

Some Environmental Effects on Photosynthesis and Water Relations of Avocado Leaves

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SUMMARY

Photosynthesis and leaf conductances of avocado leaves (*Persea americana* Mill. cv. Fuerte) were determined in the laboratory over a range of photon flux density (pfd) and temperature. Maximum rates of photosynthesis of $0.30 \text{ mg m}^{-2}\text{s}^{-1}$ were measured with saturation at c. $500 \mu\text{E m}^{-2}\text{s}^{-1}$ (25 percent of full sunlight) and a temperature optimum of 28°C . The relatively low rates of photosynthesis at which saturation occurs indicate that avocado foliage exhibits characteristics of a shade plant.

Measurements in the field gave similar results. Some leaves inside the canopy were photosynthesising at rates of up to $0.10 \text{ mg m}^{-2}\text{s}^{-1}$ at $60 \mu\text{E m}^{-2}\text{s}^{-1}$.

Xylem pressure potential and leaf diffusive conductances were determined on leaves of a field-grown Fuerte avocado tree from before sunrise to after sunset on a hot summer day (maximum pfd normal to leaf $1500 \mu\text{E m}^{-2}\text{s}^{-1}$, air temperature 35°C). Rapid stomatal opening at sunrise gave maximum values for leaf conductance (0.4 cm s^{-1}) by 0700 hours and these slowly decreased as the vapour pressure difference from leaf to air increased, until stomatal closure at sunset. Xylem pressure potential fell to a minimum of -1300 kPa several hours after the maximum of leaf conductance and remained at this level until late afternoon when it increased until almost full recovery (-300 kPa) was attained after sunset.

The importance of these findings to avocado production is discussed.

INTRODUCTION

The avocado (*Persea americana* Mill.) is a horticultural crop that has expanded in area worldwide in the last decade (9).

In Israel, California, and Australia, part of this expansion has been into areas with

different climatic and soil conditions compared to the crop's origin in the central Americas (16). Environmental factors which offer a particular contrast with present areas of cultivation include lower rainfall and humidity, high insolation, occasional frosts, and saline irrigation water. Physiological responses and adaptation to such factors are therefore of relevance to avocado tree performance under irrigation in semi-arid environments.

Field studies on the effects of irradiance and humidity on leaf transpiration and xylem pressure potential of avocados have been reported for well watered and stressed trees (19). Leaf conductances decreased as the absolute humidity difference from leaf to air increased and leaf conductances were higher under higher irradiance. The same authors (20) showed differences in leaf conductance, transpiration, and xylem pressure potential between healthy trees and those infected with *Phytophthora cinnamomi* root rot. Of particular interest to the present study were their results on the diurnal fluctuations in leaf conductance and xylem pressure potential.

Bower, Wolstenholme, and de Jager (5) enclosed whole potted avocado trees in a chamber and determined photosynthetic rates, internal water status, and stomatal conductance under varying irradiance and temperature. They concluded that the optimum conditions for photosynthesis were a leaf temperature of 20-24°C with an irradiance of approximately 300 Wm⁻². Water stress affected photosynthesis via its effect on stomatal conductance. The more recent laboratory study of the gas exchange properties of avocado leaves (12) came to similar conclusions.

The aim of the work reported here was to study the diurnal patterns of stomatal conductance and xylem pressure potential on a hot day in the field, and to determine the photosynthetic response of avocado leaves to the varying environmental conditions, photon flux density, and temperature to assess whether these responses would be likely to affect the productivity of avocado orchards in semi-arid areas.

MATERIALS and METHODS

Plant Material

The scion cultivar Fuerte was used in both the laboratory and the field, grafted onto Mexican seedling rootstocks. Laboratory studies used trees growing in 8 l pots in a glasshouse. Potted trees were in their second growing season and the field tree in its tenth season.

Field observations were made on recently irrigated trees growing in an irrigated orchard in the Murray Valley at Merbein, Victoria (Latitude 34°S). The climate of this area is semi-arid with mean annual precipitation of 275 mm, daily monthly temperature maxima of 31.8°C in January and 15.5°C in July, and daily monthly temperature minima of 16.8°C in February and 4.4°C in July.

Field Observations

Four mature, fully expanded leaves were selected at each of three levels (1-2 m, 2-3 m, 3-4 m above ground) on the tree's northern face. The following data were recorded at hourly intervals from sunrise on a day in early summer:

- (i) leaf diffusive conductance (k_s) of the marked leaves using a Lambda diffusion porometer,
- (ii) xylem pressure potential (ψ) of a similar nearby leaf using a pressure chamber (17),
- (iii) photon flux density in the plane of the leaf using a Lambda quantum sensor (400-700 nm),
- (iv) temperature of leaf, air and windspeed.

Observations began at 0600 hours (sunrise at 0700) and continued until sunset at 2000 hours. Temperature range during the day was 23.6°C to 35.5°C. The vapour pressure difference between the leaf and air (vpd) ranged from 1-7 kPa and the winds were gusty from a NE to NW direction up to a maximum velocity of 8.5 m s⁻¹. Maximum pfd normal to the leaf was 1500 $\mu\text{Em}^{-2}\text{s}^{-1}$ measured at solar noon.

Trees were well watered with 11 percent soil water content at 0.15 m depth and 16 percent at 0.45 m depth.

The field observations of photosynthesis were based on measurements made in late winter on an 11.3 cm² area of mature terminal leaves enclosed in a simple ventilated perspex chamber with the upper leaf surface exposed to the air. No control of leaf temperature was possible but leaf temperature was monitored with a thermocouple junction in contact with the lower surface of the leaf. An air stream was passed over the lower surface of the leaf and into a Hartmann and Braun infra red gas analyser in a mobile laboratory. The leaf was held incident to the solar radiation which was measured with a quantum sensor and the pfd was varied by holding screens approximately 15 cm above the leaf surface to obtain a photosynthetic response to varying pfd. Average leaf temperature was 16.2°C. Complete sets of photosynthesis measurements at varying pfd were obtained with two leaves. The net photosynthesis rates of a total of 17 leaves were determined inside the canopy of the tree where the pfd values were very low (60 $\mu\text{Em}^{-2}\text{s}^{-1}$), and the leaves were generally larger and with thinner laminae than the leaves fully exposed to the sun.

Laboratory Observations

Leaf gas exchange rates were monitored in a temperature controlled leaf cuvette that could enclose whole leaves up to 90 cm² in area. A gas stream of known CO₂ and water vapour content was passed into the cuvette and through H₂O- and CO₂- infra red gas analysers (Hartmann and Braun, Uras II). The leaf was illuminated with a low voltage quartz halide light and calibrated with a Lambda quantum sensor (400-700 nm) to provide a range in pfd from 0 to 1000 $\mu\text{Em}^{-2}\text{s}^{-1}$.

Photosynthesis/light response curves were derived for single leaves from four separate

potted Fuerte avocado trees using recently expanded leaves. Leaf temperature was maintained at 28°C. Net photosynthetic rate, stomatal conductance (k_s), and residual conductance (k_r) were derived from water vapour and CO₂ fluxes in normal and low oxygen (2 percent) gas streams. Light response curves were drawn from data points that were based on the mean of between 3 and 8 individual observations.

Photosynthetic response to leaf temperature between 15°C and 40°C was measured under saturating pfd ($850 \mu\text{Em}^{-2}\text{s}^{-1}$) in a 20 percent oxygen gas stream on mature fully expanded leaves. Rates have been averaged within each division of 4°C to accommodate slight differences in temperature between replicates.

RESULTS

Plant and Environmental Conditions

Field fluctuations in temperature, photon flux density, and vapour pressure difference between leaf and air, and the plant parameters xylem pressure potential and leaf conductance are presented in Figure 1. No systematic differences between levels within the tree were apparent, so data were pooled for presentation on a whole-tree basis.

The air temperature (Fig. 1a) increased rapidly from a minimum of 23.6°C at 0600 to 35°C at 1200 and was maintained at about this level until 1800 hours. A rapid decline occurred following sunset. Leaf temperature was generally several degrees above ambient (max. differential + 3°C) especially when leaves were exposed to direct sunlight.

Photon flux density normal to the observed leaves (Fig. 1b) attained a maximum of $1500 \mu\text{Em}^{-2}\text{s}^{-1}$ at 1200 hours with some fluctuations in the early afternoon, due to changed solar elevation and a slight build up of clouds.

Vapour pressure difference (Fig. 1a) between leaf and air peaked at 1200 hours corresponding with maxima in air temperature and pfd. The afternoon decline in vpd, despite steady air temperature, was attributed to reduced leaf temperature following lower solar elevation.

Stomata opened rapidly after sunrise when pfd normal to the leaf (Fig. 1b) was still relatively low ($100 \mu\text{Em}^{-2}\text{s}^{-1}$). Leaf conductance (Fig. 1c) was maximum at 0700 hours and decreased thereafter with a slight rise between 1300 and 1400 hours (possibly caused by the fall in vpd as discussed above). Conductance continued to fall until sunset. Although leaf conductance decreased from c. 0.4 to 0.1 cm s^{-1} between 0700 and 1800 hours, gaseous exchange continued.

Xylem pressure potential (Fig. 1d) decreased from -200 kPa before sunrise to -1300 kPa (-13 bar) by 0900 and was maintained at about this level until 1600 hours. Night time stomatal closure and a reduction in vpd allowed almost full recovery to pre-sunrise values by 2000 hours. Such recovery provides clear evidence that the trees were adequately supplied with water,

Photosynthesis

Photosynthetic response to pfd in the field is presented in Figure 2a. Photosynthesis was saturated at $500 \mu\text{Em}^{-2}\text{s}^{-1}$ and achieved a maximum rate of 0.11 to $0.12 \text{ mg CO}_2 \text{ m}^{-2}\text{s}^{-1}$. This relatively low value (c.f. laboratory data) has been attributed to sub-optimal leaf temperatures. The photosynthetic rates of leaves inside the canopy (Fig. 2b) were remarkably high (up to $0.10 \text{ mg m}^{-2}\text{s}^{-1}$) despite low photon flux density.

Saturating pfd for avocado leaves during laboratory measurements (Fig. 3a) was between 400 and $500 \mu\text{Em}^{-2}\text{s}^{-1}$ giving a maximum rate of $0.31 \text{ mg m}^{-2}\text{s}^{-1}$. Light compensation point was $63 \mu\text{Em}^{-2}\text{s}^{-1}$. Given the clear distinction between k_s and k_r in their light response characteristics (Fig. 3a), photosynthesis at sub-saturating pfd (300 - $800 \mu\text{Em}^{-2}\text{s}^{-1}$) is more likely limited by internal than by stomatal processes.

Photosynthesis showed a clear temperature optimum just below 30°C (Fig. 3b), although rates were sustained at about one-third of full capacity ($0.28 \text{ mg m}^{-2}\text{s}^{-1}$) beyond the temperature extremes measured (15 and 40°C).

DISCUSSION

The results presented here have shown that no serious physiological stress was experienced by the leaves of an avocado tree throughout a hot day in the field. However under particularly adverse environmental conditions (air temperature in excess of 40°C), or when soil moisture is limiting, low levels of xylem water potential may cause a reduction in leaf conductance for both CO_2 and water vapour, with serious effects on photosynthesis. A practical example was reported by Allan and de Jager (1) who observed that photosynthesis of macadamia leaves was zero at 40°C , and devised an intermittent sprinkler system to reduce air temperatures and hence physiological stress in an orchard where many days; in excess of 40°C were experienced.

Diurnal variations in xylem pressure potential and stomatal conductance did not show any midday stomatal closure as was reported for other woody plants (13). The conditions of high humidity and moderate temperatures in the greenhouse used by Bower (4) induced rapid stomatal opening in the early morning, but a slower decrease in ψ to a minimum of only -300 kPa by mid-afternoon compared with the minimum value for ψ of -1300 kPa that was maintained from 0900 to 1600 hours in our field study. Also under field conditions, a minimum xylem pressure potential of -1200 kPa was reported (20) but only for a short period at midday, with relatively high stomatal conductances for most of the day. This difference could have been caused by hotter and drier conditions at Merbein on the day of measurement. Diurnal patterns in ψ similar to those reported here have been seen with pear, grape (13), and apple (8).

The maximum rate of photosynthesis measured ($0.30 \text{ mg m}^{-2}\text{s}^{-1}$) at the saturating photon flux density of between 400 and $500 \mu\text{Em}^{-2}\text{s}^{-1}$ (20-25 percent of full sunlight) is similar to the findings of Bower (4) and Kimelmann (12). By comparison, the other subtropical fruit species guava (21) and citrus (14) saturate photosynthesis at pfd values much higher than the avocado.

Although photosynthesis is of prime importance in supplying carbohydrates for all plant functions, light is also essential for floral initiation in many woody species (10), and

higher levels of light may be needed for this process than have been shown to be necessary for maximum levels of photosynthesis.

Temperature optimum for photosynthesis of c. 28°C was determined with a low vapour pressure difference between leaf and air. Greater values of vpd may reduce the temperature optimum as has been reported for citrus (14), (11).

At temperatures above 30°C, enhancement of photosynthesis of 50 percent or more was obtained in a 2 percent-O₂ air stream indicating substantial photorespiration at these temperatures in normal air.

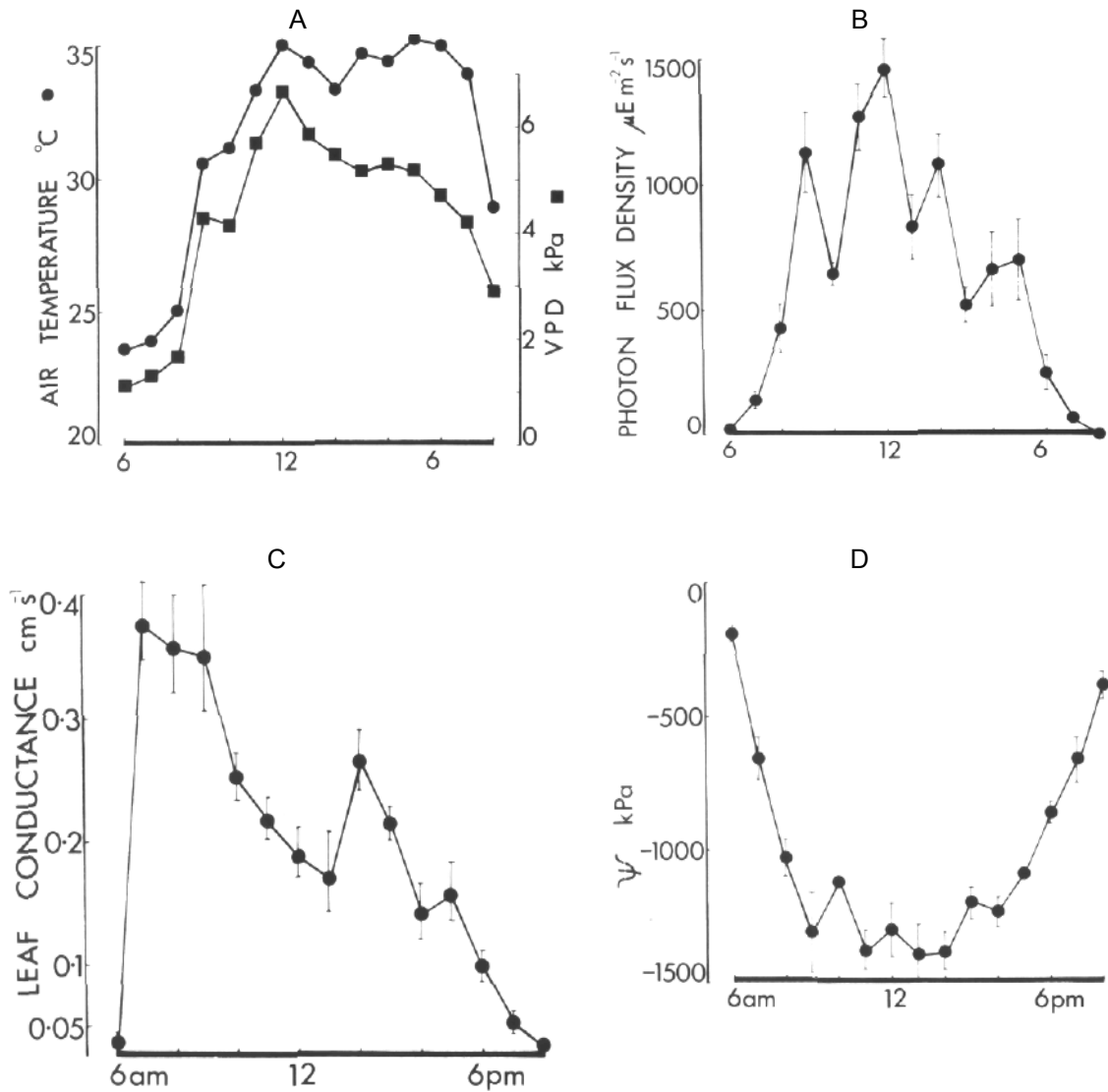
The low maximum photosynthetic rate, low light compensation point, and relatively high photosynthesis at low levels of pfd are properties that are exhibited by leaves of plants classified as "shade plants" (3).

Further support for the avocado belonging in this group of plants is found in the structure of the avocado chloroplast (6) which contained many lamellae in the grana and bears some resemblance to the rainforest species *Alocasia macrorrhiza* (7). Such structure can help explain the photosynthetic behaviour observed for avocado leaves at low pfd (Fig. 2b).

The canopy of a tree is a complex arrangement of leaves exposed at different angles to the sunlight with varying degrees of shading by other leaves. At any moment, the photosynthesis of some leaves would be saturated with respect to pfd, while others would be photosynthesising well below their maximum level. Even in full sunlight at noon, it is doubtful if a canopy would receive sufficient pfd for photosynthesis of all leaves to be saturated. The fact that the avocado had a low pfd for saturation of photosynthesis ensures that the tree produces proportionally more of its potential yield of photosynthate than would a similarly shaped tree whose leaves saturated at a higher pfd.

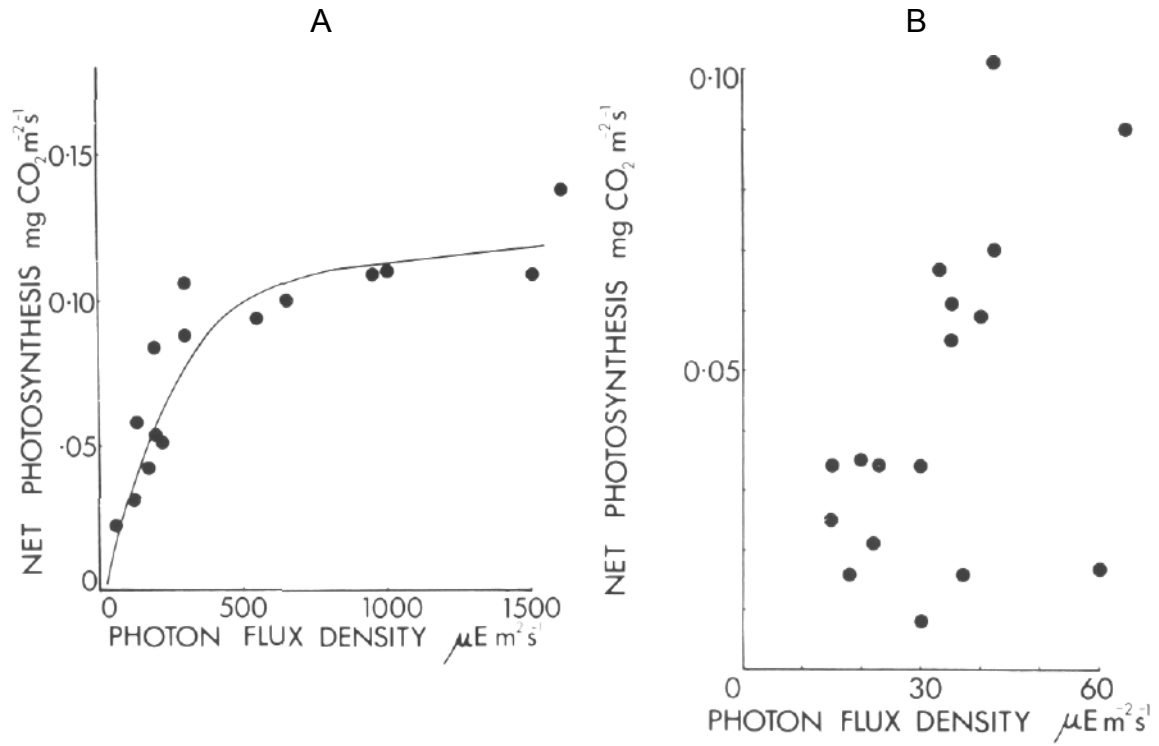
The maximum rate of photosynthesis for avocado leaves reported here (0.30 mg m⁻²s⁻¹) is low when compared with those reported for the perennial horticultural crops grapevine (0.56 mg m⁻²s⁻¹ (15)), peach (0.74 mg m⁻²s⁻¹ (18)), and apple (0.97 mg m⁻²s⁻¹ (2)). However these species are all deciduous, and by comparison with evergreen plants, are able to photosynthesise for a 30 percent shorter period of the year. The low rates of photosynthesis of the evergreen tree species avocado, citrus (14), and macadamia (1) may not be a handicap if an annual carbon balance is calculated for the trees.

FIGURE 1



Changes in (a) air temperature ($^{\circ}\text{C}$) and vapour pressure difference (vpd) between leaf and air, (b) photon flux density, (c) leaf conductance (ks) and (d) xylem pressure potential (Ψ), of Fuerte avocado leaves measured at hourly intervals from 0600 to 2000 hours. (Bars represent 2 x SE).

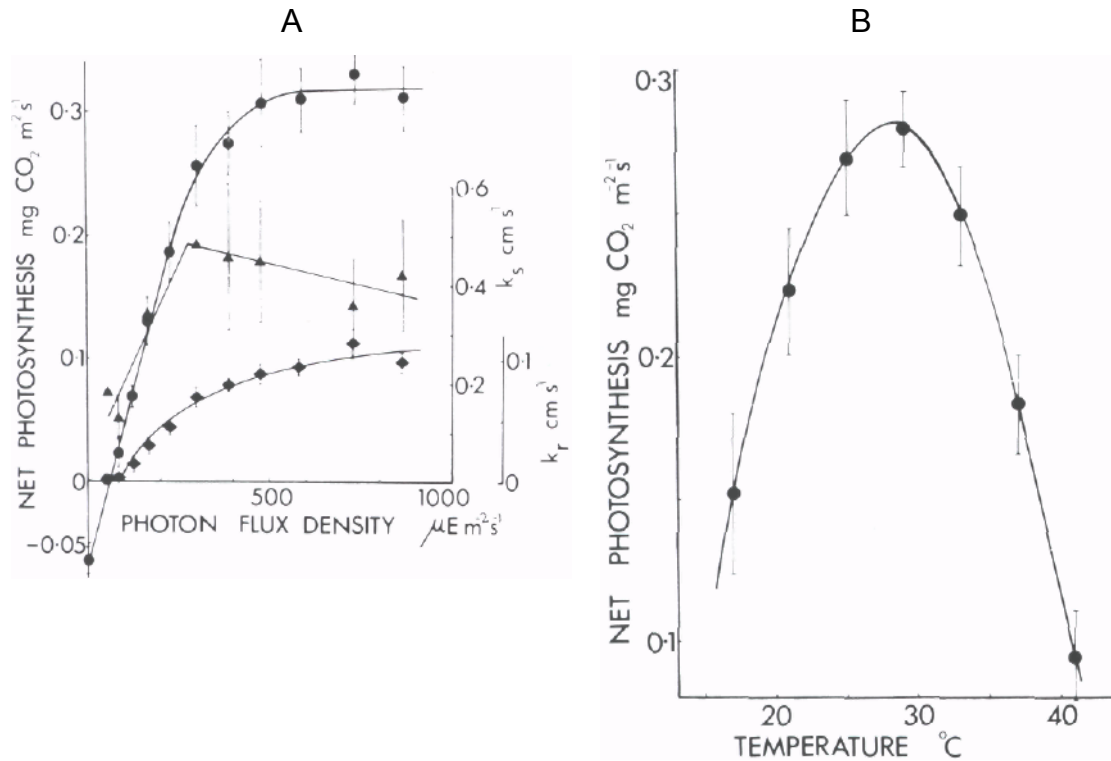
FIGURE 2



(a) Net photosynthesis of Fuerte avocado leaves measured at varying photon flux density.

(b) Net photosynthesis of individual leaves measured within the canopy of a Fuerte avocado tree.

FIGURE 3



(a) Net photosynthesis (\bullet) and stomatal (k_s) (\blacktriangle) and internal conductance (k_r) (\blacklozenge) of Fuerte avocado leaves measured at varying photon flux density. (Note different scale used for k_s and k_r).
 (b) Net photosynthesis of Fuerte avocado leaves at varying leaf temperature. (Bars represent $2 \times \text{SE}$).

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