoot and spur leaves increased as VPD, PAR and temperature increased until the 10:00 reading when VPD reached ca. 1.9 kPa (Figure 8). Thereafter, VPD increased and  $g_s$  decreased at similiar rates (Figure 8). Transpiration remained fairly intermediate between  $g_s$  and VPD, fluctuating somewhat for spur leaves and dropping slightly for both as the day progressed. On day 222 (8/10/83), overcast with some precipitation, values for VPD, PAR and temperature of spur and shoot leaves were relatively low (Table 6). Although VPD and T increased, the maximum mean was never higher than 1.57 kPa.

## Short-term oscillation

Stomatal conductance of all leaves monitered at least 30 minutes appeared to cycle (Figures 10 and 11). Time between the troughs was about 20 minutes. Oscillation was less clear in the leaf monitered only 18 minutes (Figure 12), and not at all clear in the leaf monitered 11 minutes (Figure 13). Leaf temperatures were between  $27.4-30.3^{\circ}$ C and relative humidity between 41.6-45.1%. PAR was 1600-1700 umol m<sup>-2</sup> s<sup>-1</sup>. **Fruit.** 

 $g_s$  and TR of shoot leaves on de-fruited branches were ususally higher than  $g_s$  on fruited branches early in the season (Figure 14, Table D1). Spur leaf  $g_s$  and TR were similiar for leaves on de-fruited and fruited branches. Spur leaf  $g_s$  was significantly lower than shoot leaf

	Temper	ature		
Time	Shoot1	Spur <sup>2</sup>	VPD3	
		<del></del>		
8:00	15.6	15.5	0.60	
10:00	18.6	18.6	0.99	
12:00	22.5	21.9	1.47	
14:00	22.9	22.6	1.28	
Means	19.9	19.6	1.08	
1 <sub>LSD, 5%</sub>	= 1.00C	<del></del>		<u> </u>
<sup>2</sup> LSD. 5%	= 0.653°C			

3LSD, 5% = 0.19 kPa

Table 14. Diurnal temperature (°C) and vapor pressure difference (VPD)(kPa) by time and direction for spur leaves on day 222 (8/10/83).

Figure 10. Timecourse of stomatal conductance and transpiration on four week old leaf, day 214 (8/2/83). (Potted tree, natural conditions.)



Figure 11. Timecourse of stomatal conductance and transpiration on four week old leaf, day 214 (8/2/83). (Potted tree, natural conditions.)

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Figure 12. Timecourse of stomatal conductance and transpiration on two week old leaf, day 214 (8/2/83). (Potted tree, natural conditions.)

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Figure 13. Timecourse of stomatal conductance and transpiration on two week old leaf, day 214 (8/2/83). (Potted tree, natural conditions.)



Figure 14. A) Stomatal conductance and C) transpiration for shoot and spur leaves on fruited and de-fruited branches, in relation B) the phenological development, 1983. All leaves 3-5 nodes from base in whorl sequence. Standard error bars included.



gs on all dates. Transpiration on day 179 (6/28) was very low, corresponding to a cool, humid day and very wet soil due to rainfall (Figure 14). The greatest difference in  $q_s$  and TR between shoot leaves fruited and de-fruited, and spur leaves fruited and de-fruited appears to be during Stage II. The exponential phase of cherry fruit growth (Stage III) (by weight) occurred from ca. day 179 through ca. 188 (6/28 Average number of leaves per shoot was 14.5 for fruited - 7/7). branches versus 15.8 for defruited branches, and per spur, 4.6 leaves for fruited trees versus 5.3 leaves for defruited trees. Shoot expansion of fruited trees ended between days 178 and 188 (6/27, 7/7) (Figure 1); no differentiation was made between terminal bud set dates of fruited and defruited branches. No significant differences in  $g_s$  or TR occurred mbetween spur leaves within 2.5 centimeters of fruit or more than 5 centimeters from fruit, although values appeared to be higher for leaves over 5 centimeters from fruit (Table 15).

## Prediction Equations

Initial step  $R^2$  values are presented in Table 16. Coefficients of multiple determination ( $R^2$ ) for quadratic equations of combined trees, leaf age group "A", are also listed in Table 16. Except for one tree (tree 1) of age group "B", day of the year consistently accounted for the greatest percent variability in transpiration. (Air vapor pressure and air vapor pressure squared had the highest  $R^2$  for age group "B", tree 1.)  $R^2$  values for individual trees were higher than trees combined; trees 3 and 4 had the higher  $R^2$  values than trees 1 and 2.

Time was used as the first term in the regression since regressions of TR with the time (day of year) parameter for combined trees of leaf age group "A" yielded the highest  $R^2$ . The addition of PAR, temperature

Table 15. Mean stomatal conductance  $(g_s)(cm s^{-1})$  and transpiration  $(TR)(\mu g cm^{-2} s^{-1})$  for leaves of spurs within 2.5 cm of fruit (<2.5) and greater than 5 cm from fruit (>5.0) in 1983.

Day		9	s		TR		
Year	Date	<2.5	>5.0	<2.5	>5.0		
165 172 179 186 193 201 220 235	6/14 6/21 6/28 7/05 7/12 7/20 8/08 8/23	0.366 0.284 0.401 0.573 0.295 0.398 0.217 0.334	0.383 0.288 0.443 0.599 0.343 0.477 0.274 0.395	11.30 11.80 2.30 8.29 10.69 11.96 5.25 4.30	11.95 12.50 2.55 8.65 12.14 14.66 6.12 5.29		

								ree			
		Ą	je Grou	<b>р</b> "А"				Age	Group	"B"	
Term	1	2	3	4	A11	A11	1	2	3	4	A11
PAR	.061	.21*	.37**	X	.08*		.22	X	X	.15	.02
PAR <sup>2</sup>	•10	.23*	.41**	X	.10**	.11	.18	X ·	X	.14	.20
logPAR	X	.15	.29*	X	.05*		.25*	X	X	.15	.02
	-12	X	.12*	X	.04	~.	.19	.16	•31×	X	.10**
	•1	X	•	X	•04	-08	.20	.1/	.చూ	×	•10**
AIRVP	X	X	X	X	X	~~	.30**	.16	.12	.05	.03
AIrve	X	. X	X	X	X	-03	• 30***	.15	.15	X	.04
IOGATEVP	.0/	X	X	X	X		•29*	•10	-08	.06	.03
Day 2	.40**	./3**	./0**	.80**	•04**		X	.4/**	.54**	•85**	.43**
Day-	.48**	./1**	.//**	./5**	.00**		X	.49**	.00**	·91**	.45**
Day David	.40**	•00***	•0/**	•08**	.50**		-06	•52**	·03**	./0**	.03**
loguay	•48** 1c	./0^~	./9**	•00^^^	-00^^	•	Å	•44^~	.50~~	.00^^	.41^^
	-10	•29°	.50	×.	•1100		.00	× 12	.05	•12	.00.
	.10 V	(.10)	• 30~~ V	Ŷ	.05		∧ 2/1★	10	•15 21	Ŷ	.04
	â	12	30**	Ŷ	n3		• <b>34</b> ··· 12	16	·21 23*	Ŷ	.00*
	.09 Y	۲. ۲.	•.J9····	10	••••		•12 26*	10	• 2011	Ŷ	.00 F0
TyD	Ŷ	27 <b>*</b>	36**	65**			.20	.10	â	.71**	.12**
	Ŷ	08	22*	 ⊰i★	12**		25*	· · · · · · · · · · · · · · · · · · ·	••• x	35**	· T
PyTyD	Ŷ	.05	.15	.16	X		.10	Ŷ	Ŷ	- x	Ŷ
PxAxD	x	X	X	28*	X		X	x	x	.09	X
TxAxD	x	x	.09	.20*	.05*		.28*	.06	x	.22**	x
PxTxAxD	X	X	.06	.21	X		(.09)	X	.08	.08	X

Table 16.  $R^2$  for regressions of photosynthetically active radiation (PAR or P)(µmol m<sup>-2</sup> s<sup>-1</sup>), temperature (Temp or T)(°C), air vapor pressure (AirVP or A)(kPa) and day of year (Day or D) terms.

\* Significant F, 5%

**\*\*** Significant F, 1%

X Residual varience exceeds varience of Y-variate

df: Tree 1) 1/16; 2) 1/18; 3) 1/16; 4) 1/18; A11) 1/74

"A" 3-5 nodes from shoot base

"B" 5-7 nodes from shoot base

or air vapor pressure logged or squared, or an interaction of variables did not significantly (F,5%) account for a greater percent of the variablility. The greatest increases in  $R^2$  by the addition of another term are presented in Table 17. The prediction equation derived from TR data of leaves 3-5 nodes from the base and from 4 trees is,

TR = 192.205 - 79.963 D,

where D = day of year. Standard errors and t values for the constants are listed in Table 18.

From the  $R^2$  values listed in Table 16, linear PAR was chosen as the first term to include in the equation. (While PAR<sup>2</sup> had a higher R<sup>2</sup>, than linear PAR, the full quadratic model is incomplete without linear PAR; the increase from one to two terms (PAR to PAR and PAR<sup>2</sup>) was not significant at F, 5%). The second term which produced the highest R<sup>2</sup> in the next series of regressions was temperature (see Figure 15). Although the R<sup>2</sup> values for the linear temperature model and linear air vapor pressure model were insignificant, a linear multiple regression of the temperature and air vapor pressure had a higher R<sup>2</sup> than any other two term combination (Figure 15). The final equation included linear terms of PAR, temperature, and air vapor pressure, and accounted for 24.2% of the variability in transpiration. The regression was significant (F, 5%; Figure 15). Table 19 lists constant estimates, standard errors and t values for each equation in the progression.

The two final models (1) day of year model, and 2) PAR, temperature, air vapor pressure model) were tested and compared with diurnal experiment data from the 14:00 reading of day 207 (7/26); predictions were not similiar (Table 20).

	Ter	ms		
Equation	×ı	X2	R2	F
$Y = a + bX_1$	log (Day of Year)	_	.66	
$Y = a + bX_1 + cX_2$	10	PAR Temp. Air V.P.	.67 .67 .66	0.790ns
Y = a + bX <sub>1</sub> + cX <sub>2</sub> + dX <sub>3</sub> + dX <sub>4</sub> + eX <sub>5</sub> , where $X_1X_5$ = log	(Day of Year)	, PAR, PAR <sup>2</sup> ,	.67 Temp., /	Air V.P.,

Table 17. Prediction equations and  $R^2$  values for respective X terms for transpiration of shoot leaves 3-5 nodes from shoot base (Age group "A").

Table 18. Estimates, standard errors and T test for constants a and b, where  $Y = a + bX_1$  and where Y = transpiration and  $X_1 = \log$  (Day of year).

Constant Estimate	S.E.	т
a b	14.64 13.13	6.64 -12.04

Error df=74



Figure 15. Equations containing terms proceeding a final equation for the prediction of transpiration  $(\hat{Y}, \mu g \, m^{-2} \, s^{-1})$  from environmental parameters: photosynthetically active radiation (P, umol  $m^{-2} \, s^{-1}$ ), temperature (T,°C) and air vapor pressure (A, kPa). F tests the significance in the change between R<sup>2</sup> values for the model before and after the addition of another term.

Equation	Constant	Estimate	S.E.	Т
 V=a+bD		0 11055	2 08266	5 31
i-a · ur	b	0.00542	0.00213	2.54
Y=a+bP+cT	a	-1.98626	6.34864	-0.31
	b C	0.00595 0.42870	0.00209 0.19772	2.84 2.17
Y=a+cT+dA	a	-10.55664	7.15855	-1.47
	c d	1.31438 -0.73478	0.32583 0.20401	4.03 -3.60
Y=a+bP+cT+dA	a	-14.27002	7.13739	-2.00
	Ь	0.00467	0.00202	2.31
	c d	1.243/5 -0.64047	0.31801 0.20236	3.91 -3.16
<b>D D A D</b>		* *		-
Vapor Pressu	m-2 s-1); ire (kPa).	I=lempera	ture ( <sup>UC</sup> );	A=A1r

Table 19. Constant estimates, standard errors, and t-values for the step-wise equations in the transpiration prediction model, Figure 15.

Table 20. Comparison of two equations to predict transpiration (TR,  $\mu g \, cm^{-2} \, s^{-1}$ ). (Values given represent actual mean values of data collected in diurnal study, 14:00 reading.)

	<u> </u>					
Given: Day of Year Photosynthetically Active Radiation Temperature Air Vapor Pressure	207 1770 30.9 15.0	µmol oc kPa	m-2 s <sup>-1</sup>			
Method			TR			
Predictive: Y = a + b(log(Day of Year))			7.0			
Y = a + b(PAR) + c(Temp.) + d(Air V.P.)						
Actual (Mean)			15.3			

## Discussion

Leaf age. In general, the most immature and mature leaves on the shoot had lower stomatal conductances than recently matured leaves (Figures 4 and 5). Work by Sams and Flore (1982) on 'Montmorency' sour cherry photosynthesis support these findings. They found that photosynthesis (Pn) rates increased as leaves approached 80% full expansion, plateaued for 2-4 weeks, then declined.

The differences related to age may be due to immature stomata and less developed photosynthetic systems in the younger leaves (Sams and Flore, 1982, for sour cherry; after Slack, 1974, for apple) and the onset of normal leaf senescence in the older, more basal leaves (Sams and Flore, 1982). Although leaf area and stomatal conductance appear to follow similiar patterns as leaf distance from shoot base increases, they do not appear to be highly correlated (Figure 5; Table 5). Since the trees were bearing fruit, competition for assimilate and water between fruit and various leaves on the shoot may have also affected ge and TR (see Figures 1 and 3). The peak in transpiration on day 202 (7/21/83) (Figure 4) may be related to the harvest of fruit on day 200 (7/19/83); although temperature and relative humidity were high, they do not appear to adequately explain such a peak (Table 1). The rainfall pattern of 1983 appeared to influence  $q_s$  and to a lesser degree, TR; peaks in g<sub>s</sub> tended to correspond to periods when the moisture supply was high, such as on days 180 and 224 (6/29, 8/12) (Figures 3 and 4). Lakso (1979) encountered a similiar situation in which the rainfall pattern appeared to influence the water potential required for stomatal closure in apple. Soil moisture factors appeared to affect g<sub>s</sub> more than they affected TR (Lakso, 1979).

A sesonal trend towards decreasing use of water by peach trees was also observed by Worthington <u>et. al.</u> (1984). He found that weekly crop coefficients for peach ranged from 0.982 early in the season to 0.399 late in the season despite increasing foliage, and associated this trend with physiological changes in the trees (Worthington <u>et. al.</u>, 1984).

Leaf type. Leaf type did not significantly affect stomatal conductance or transpiration; however, spur leaves did have relatively lower  $g_s$  and TR values than terminal or lateral shoots (Figure 7). While of a lesser magnitude, terminal shoot leaves tended to have slightly higher (but not significantly )  $g_s$  and TR than lateral shoot leaves after day 164 (6/13) (Figure 7). Significance may have been more evident had the sample size been larger.

An analysis on initially less mature leaves would be of interest since initial measurements on day 164 (6/13) showed significant differences between spurs and shoots, and relatively higher values of  $g_s$  and TR (Figure 7).

It is also important to note that leaf location with the canopy may affect stomatal opening to a greater degree than actual physiological differences between leaf type. As seen in the diurnal study, (Figure 8), PAR received by shoots was greater than that received by spurs. Spurs are generally not as exposed to the sunlight as shoots. Even the basal end of lateral shoots are often not as well exposed as are terminal shoots. Tree pruning, training and spacing, etc. all affect leaf receptivity to the sun. Although attempts were made to allow for maximum exposure to sunlight, the effects of shading cannot be ruled out.

The difference which occurred between leaf types on day 272 (9/29)

(Figure 7) seems unlikely, and may be a result of using fewer experimental units on that day.

<u>Diurnal.</u> Diurnal characterization of  $g_s$  and TR of 'Montmorency' sour cherry on two days, 1) clear, and 2) cloudy to overcast with some precipitation, reveled variations in stomatal movement and water loss daily and between days (Figures 8 and 9). Sams and Flore (1983) found strong diurnal variation in whole tree Pn of potted trees under natural sunlight and constant temperature. Under constant, optimum conditions, Sams and Flore (1983) found no significant change in Pn of leaves on a diurnal basis. Since factors such as VPD, PAR and temperature vary between and within days (Tables 2, 3, 6, 9), it is likely that  $g_s$  and TR, both of which are affected by the environment, would vary.

As in a study by Sams and Flore (1983) where maximum Pn occurred before solar noon and decreased before PAR decreased,  $g_S$  on day 207 (7/26) reached a maximum prior to maximum PAR and decreased before a decrease in PAR (Table 6; Figure 8).

On day 222 (8/10),  $g_s$  was initially high, but then decreasesd for shoot leaves (Table 6). Low VPD, or seasonal, diurnal or leaf age effects may have been contributing factors. The relationship between spur leaf  $g_s$  and shoot leaf  $g_s$  on the overcast day (Figure 6) may be due to differences in leaf age (since shoot and spur leaves were of different ages), or a preconditioning to lower radiation levels by the past environment. PAR levels were similiar for both shoots and spurs under an overcast sky.

Chalmers <u>et.</u> <u>al.</u> (1983) found that maximum stomatal conductances in the uppermost layer of peach trees occurred before 10:00, but then steadily decreased. Maximum  $g_s$  for lower layers occurred later in the

morning. On day 207 (7/26) of the present study, in which measurements were taken from the mid portion of the tree on the clear day, maximum conductance occurred about 10:00 (Table 6; Figure 8). Houle (1984) reported that light and humidity appear to be more closely related to diurnal fluctuations than soil moisture. In the present study, PAR and VPD (or humidity) appear to be closely related to the diurnal fluctuations of day 207 (7/26), 1983 (Table 6).

As the sun moved across the sky from east to west, PAR levels on day 207 (7/26) within each quadrant of the tree varied (Table 6). However,  $g_s$  and TR were not affected, probably due to sufficient levels of PAR.

<u>Short-term</u> <u>oscillations</u>. While the stomata showed signs of oscillations, more extensive measurements are necessary to determine whether oscillations in sour cherry are spontaneous or induced. Although environmental parameters (RH, T, PAR) were fairly stable during the  $g_s$  and TR monitering period, the affect of the porometer itself on the plant is not known.

<u>Fruit.</u> The stomatal response to a fruit load was characterized for both spurs and shoots of 'Montmorency' sour cherry (Table 14). Fruited branches had lower conductances than defruited branches during both slow (Stage II) and rapid (Stage III) fruit development. In research by Sams and Flore (1983) on 'Montmorency' sour cherry, variation in Pn rates was found between seasons and growth stages. Stage II and III of the first season were characterized by higher Pn rates of fruited than non-fruited shoot leaves, while Stages I and III of the second season were characterized by insignificant, though, slightly higher Pn rates for fruited than non-fruited shoot foliage. Stage II and post harvest Pn rates, in the second season, were higher in non-fruited than fruited shoot leaves (Sams and Flore 1983).

In peach, while Chalmers <u>et. al.</u> (1983) observed lower transpiration in fruited than defruited trees during the stage of slow fruit growth, he found higher tranpiration in fruited than in defruited trees during the second stage of rapid fruit growth. This may be a result of continued high demand for assimilate for vegetative growth of defruited trees during the slow fruit growth stage. Chalmers <u>et. al.</u> (1983) suggested that fruits inhibited vegetative growth of fruited trees during the first period of rapid fruit growth by out-competing for assimilate. Defruited trees, on the other hand, did not have that fruit sink, and vegetative growth was promoted (Chalmers <u>et. al.</u>, 1983).

<u>Prediction.</u> While many combinations of environmental parameters were tried, (temperature, PAR, air vapor pressure) none improved on a seasonal-change based model to predict transpiration. It appears that much more variability exists than can be accounted for by temperature, PAR or air vapor pressure.

The trend in transpiration from some point in the season (beginning with day 160 (6/9) for leaf age group "A" and later for younger leaves (Figure 4)) was to decrease. Prior to that time (as evidenced by the younger leaves of leaf age group "B", days 160-200), a plateau occurred. Environmental parameters may more greatly affect transpiration during the plateau period than during the decline. Therefore, it may be of interest to segregate parts of the season by stage of vegetative or reproductive development. A preliminary identification of data points suggested a segregation of points by time of season.

The overall need for a model is to predict transpiration for whole

trees and plantings and not individual leaf age groups. However, the extent of variability between trees due to internal and external factors was not known. To minimize variability of transpiration due to leaf age, model regressions were done on an individual leaf group. As shown in Table 16, the percentage variability in transpiration accounted for by any one term varied between trees. The amount of fruit on each tree seemed to vary between trees.

## Conculsions

Differences in leaf age appear to affect stomatal conductance and transpiration; as individual leaves mature, stomatal conductance increases, remains level for a period, then decreases. Transpiration (TR) is consistent for a period, then declines. Leaf or shoot type did not appear to affect stomatal conductance  $(g_S)$  or transpiraton (TR) leaves 3-5 nodes from the shoot base. A diurnal pattern in all parameters measured was detected. Peak conductance appeared to occur about 10:00 under conditions of a clear sky. Oscillation of stomata occurred as evidenced  $g_S$  and TR readings. Fruit appeared to influence  $g_S$  and TR since fruited branches had lower conductances than defruited branches during both slow and rapid fruit development. The day of the year was more significant in the prediction of transpiration than were all combinations of environmental parameters PAR, temperature and air vapor pressure.

APPENDICES

APPENDIX A

		Anj	"B	,u	"C		Me	an		LSD	
of Date Year 1983	X	S.E.	X	S.E.	X	S.E.	X	S.E.	5%	1%	0.1%
164 6/13   167 6/16   171 6/20   175 6/24   180 6/29   187 7/06   195 7/14   202 7/21   224 8/12   236 8/24   272 9/29	.672 .870 .596 .461 .865 .552 .436 .436 .436 .805 .279 .298	.066 .082 .077 .030 .061 .036 .042 .026 .041 .026 .020	.482 .685 .594 .561 1.115 .752 .692 .672 .907 .364 .349	.034 .040 .083 .043 .063 .095 .086 .057 .059 .045	 .458 .390 .413 .502 .259 .471 .509 .773 .317 .255	027 .029 .026 .012 .037 .035 .035 .055 .035 .055 .055	.577 .671 .527 .478 .827 .521 .533 .532 .828 .320 .301	.043 .046 .048 .023 .060 .048 .046 .038 .030 .034 .035	.122 .125 .101 .125 .125 .125 .125 .125 .125 n.s.	.172 .167 .158 n.s. .167 .167 .167 n.s.	n.s. .176 n.s. .176 .176 .176 .176

Table A1. Stomatal conductance  $(g_s)(cm s^{-1})$  of leaves of different physiological ages on terminal and lateral shoots on "Montmorency" sour cherry, East Lansing, 1983.

<sup>1</sup>Physiological age groups: "A", and "B" (same leaf monitered throughout season) are 3-5 nodes from base and 12-15 days unfolded (90° angle between blade halves), and 5-7 nodes from base and 0-3 days unfolded, respectively; Group "C" (leaf most recently unfolded on day of experiment - nodes 5-19; after terminal bud set, same leaf monitered throughout season).
Day	"A"	\"l	"B"		"C"		MEAN			LSD	
of Date Year 1983	X	S.E.	X	S.E.	X	S.E.	x	S.E.	5%	1%	0.1%
164 6/13 167 6/16 171 6/20 175 6/24 180 6/29 187 7/06 195 7/14 202 7/21 224 8/12 236 8/24 272 9/29	24.35 24.93 20.31 16.22 18.59 13.66 13.07 16.12 10.00 5.69	1.77 2.19 2.02 0.83 0.98 0.71 0.97 1.32 0.50 0.38 0.16	18.84 21.07 19.38 19.27 22.12 16.99 18.52 22.59 11.15 7.25 4.25	1.21 1.64 2.92 1.02 0.96 1.06 1.87 2.89 0.78 1.09 0.52	15.45 14.71 15.67 13.32 7.50 14.63 19.47 10.17 6.55 2.24	1.04 2.14 0.99 0.76 0.27 1.74 1.35 0.58 0.96 0.20	21.59 20.48 18.03 17.05 18.01 12.72 15.41 19.39 10.44 6.50	1.26 1.24 1.49 0.62 0.90 0.92 0.99 1.23 0.36 0.49 0.22	3.26 3.06 3.80 3.06 3.06 3.06 3.06 3.06 n.s. n.s.	4.68 4.07 n.s. n.s. 4.07 4.07 4.07	n.s. 5.32 5.32 5.32 5.32 5.32

Table A2. Transpiration  $(TR)(\mu g \text{ cm}^{-2} \text{ s}^{-1})$  rates of leaves of different physiological ages on teminal and lateral shoots on "Montmorency" sour cherry, East Lansing, 1983.

<sup>1</sup> Physiological age groups: "A", and "B" (same leaf monitered throughout season) are 3-5 nodes from base and 12-15 days unfolded (90° angle between blade halves), and 5-7 nodes from base and 0-3 days unfolded, respectively; Group "C" (leaf most recently unfolded on day of experiment - nodes 5-19; after terminal bud set, same leaf monitered throughout season).

APPENDIX B

Table B1. Leaf area (LA,  $cm^2$ ), stomatal conductance ( $g_s$ ,  $cm s^{-1}$ ) and transpiration (TR,  $\mu g cm^{-2} s^{-1}$ ) for all leaves on 'Montmorency' sour cherry shoots a) prior to terminal leaf expansion (7/6/83), and b) after full leaf and shoot expansion (8/4/83).

	loaf		Shoot	1	S	Shoot 2			Shoot 3	
	No.	LA	9s	TR	LA		TR	LA	<u>9</u> s	TR
A)	DATE	: July	6, 19	33	17 67		10.00	16 51	050	6 01
	1	9.02	.4/6	13.12	1/.5/	.442	12.66	16.51	•258	6.8L
	2	22.30	.493	12.00	26.22	.000 276	14.20	25.40	•300 604	10.92
		20.00	· 495	10.75	20.23	.370	13 68	35.49	-054 813	18.89
	5	38.04	.285	8.12	29.35	.505	12.57	45.15	.847	19.88
	6	38.51	.578	14.49	33.45	.685	18.18	43.06	.935	19.63
	7	33.92	.565	15.49	30.41	.614	16.62	42.40	1.087	22.50
	8	31.06	.671	16.49	32.04		2.08	43.70	1.010	18.40
	9	28.55	.625	14.99	32.25	.360	10.84	44.23	.980	20.34
	10	26.70	.633	15.99	20.47	.379	11.35	36.45	1.149	22.08
	11	24.11	.532	13.99	23.15	<b>.</b> 483	13.85	32.10	1.299	22.57
	12	24.60	.397	9.95	21.48	.356	9.96	28.21	.870	18.98
	13	27.73	.467	12.84	22.19	.317	9.22	32.88	.552	12.32
	14	26.29	.274	7.99	26.49	.141	4.57	28.72	.524	12.15
	15	2/.24	.300	10.16	19.35	.159	4./1	31.43	-385	10.10
	10	చ.రు నిర	.1/4	5.42	14.40	.1.34	4.54	22.10	.100	4.34
	10	دد ہے۔ مح	•120	4.00	8.45	•050	1./8	10 10	-103 121	4.4/
	مر 10	0.72	.0/9	2.42				11 22	.1.51	2 24
									.0/5	C•C7
2)	DATE:	August	: 4, 19	83						
	1		.252	4.18	22.20	.862	11.49	13.92	.800	16.36
	2	25.05	.500	7.44	29.29	1.177	15.42	8.03	1.639	26.78
	3	28.49	.535	/.90	28.65	.813	13.07	36.87	2.222	31.12
	4	3/.61	.524	/.66	30.38	1.190	18.78	30.18	1.88/	24.21
	5	41.03	.595	8.05	32.09	1.3/0	20.14	49.08	2.381	20.13
	07	3/.58	-003 400	8.91 7.06	28.88	1.351	20.00	48.0/	2.110	27.51
	0	20.90	•490 205	1.00	30.21 22 12	1 471	21 72	41.51	2.110	29.00
	o Q	20.40	•295 0/3	<b>4.40</b> 12 <b>27</b>	21 50	1 163	18 04	49.00	2 041	27 79
	10	25 13	. <del></del>	10.81	26.28	1.103	16.63	37 90	2.632	26.50
	11	27.36	.870	11.90	29.36	1.539	22.87	33.29	3.226	26.71
	12	31.46	.952	12.56	26.09	1.471	22.48	29.39	2.128	23.18
	13	24.82	.971	12.40	28.17	1.299	20.45	32.22	3.448	25.64
	14	30.03	1.515	16.65	26.16	1.250	21.76	29.01	2.564	24.06
	15	27.24	1.471	15.95	29.75	1.205	22.02	33.46	2.041	21.14
	16	30.52	1.219	14.26	29.97	1.053	21.53	25.95	1.190	14.18
	17	33.15	1.539	17.84	25.57	.758	17.36	39.75	1.923	19.01
	18	28.79	.402	6.37				41.80	.980	12.99
	19							43.33	1.235	14.46
	20							19.89	.358	6.12

T	Leef		Shoot	1	· · ·	Shoot	2
No.	No.	LA	g <sub>s</sub>	TR	LA	gs	TR
1	1 2 3 4 5 6 7 8	7.75 13.47 15.25 20.16 17.89 21.57 19.94 10.50	.81 .99 1.01 .99 .83 .68 .68 .48	11.13 13.57 13.24 13.35 12.51 10.63 10.13 7.96	6.92 10.50 11.57 14.76 15.41 14.78 16.13	.43 .71 .48 .72 .75 .45 .25	7.13 11.59 7.82 11.59 11.99 7.75 4.30
2	1 2 3 4 5 6 7 8 9	7.56 18.62 11.42 19.15 18.65 14.32 13.89 14.70	.65 .69 .28 .91 .74 .50 .35	10.64 11.55 4.90 14.70 12.30 13.88 8.62 6.20	8.51 12.32 17.56 21.29 20.75 22.66 22.67 18.33 10.92	.36 .39 .59 .68 .50 .50 .38 .31	6.38 6.79 9.68 9.66 11.45 9.60 8.76 6.56 5.81
3	1 2 3 4 5 6 7 8 9	17.64 30.94 34.65 38.96 41.96 39.27 43.90 23.94 10.25	.59 .63 .59 .94 .75 .47	10.11 11.21 10.25 15.03 13.89 14.29 11.92 7.93	21.00 26.80 35.35 33.81 39.69 32.57 22.05 10.58	1.11 .94 1.19 1.24 .94 .65 .38 .23	17.87 15.40 18.31 18.92 15.26 11.26 7.02 4.24
4	1 2 3 4 5 6 7 8 9	9.25 14.62 19.11 20.75 26.19 16.60 16.13	.36 .56 .54 .54 .58 .48 .48 .32	6.56 9.81 7.98 9.47 9.86 8.22 4.41 5.75	12.47 13.57 24.08 27.09 28.34 26.73 25.87 17.85 8.37	.52 .47 .58 .78 .65 .48 .28 .25	9.07 7.93 10.21 12.95 13.35 11.18 8.61 5.18 4.68

Table B2. Leaf area (LA)( $cm^2$ ), stomatal conductance ( $g_s$ )( $cm s^{-1}$ ) and transpiration for each leaf of an expanding shoot on June 12, 1984.

Table B3. Leaf area (LA)  $(cm^2)$ , stomatal conductance  $(g_s)$   $(cm s^{-1})$ , and transpiration (TR) ( $\mu g \ cm^{-2} \ s^{-1}$ ) for each leaf of fully expanded shoots, 'Montmorency' (Day 201, 7/19/84).

	Trac	5	Shoot	1	S	hoot	2	Troo	S	ihoot	1	S	shoot	2
No.	No.	LA	9 <sub>S</sub>	TR	LA	9s	TR	No.	LA	9s	TR	LA	9s	TR
1 2 3 4 5 6 7 8 9 10 11 23 14 15	1	8.73 13.97 16.91 21.55 21.28 27.41 28.67 22.02 26.79 27.72 24.92 28.98 23.75 18.71 18.02	.42 .49 .44 .57 .57 .57 .57 .57 .57 .57 .57 .57 .57	7.68 8.17 8.01 7.50 10.47 9.30 8.87 9.19 8.66 8.35 8.04 7.43 8.25 7.73 6.14	10.71 11.98 15.94 16.13 17.14 19.64 16.40 17.85 17.37 22.88 16.35	.23 .29 .40 .53 .45 .46 .58 .42 .54	7.34 5.29 7.09 8.97 7.43 8.14 9.83 8.24 11.23 7.61 9.62	3	18.37 30.70 34.65 38.96 42.71 43.37 51.24 31.75 26.60 36.19 32.90 34.27 30.59 27.64 28.52	.70 .14 .15 .18 .17 .30 .31 .33 .47 .41 .47 .48 .37 .41 .47	1.31 2.58 2.74 3.35 2.94 5.13 5.32 5.89 7.89 6.65 7.86 7.58 6.03 7.27 8.00	5.78 27.41 34.64 35.53 38.22 38.50 42.69 35.74 26.88 25.59 28.34 32.20 33.94 31.50	- &	4.29 10.23 8.10 10.68 8.27 7.32 10.22 9.20 9.42 8.41 8.41 9.76 9.09 9.20
1 2 3 4 5 6 7 8 9 10 11 12 13 14	2	8.68 19.11 11.78 20.48 19.95 15.93 16.66 20.72 9.63 10.01 14.11	.36 .16 .36 .46 .41 .50 .49 .49 .45 .51	6.50 3.03 6.38 8.02 6.80 8.87 7.04 8.66 8.02 8.05 8.98	9.14 12.71 18.09 21.84 22.11 24.40 24.69 22.02 18.09 17.89 14.96 16.17	.16 .12 .21 .27 .27 .31 .22 .30 .30 .32 .30 .32 .33 .28 .40	3.01 2.09 3.76 4.79 3.99 5.64 3.93 5.67 5.70 5.19 7.18	4	9.45 19.60 14.46 21.28 27.41 17.40 26.18 22.93 12.54 14.70	.09 .25 .15 .13 .23 .18 -23 .27	1.60 4.49 2.73 2.27 3.95 3.09 4.29 3.77 5.49 4.54	12.85 14.46 23.78 28.03 29.93 30.45 33.25 27.69 23.52 22.93 23.53 29.30 18.91 14.97	.16 .20 .15 .32 .32 .37 .4 .4 .5 .28 .33 .33 .4 .5 .28 .33 .33 .33 .33 .33 .33 .33 .33 .33 .3	2.76 3.35 2.47 5.36 4.71 5.26 3.91 6.38 5.99 7.54 6.36 4.78 5.55 5.86

APPENDIX C

Table (1. Stomatal conductance (cm s<sup>-1</sup>) of terminal, lateral and spur leaves of a similiar physiological age (3-5 nodes from base, 12-15 days unfolded on day 164, 6/13/83, age group "A") in 'Montmorency' sour cherry.

Day of Year	Date 1983	Terminal	Lateral	Spur	5% LSD
164	6/13	0.655	0.689	0.419	0.195
167	6/16	0.930	0.810	0.638	n.s.
171	6/20	0.655	0.537		*
175	6/24	0.493	0.429	0.341	n.s.
180	6/29	0.889	0.841	0.612	n.s.
187	7/06	0.569	0.536	0.544	n.s.
195	7/14	0.459	0.413	0.375	n.s.
202	7/21	0.403	0.429	0.351	n.s.
224	8/12	0.810	0.800	0.701	n.s.
236	8/24	0.294	0.265	0.287	n.s.
272	9/29	0.327	0.270	0.301	0.016

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Table C2. Transpiration ( $\mu$ g cm<sup>-2</sup> s<sup>-1</sup>) of terminal, lateral and spur leaves of a similiar physiological age (3-5 nodes from base, 12-15 days unfolded on day 164, 6/13/83, leaf age group "A") in 'Montmorency' sour cherry.

Day of Date Year 1983	Terminal	Lateral	Spur	5% LSD
164 6/13	24.01	24.68	16.38	5.70
167 6/16	26.24	23.62	19.32	n.s.
171 6/20	22.02	18.59		*
175 6/24	17.36	15.08	11.70	n.s.
180 6/29	18.72	18.46	14.26	n.s.
187 7/06	14.21	13.10	13.13	n.s.
195 7/14	13.67	12.47	11.37	n.s.
202 7/21	15.68	16.56	12.99	n.s.
224 8/12	10.14	9.87	8.85	n.s.
236 8/24	5.92	5.46	6.21	n.s.
272 9/29	4.13	3.69	3.83	0.27

APPENDIX D

			Shoots				Spu				
Day			F		N		F		N	LSD	, 5%
Year	Date	9 <sub>S</sub>	TR	9s	TR	9s	TR	9s	TR	9s	TR
105	6/14	.67	19.33	.81	22.97	.37	11.30	.50	15.33	0.14	3.85
172	6/21	.43	16.43	.64	23.60	.33	11.79	.37	15.02	0.11	3.86
179	6/28	.64	3.31	.79	2.30	.40	3.84	.45	2.44	0.07	0.40
186	7/05	.80	10.74	.89	11.86	.57	8.29	.70	9.50	0.12	1.43
193	7/12	.47	15.61	.53	18.16	.30	10.69	.33	11.78	0.14	4.31
201	7/20	.65	17.83	.73	20.77	.40	11.96	.43	13.64	0.18	5.14
220	8/08	.38	8.13	.35	7.40	.25	5.25	.29	6.18	0.08	1.67
235	8/23	.50	5.96	.53	6.84	.33	4.30	.40	4.89	0.09	1.12
	Mean	57	12,17	- 66	14.24	. 37	8.43	.43	9.85		
	Mean <sup>1</sup>	.56	13.43	.64	15.94	.36	9.08	.43	10.91	0.09	2.24

Table D1. Stomatal conductance  $(g_s)(s \text{ cm}^{-1})$  and transpiration  $(TR)(\mu g \text{ cm}^{-2} \text{ s}^{-1})$  values for fruited (F) and non-fruited (NF) "Montmorency" sour cherry shoots and spurs in 1983.

<sup>1</sup>Excludes day 179 due to imbalance of experimental units (4 trees, rather than 5 were used).

 $g_{s}$ : LSD,5% (vertical, excluding day 179) = 0.12.

TR: LSD, 5% (vertical, excluding day 179) = 3.03.

APPENDIX E

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Tree to tree variability.

Tree to tree variability was not included as a part in the above study. However, it is of interest for sampling procedures in future studies. Therefore, the stomatal conductance and transpiration data from the diurnal study was separated by tree and time of day, and is listed in Table E1. Tree to tree variability may occur due to differences in time of measurement (sequential rather than simultaneous measurements), soil factors (such as moisture availability, nutrients, etc.), tree size, disease or some other factor.

Table E1. Diurnal  $g_s$  (cm s<sup>-1</sup>) values by tree on day 207 (7/26/83). Two leaves, 5 to 8 nodes from shoot base, per quadrant on both terminal and lateral shoots, were averaged.

<u></u>		Tree		
Time	<u> </u>	II	III	Mean
8:00 10:00 12:00 14:00 16:00	.531 1.200 1.002 .877 .737	.495 .517 .292 .198 .205	.529 .717 .447 .335 .301	.518 .811 .580 .470 .414

APPENDIX F

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## APPENDIX F

Inside oscillatory behavior.

As noted in the literature review, oscillatory behavior of the stomata has been often documented. Since potted trees are often taken into the laboratory for photosynthesis, transpiration or stomatal conductance measurements on a gas exchange system, it was of interest to also observe any short-term oscillatory behavior inside the laboratory. As a preliminary to possible further documentation (day 210, or 7-29-83, 15:15-16:00), a potted sour cherry tree was taken into the lab one hour before being placed beneath a high intensity discharge (HID) lamp at 2000  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>. Measurements were begun 5 minutes later (15:15).

Oscillations of 20 minutes between troughs were evident for both  $g_s$  and TR, respectively (Figure F1). Temperature remained between 30-32°C, and relative humidity was about 42.7-43.1%.

How the movement of the plant indoors, and the prolonged presence of the porometer affected the results is not known. Figure F1. Timecourse of stomatal conductance and transpiration on leaf of potted tree. Measurements taken with leaf porometer inside the laboratory.



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