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INCOMING SOLAR RADIATION AND INTERNAL WATER STATUS AS STRESS FACTORS IN AVOCADO, *PERSEA AMERICANA* (MILL.) CV EDRANOL

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ABSTRACT:

The rate of CO_2 exchange of the avocado, *Persea americana* (Mill.) cv Edranol, was studied under varying conditions of solar radiation flux density and temperature, using the chamber method. Internal water status and stomatal resistance were monitored using a pressure bomb and diffusion porometer. It was found that *Persea americana* is a typical C_3 plant, with maximal CO_2 exchange of 0,40 mg m^{-2} s^{-1} occurring in the temperature range 20-24°C. The point of inflection on the photosynthesis incident radiation response curves was approximately 200 Wm^{-2} for temperatures between 10 and 30°C. Under increasing water stress, stomates closed rapidly at leaf water potentials of less than -900 kPa, corresponding to soil water potentials less than -70 kPa. Leaf temperatures exceeded air temperatures by up to 6°C in stressed plants. The practical significance of the results is discussed from the points of view of high density planting and irrigation scheduling.

INTRODUCTION

The main avocado cultivars grown in South Africa are Fuerte, Edranol and Hass. The experiments reported here were on Edranol, representative of the Guatemalan horticultural race (Bergh, 1975). Guatemalan type avocados are adapted to highland tropical or cool sub-tropical, moist and humid climates (Wolstenholme, 1977), and have the reputation of being particularly sensitive to heat and moisture stress. Apart from the recent report of Sterne, Kaufmann & Zentmyer (1977), very little critical work on photosynthetic and internal water relations of the avocado has been published.

The avocado has been affected by the modern trend towards high density orchards. It is standard practice to double plant in California, removing excess trees when crowding and shading occur (Lee, 1974). Cain (1969) emphasized that production per unit area, and not solely per tree, is the most important criterion for orchard profitability. In widely spaced standard apple orchards, only 40% of the land is effectively utilized in the long term (Cain, 1970). It has even been suggested that solar radiation stress should dictate tree spacing (Fochessati, 1972).

The effect of shading on avocado tree performance is a controversial topic, and in the absence of research guidelines, tree espacement and thinning programmes are largely subjective. The large leaf and very large seed of the Guatemalan type avocado, as well as what is known of its native habitat, are on basic ecophysiological principles (Janzen, 1975; Larcher, 1975) suggestive of evolutionary adaptation to a shaded, humid forest environment. On the other hand, the leathery nature of the mature leaf is indicative of at least fair tolerance of drought (from a survival point of view).

In respect of water relations, the avocado grower is faced with a dilemma. He must compromise between the limited root system and the high water requirements of the tree (Bredell, 1971), and the high oxygen requirements of the roots (Curtis, 1949) and their intolerance of poor drainage, especially in the presence of the soil fungus *Phytophthora cinnamomi* (Wager, 1942; Zentmyer, Paulus, Gustafson, Wallace & Burns, 1965).

Hsiao (1973) concluded that moisture stress in plants is indicated by internal water potential. There is a threshold potential, apparently fairly species specific (Meidner & Mainsfield, 1968), in excess of which stomates close rapidly, with adverse effects on CO_2 uptake and photosynthesis.

This research was conducted to give a better ecophysiological understanding of the avocado's response to radiation, temperature and internal moisture stress, aspects that have important field applications.

PROCEDURE

The experiments were conducted on two-year old grafted trees (cv Edranol) growing in a soil-based nursery mix in 18ß black polyethylene nursery bags.

Net CO_2 exchange

Net CO_2 exchange under varying conditions of incoming solar radiation, temperature and plant water stress were measured by the chamber methods similar to that of Baker & Musgrave (1964). The perspex chamber measured 600 x 600 x 960 mm, with the top surface covered by clear "Uvidek 602" polyethylene sheeting. The temperature within the chamber was controlled by an air-conditioner.

Net photosynthesis was monitored by a Beckman infrared gas analyser, (model 215A), using a null point technique. Air was passed through calcium chloride to remove water vapour. Ambient air was passed through the reference cell of the gas analyser (for CO_2 comparisons). The chamber was connected to the other cell by plastic tubing. To eliminate pressure differences between the cells, the system was initially run with the chamber empty so as to set the gas analyser at zero.

When the CO_2 concentration in the chamber equalled that of ambient air, deflection of the scale on the gas analyser was zero. Pure CO_2 was then introduced into the system for 120 s, through a previously calibraed flow meter (Rotameter). The total amount of CO_2 added as adjusted according to room temperature and pressure. The time taken for one cycle from zero reading to zero, with trees in the chamber, was noted. The total adazial surface leaf area of the trees was determined with a Lambda LI 3000 electronic area meter. Net CO_2 in mg m^{-2} s^{-1} could then be computed. A correction factor for leakage of CO2 to the outside atmosphere (from the sealed system with empty chamber) was applied.

To eliminate the considerable CO_2 release from root respiration (Milthorpe & Moorby, 1974) each pot was placed in a large plastic bag and sealed around the stem with masking tape. Three trees were placed in the chamber with the foliage simulating a natural canopy as far as possible.

Incoming radiant flux density (r.f.d.) was measured within the chamber, above the canopy, with a Lambda radiometer (model LI 185). "Saran" shade cloth was used to control incoming radiant flux density when necessary. Leaf and air temperatures were measured using thermocouples, a direct read-out being obtained with a Bailey amplifying thermocouple (model BAT 4). A wet and dry bulb thermometer monitored relative humidity in the chamber, and air movement was measured with an anemometer.

Plant water stress

The effect of a drying cycle on CO_2 exchange, stomatal aperture and internal water potential was studied. In the case of net CO_2 exchange determination during water stress conditions, all measurements were made at a r.f.d. of approximately 400 Wm^{-2}, and a chamber temperature of 20°C to 24°C. Leaf water potential ($\psi\ell$), soil moisture status and the corresponding stomatal resistance to water vapour diffusion were measured using the same plants, outside the chamber.

Stomatal resistance to water vapour transfer was measured with a Lambda diffusion porometer (model LI 60), of the type designed by van Bavel, Nakayama & Ehrler (1965) and modified by Kanemasu, Thurtell & Tanner (1969). Diffusive resistance of the abaxial leaf surface was determined by recording the time for a given quantity of water vapour to diffuse from the leaf into a sensing cup and be absorbed by the humidity sensing element (Rutherfoord & de Jager, 1975). Since the diffusion rate is temperature dependent, values were corrected for temperature variations.

Leaf water potential ($\psi\ell$) was determined immediately afterwards for the same leaves, using a P.M.S. pressure chamber. The leaf was placed in the chamber with the cut petiole protruding through the rubber bung. Pressure inside the hermetically sealed chamber was gradually increased using dry compressed nitrogen. The pressure at which a droplet of xylem sap just appeared at the cut petiole surface, gave an estimate of $\psi\ell$ (Slavik, 1974; Rutherfoord & de Jager, 1975). It has recently been shown that xylem pressure potential is an adequate estimate of leaf water potential in the avocado (Sterne, Kaufmann & Zentmyer, 1977).

Soil matric potential in the pots was determined by tensiometers.

RESULTS

The influence of incoming solar radiation

Fig. 1 shows that the avocado cv Edranol exhibits the net photosynthesis-incoming solar radiation response curve of a typical C_3 type of plant, as outlined by Leopold & Kriedemann (1975).

In common with most C_3 plants, solar radiation saturation occurred at a relatively low level. Thereafter, providing that leaf temperature could be maintained fairly close to ambient air temperature, the rate of net CO_2 exchange did not alter appreciably with increasing incoming r.f.d., within the temperature range 10 to 30°C.

The maximal rates of net CO_2 exchange in well watered plants varied according to temperature. The air temperature for maximal net photosynthesis was found to be between 20°C and 24°C. Under these conditions (Fig. 1c) the maximal rate of net CO_2 uptake was approximately 0,4 mg m^{-2} s^{-1}. Within 5°C above and below these temperatures (Figs. 1b and 1d respectively) maximal net CO_2 uptake decreased to approximately 0,33 mg m^{-2} s^{-1}.

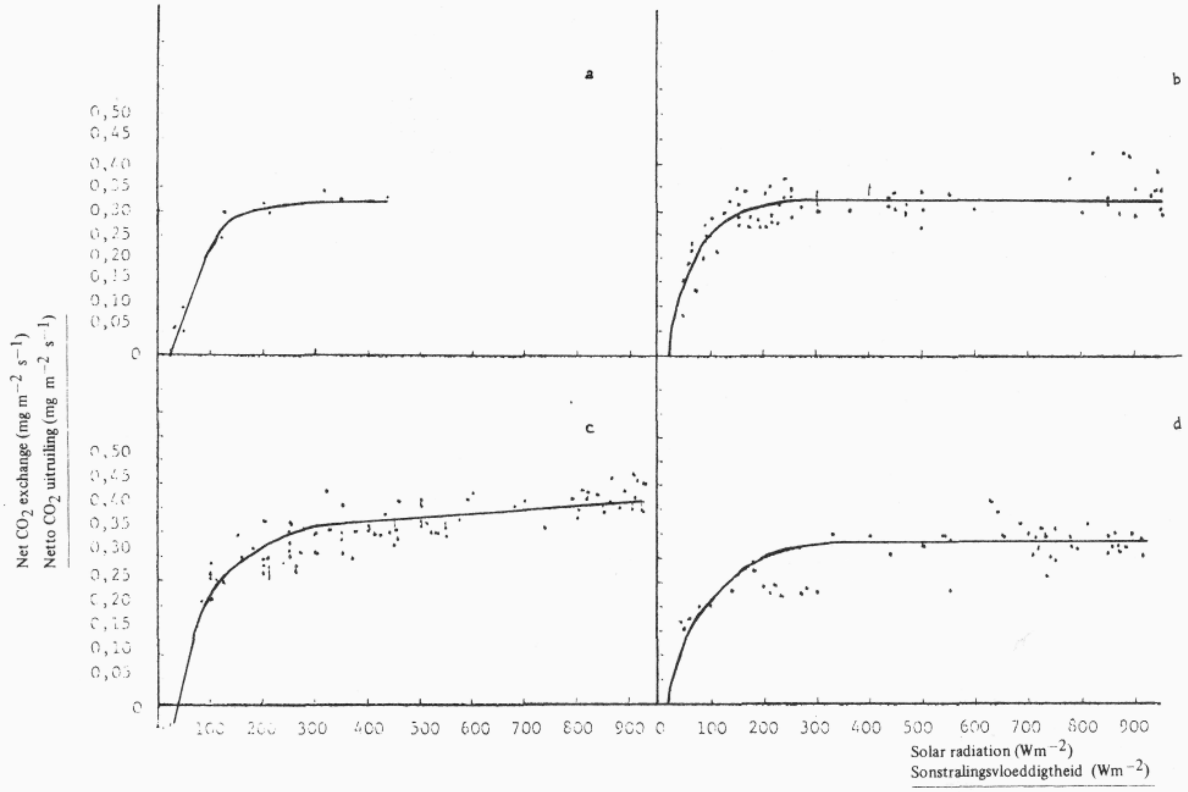
No significant differences between air and leaf temperatures were recorded in the chamber in well watered plants, indicating that the air-conditioner maintained sufficient air movement, and transpiration was sufficient to dissipate the incoming radiation heat load. Leaf temperature averaged 0,6c-C higher than air temperatures. While the mean measured difference over the entire drying cycle was 2,6oc, leaf temperature was up to 6oc above ambient temperature under extreme water stress conditions.

Of particular significance is the fact that under all temperatures normally encountered and tested, both the overall shape of the net photosynthesis-incoming solar radiation response curves (Fig. 1) and the point of inflection where a further decrease in incoming solar radiation resulted in a decrease in photosynthetic output, as portrayed by the net rate of CO_2 uptake, were similar. Only the maximal rates of net CO_2 uptake differed. The point of inflection occurred between 200 and 250 Wm^{-2}. The decrease in net CO_2 exchange was at first moderate, increasing with decreasing incident solar radiation and following the typical rectangular hyperbola relationship reported by many authors.

As it was not possible to reduce ambient temperatures within the chamber to below 10°C, or to maintain temperatures above 30°C, the effects of extreme temperatures were not investigated.

Fig. 1. *Net photosynthesis solar radiation response curves at ambient CO_2 concentration, and temperatures between a) 10 to 15°C, b) 16 to 19°C, c) 20 to 24°C and d) 25 to 30°C*

Fig. 1. *Invloed van sonstralingsvloeddigtheid op nettofotosintese teen normale CO_2 konsentrasie, en temperature tussen a) 10 tot 15°C, b) 16 tot 19°C, c) 20 tot 24°C en d) 25 tot 30°C*



The influence of water stress

The internal water status of the leaf affected net CO_2 uptake by altering stomatal aperture.

Fig. 2 shows that resistance to water vapour movement through the stomates remained constant with change in xylem pressure potential up to approximately -400 kPa. Thereafter, the stomata presumably closed slowly with decreasing (more negative) xylem pressure potential. Within the range -800 to -1000 kPa closure became more rapid, with total closure occurring at xylem pressure potentials of lower than -1000 kPa.

The influence of stomatal closure on net photosynthesis was evidenced by increasing stomatal resistance to water vapour movement, as shown in Fig. 3.

It would seem that net CO_2 uptake by the plant decreased linearly with increased stomatal resistance until full closure was achieved. The photosynthetic rate of the plant was reduced by 0,033 mg m^{-2} s^{-1} per unit increase in stomatal resistance.

Of importance to irrigation management, is the effect of decreasing soil moisture on the plant, shown in Fig. 4. For soil moisture potentials of zero to -40 kPa, very little increase in stomatal resistance was found. Thereafter however, stomatal resistance increased steadily to a soil moisture potential of -70 kPa, after which the stomata appeared to close rapidly, being completely closed by -80 kPa soil moisutre potential.

Fig. 2. *Relationship between stomatal resistance and leaf water potential*

Fig. 2. *Verwantskap tussen die diffusieweerstand van huidmondjies en blaarwaterpotensiaal*

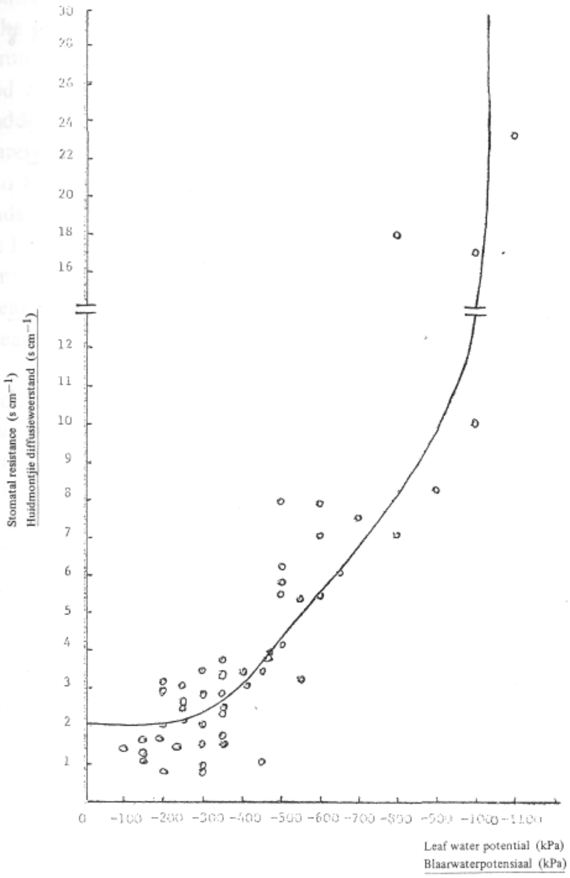
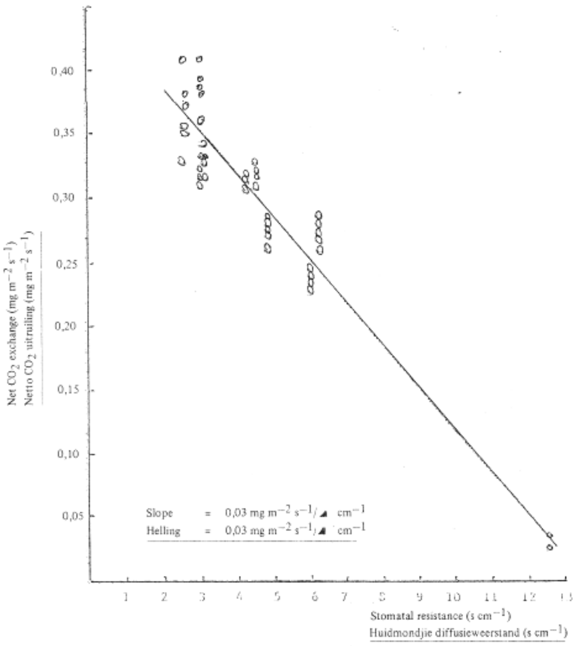


Fig. 3. *Relationship between net CO_2 exchange and stomatal resistance under conditions of increasing water stress*

Fig. 3. *Verwantskap tussen netto CO_2-uitruiling en diffusieweerstand van die huidmondjies vir toestande van toenemende vogstremming*



DISCUSSION AND CONCLUSIONS

The results indicate that the avocado, *Persea americana* cv Edranol, as a C_3 plant is fairly well adapted to shade conditions. Incoming solar radiation saturation for a simulated canopy occurred at approximately 20% of incoming solar radiation during summer in Pietermaritzburg. Furthermore, at only 15% of the maximal incoming solar radiation of ± 1 100 Wm^{-2}, the plants were able to maintain approximately 15% of their maximal photosynthetic rate, within the 20°C to 24°C temperature range. This means that from a photosynthetic point of view these plants could be well suited to high density plantings. It must be emphasised however, that the influence of solar radiation and shading on flowering and fruit set in spring has not been studied.

It thus seems that under conditions of no water and temperature stress, incoming solar radiation should not be considered a serious stress factor. On the other hand, it must be remembered that in an orchard situation a high percentage of leaves are in fact shaded at any particular time.

Water stress has been shown to have serious effects on photosynthesis. Field experience indicated that the avocado is fairly drought tolerant from a tree survival point of view. But flowering and fruiting become seriously affected, as in order to effect this drought tolerance, the stomates close. Fig. 2 indicates that this occurs at a relatively high leaf water potential in Edranol (approximately -900 kPa). In the Mexican cultivar Bacon, Sterne *et al.* found stomatal closure to occur at about -1200 kPa. These potentials compare favourably with those reported for herbaceous crops, e.g. -700 to -900 kPa for tomatoes (Duniway, 1971) and -1050 kPa for potatoes (Rutherfoord & de Jager, 1975).

This suggests that irrigation should be applied when the soil moisture potential is approximately -60 kPa. To what extent these results can be extrapolated to the field situation is not yet known.

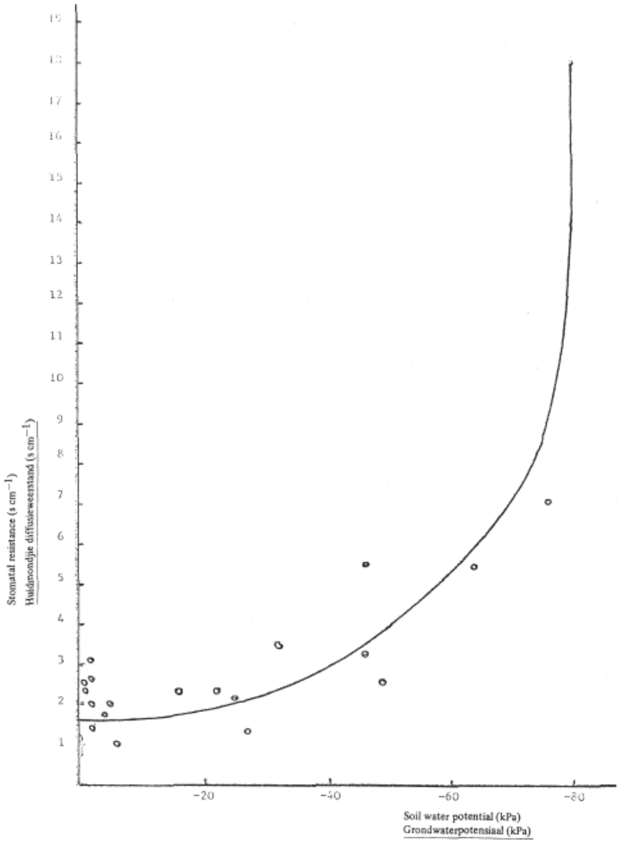
Should plants become moisture stressed, it was found that re-wetting did not restore previous stomatal apertures nor maximal photosynthetic rates for up to 4 to 6 days, depending on the duration of stress. Sterne *et al.,* (1977) found that 5 days after re-wetting, stressed avocado cv Bacon trees had not yet returned to normal. This, according to Beardsell & Cohen (1975), is due to the stress-induced accumulation of abscisic acid in leaves, which prevents stomatal opening.

Should water stress conditions occur, high levels of incoming solar radiation, by increasing leaf temperatures, will aggravate the stress situation.

Thus radiation, temperature and especially water stress have adverse and rapid effects on photosynthesis, the tree "shutting down" in order to survive. As avocado fruits have a high oil content, their growth and development mobilizes a substantial proportion of the tree's carbohydrate reserves. Thus, any stress, by reducing photosynthesis, will have serious effects on yield and increase the problem of alternate bearing. Solar radiation, temperature and especially water stress should therefore be limited to the minimum, making light but frequent irrigation most important.

Fig. 4. *Relationship between stomatal resistance and soil water potential (drying cycle)*

Fig. 4. *Verwantskap tussen diffusieweerstand van die huidmondjies en grondwaterpotensiaal*



OPSOMMING

Somtralinsvloeddigtheid en interne waterpotensiaal as Stremmingsfaktore in Avokado, Persea Americana *(Mill.) cv edranol*

Die tempo van CO_2 uitruiling van die avokado *Persea americana* (Mill.) cv Edranol is onder verskillende toestande van sonstralingsvloeddigtheid en temperatuur bestudeer. Daar is gevind dat die avokado 'n C_3 plant is, en dat die tempo van netto CO_2-uitruiling 'n maksimale waarde van 0,40 mg m^{-2} s^{-1} teen 'n temperatuur van 22°C bereik. Die diffusieweerstand van die huidmondjies het skielik toegneem teen 'n blaarwaterpotensiaal van -900 kPa. Klaarblyklik stem hierdie blaarwaterpotensiaal met 'n grondwaterpotensiaal van ongeveer -70 kPa ooreen. Maksimale netto CO_2 uitruiling kom voor teen die lae sonstralingsvloeddigtheid van omtrent 200 Wm^{-2}.

Daar word dus afgelei dat hierdie avokado kultivar redelik dig aangeplant mag word sonder om stralingsbeperkings op fotosintese te veroorsaak. Nietemin sal dit teen die relatiewe lae grondwater potensiaal van -70 kPa vogstremming toon, en verg dus sorgvuldige besproeiingspraktyke.

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References

BAKER, D.N. & MUSGRAVE, R.B., 1964. Photosynthesis under field conditions. V. Further plant chamber studies of the effects of light on corn. *Crop Sci. 2,* 127 - 131,

BEARDSELL, M.F. & COHEN, D., 1975. Relationship between leaf water status, abscisic acid levels, and stomatal resistance in maize and sorghum. *Pl. Physiol.* 56, 207 - 212.

BERGH, B.O., 1975. Avocados. In: Advances in fruit breeding. Ed. J. Janick & J.N. Moore. West Lafayette: Purdue Univ. Press.

BREDELL, G.S., 1971. Waterverbruik van sommige subtropiese vrugtesoorte. *Citrus & Subtrop. Fruit J.* No. 456,15 - 20.

CAIN, J.C., 1969. Tree spacing in relation to orchard production efficiency. *Cornell Univ. Agric. Exp. Sta. Res. Circ.15.* 1970. Optimal density of apple orchards. *HortScience* 5, 232 - 234.

CURTIS, D.S., 1949. Effect of soil oxygen supply in nutrient solution on avocado and citrus seedlings. *Soil Sci.* 67, 253-260.

DUNIWAY, J.M., 1971. Water relations of fusarium wilt*. Physiol. Pl. Pathol.* 1, 537 - 546.

FOCHESSATI, A., 1972. A hedgerow training method for apple *trees. Decid. Fruit Grow.* 22, 85 - 93.

HSIAO, T.C., 1973. Plant responses to water stress. *Ann. Rev. Pl. Physiol.* 24, 519-570.

KANEMASU, E.T., THURTELL, G.W. & TANNER, C.B, 1969. Design, calibration and field use of a stomatal diffusion porometer. *Pl. Physiol.* 44, 881 - 885.

JANZEN, D.H., 1975. Ecology of plants in the tropics. London: Edward Arnold.

LARCHER, W., 1975. Physiological plant ecology. Berlin: Springer-Verlag.

LEE, B.W., 1974. A planting plan for avocados. *Calif. Avocado Soc. Yrbk.* 57, 76 - 81.

LEOPOLD, C.A. & KRIEDEMANN, P.E., 1975. Plant growth and development. 2nd Ed. New York: McGraw Hill.

MEIDNER, H. & MANSFIELD, T.A., 1968. Physiology of stomata. London: McGraw Hill.

MILTHORPE, F.L. & MORBY, J., 1974. An introduction to crop physiology. Cambridge: Cambridge Univ. Press.

RUTHERFOORD, R.J. & DE JAGER, J.M, 1975. Water status and stomatal behaviours of BPI potatoes and their effect upon yield. *Crop Prod.* 4, 125 - 128.

SLAVIK, B., 1974. Methods of studying plant water relations. Berlin: Springer-Verlag.

STERNE, R.E., KAUFMANN, M.R. & ZENTMYER, G.A., 1977. Environmental effects on transpiration and leaf water potential in avocado. *Physiol. Plant.* 41, 1 - 6.

VAN BAVEL, C.H.M. NAKAYAMA, F.S., & EHRLER, W.L., 1965. Measuring transpiration resistance of leaves. *Pl. Physiol.* 40, 535 - 540.

WAGER, V.A., 1942. *Phytophthora cinnamomi* and wet soil in relation to the dying back of avocado trees. *Hilgardia* 14, 519 - 532.

WOLSTENHOLME, B.N., 1977. A simple climatic classification for tropical and subtropical areas and fruits in South Africa. *Crop Prod.* 6, 35 - 39.

ZENTMYER, G.A., PAULUS, A.O., GUSTAFSON, C.D., WALLACE, J.M. & BURNS, R.M., 1965. Avocado diseases. *Calif. Agric. Exp. Sta. Ore.* 534.