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The Effect of Temperature on Growth and Dry Matter Production of Avocado Plants

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Abstract

Grafted cv. Fuerte and cv. Hass avocado plants were grown for 81 days in sunlit growth chambers at day/night temperatures of 17/10, 21/14, 25/18, 29/22, 33/26 and 37/30°C. Stem diameter, length of side branches, the number of leaves, leaf area and plant height, were all greater in the 21/14 to 33/26°C temperature range, than at temperatures of 17/10°C and especially 37/30°C, which restricted growth in both cultivars.

Total dry matter accumulation by Fuerte was greatest at 25/18°C, while Hass was less affected by temperature extremes. High temperatures produced maximum dry matter in the leaves, while low temperatures produced it in the roots. Temperatures of 37/30°C reduced root growth and dry matter accumulation by 60-70% as compared with the optimal treatments. It is suggested that under high temperature conditions measures should be taken to cool the soil.

The Fuerte plants were more affected by temperature extremes than were the Hass plants which had a broader range of optimal growth response. Therefore cv. Hass could be expected to adapt better to extreme temperature conditions. Hass plants grown under high temperatures exhibited a greater leaf diffusive resistance than Fuerte and are therefore more capable of reducing water loss from the leaves.

As temperatures decreased, more red pigment was evident in the young flush of both cultivars.

Introduction

The avocado (*Persea americana* Mill.) is native to the subtropics of Central America (15-20°N.) and grows at elevations as high as 2500 m. Avocado is grown commercially up to latitude 35°. The expansion of avocado plantings in the last decade to marginal areas is subjecting trees to very wide seasonal and diurnal temperature fluctuations. Planting in cooler areas has produced slower growth and development of trees and fruit (Oppenheimer 1978). The effect of high temperatures on avocados is much less known.

Although the avocado grows in very diverse climates there are only two reports on the response of tree growth to various temperature regimens. Haas (1939) grew 'Puebla' seedlings at five different root temperatures (10-38°C). The temperature of the canopy was not controlled. Greatest fresh and dry weight of leaves and trunk was attained at 31°C root temperature, while maximum root growth was at 24°C. Yusof *et al.* (1969) examined growth of 'Mexican' seedlings under three different temperature regimens. More growth occurred between 21 and 27°C than at 32°C, where the growth was reduced and the seedlings were short and spreading.

Our objective was to determine the effect of a range of temperatures on growth habit and on dry matter production of the two most commonly grown avocado cultivars: Fuerte and Hass.

Materials and Methods

Eight-month-old trees grown in 5-1. containers were placed in controlled-temperature growth chambers for 81 days under a 12.5-h photoperiod. Scion wood of each cultivar was collected from single mother trees and was grafted onto 'Guatemalan' seedlings from single parent trees. The trees of the cultivar, Fuerte, were grown in a sand, peat, and Styrofoam mix while the cv. Hass trees were grown in a sawdust-metal-dust mix. The plants were grown in sunlit growth chambers at Wollongbar, N.S.W. (lat. 29° S.). Three plants of each cultivar were subjected to the following day/night temperatures: 17/10, 21/14, 25/18, 29/22, 33/26, 37/30 ± 1°C. Each plant was irrigated daily with 1 1. of tap water and fertilized with 1 g of NH_4NO_3 twice a week. No other fertilizer was applied, and no deficiency symptoms were observed.

At the start of the experiment four plants of each cultivar were harvested to determine stem diameter, stem length, number and length of side branches, and fresh and dry weights of roots, stem and leaves. After 81 days all plants were harvested and analysed as above.

From these data the following were estimated: total fresh and dry weights, distribution of dry matter within the plant, root/top ratio, and number of leaves produced. Leaf thickness was measured with a micrometer and the total leaf area with an electronic planimeter. Stem height was measured weekly. The relative growth as dry weight/height ratio was calculated after harvest. The degree of red pigmentation of the young flush was estimated with a colour dictionary (Mearz and Paul 1963).

Since humidity was not controlled, there was some concern that water stress may have influenced some treatments, especially those involving high temperatures. To assess the development of water stress, leaf diffusive resistance and relative water content were measured.

Ten discs, each 8 mm in diameter, were punched from a single leaf and floated in distilled water for 24 h to give relative water content (φ), such that $9 = 100(D_f - D_w)/(D_t - D_w)$, where D_f, D_t, and D_w are the fresh, turgid and dry weights of the discs respectively.

The leaf diffusive resistance (TI) was measured on. the abaxial side of the leaf around noon on a sunny day, by using a Li-cor automatic diffusive resistance meter. The sensor was calibrated at 29°C and temperature adjustments were made, using a calibration curve. At the same time, leaf temperature and soil moisture tension were also measured.

As the leaf diffusive resistance measurements were taken, photosynthetically active radiation was measured with a Li-cor LI-190S quantum sensor. The net radiation was measured with a Middleton miniature net pyranometer. Vapour pressure deficits in the chambers were measured every 15 min using shielded, unventilated wet and dry thermocouples.

All data are presented as means ± standard errors for each cultivar in each chamber.

Results

At the start of the experiment the Fuerte trees were about twice as large as the Hass trees (mean total dry weights per plant were 29 and 13 g respectively), and this difference was reflected in all the results.

Vegetative growth was maximized at the 21/14 to 33/26°C range, while the two extreme regimens (17/10 and 37/30°C) restricted growth in both cultivars. Stem diameter, length of side branches (representing also number of side branches), and relative increase in height were all greater in the 21/14 to 33/26°C range than at lower or higher temperature regimens (Fig. 1). Growth peaks were found at 29/22°C in the stem diameter of Fuerte plants (Fig. l*a*) and in the length of side branches of the cv. Hass (Fig. 1*b).*

The effect of temperature on tree height was difficult to assess because of the cyclic growth pattern of the avocado (Fig. 2). For instance, at the beginning and end of the experiment the Fuerte plants grown at 33/26°C were taller than those grown at 29/22°C; during the 22nd to 54th days of the experiment, the reverse was observed. The same occurred with the cv. Hass, where the plants grown at 37/30°C were sometimes taller than those grown at 29/22°C.

The number of new leaves and their total area increased with temperature up to 33/26°C (Fig. 3). The average single leaf area decreased sharply at the 37/30°C temperature regimen, resulting in a significant decrease in the total leaf area. Temperature extremes resulted in thinner Fuerte leaves, while thin Mass leaves were formed only under high temperatures (Fig. 3).

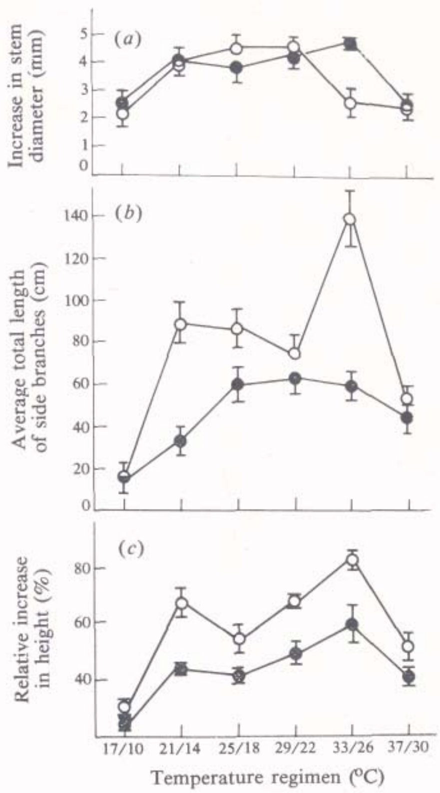

Fig. 1. The effect of ambient temperature during 81 days on (*a*) the increase in avocado stem diameter, (*b*) total length of side branches and (*c*) relative increase in height. Data are means ± s.e. of three plants from each cultivar. ● Hass, ○ Fuerte.

The accumulation of total dry matter and the relative dry matter production as a response to temperature produced a curve in Fuerte with a peak at 25/18°C, while Hass plants showed a less pronounced temperature optimum (Fig. 4). At relatively high temperatures maximal dry matter was produced in the leaves, while at medium temperatures greatest dry matter accumulation occurred in the stems, and at relatively low temperatures in the roots (Fig. 5). Thus, with Fuerte plants at 33/26°C, almost 50% of the dry matter was found in the leaves and only 19% in the roots. The corresponding values for the 21/14°C temperature regimen were 37 and 33 %. In the cv. Hass even more dry matter was found in roots (42%) than in leaves (26%) at 21/14°C. The reduced root growth and dry matter production at high temperatures can be seen also in Fig. 6 and in the top/root ratio (Fig. 4*c*).

The temperature treatments affected the growth of side branches (Fig. 1*b)* as well as the apical growth (Figs 1*c*, 2). The height (H) was proportional to the total plant dry weight (W). The W/H ratio varied among temperature treatments (Fig. 4*d),* being low in cold and hot treatments, and high at 25/18-29/22°C with the cv. Fuerte and 29/22-33/26°C with the cv. Hass.

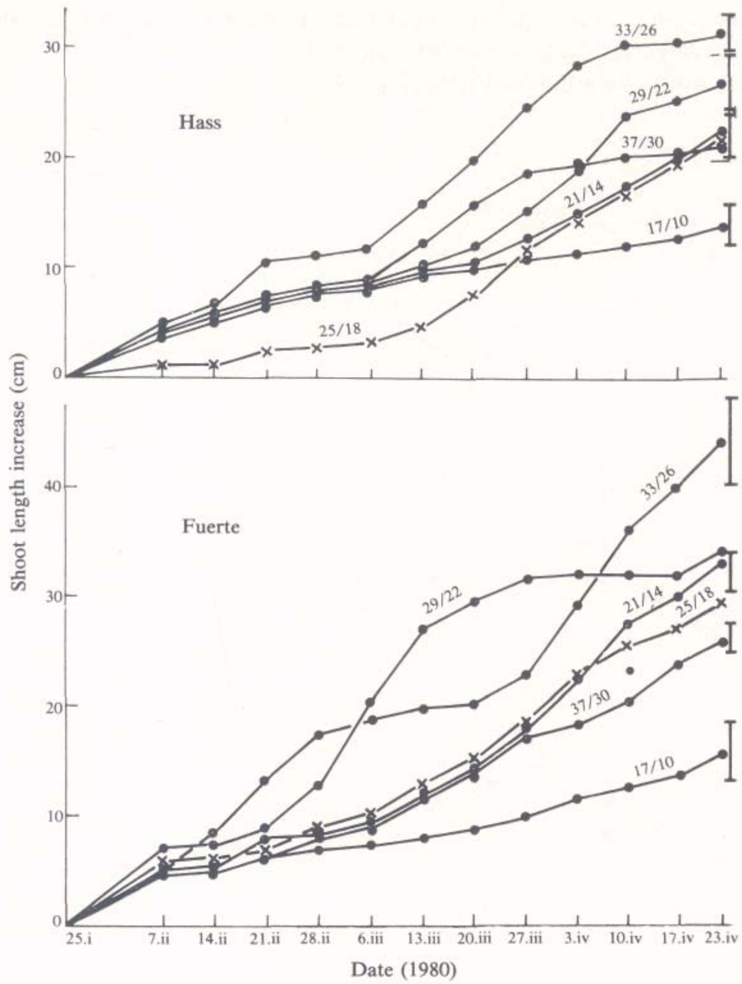

Fig. 2. The effect of ambient temperature on the cumulative increase in height of avocado plants during 81 days. Vertical bars indicate standard errors on 23 April 1980.

Table 1. The effect of temperature on the colour of the flush (Mearz and Paul 1963)

Temp. (°C)	cv. Fuerte		cv. Hass	
17/10	8-L-6	Mirador	8-L-4	Andorra
21/14	16-A-12	Biskra	8-L-6	Mirador
25/18	15-H-8	Rubber	8-L-9	Maraciabo
29/22	15-L-4	Olive green	16-E-8	
33/26	22-L-7	Art green	15-L-11	Buffalo
37/30	22-L-5	Cerro green	22-L-5	Cerro green

Temperature affected the colour of the flush considerably (Table 1). In the hot chamber the flush was green while under cool conditions it was red. The colour changed gradually from green to red with the decrease in temperature.

Maximum relative water content was found in 33/26°C leaves of cv. Hass; with cv. Fuerte the trend was not clear (Fig. 7*b)*.

Temperature gradually influenced the relative leaf diffusive resistance of cv. Hass from 17/10 to 33/26°C but most sharply at 37/30°C; the trend in Fuerte was more gradual (Fig. 7*a)*.

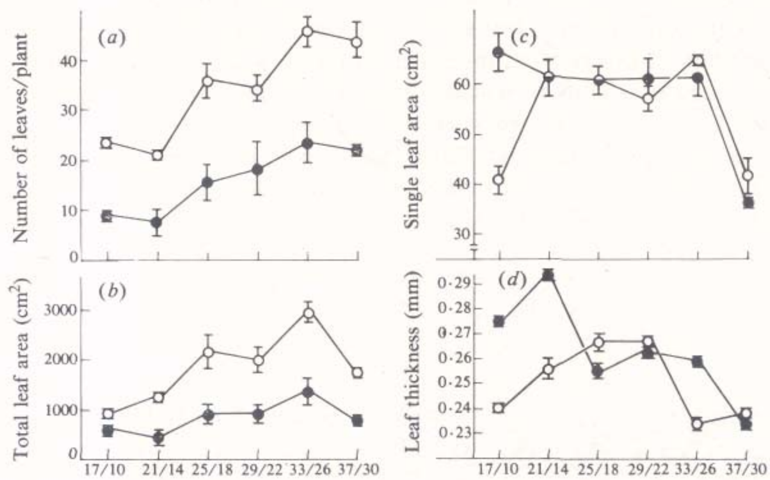

Fig. 3. The effect of ambient temperature on (*a*) the number of new avocado leaves formed, (*b*) total leaf area, (*c*) the average single leaf area, and (*d*) leaf thickness at the end of the experiment. Data are means ± s.e. of three plants from each cultivar. ● Hass, ○ Fuerte.

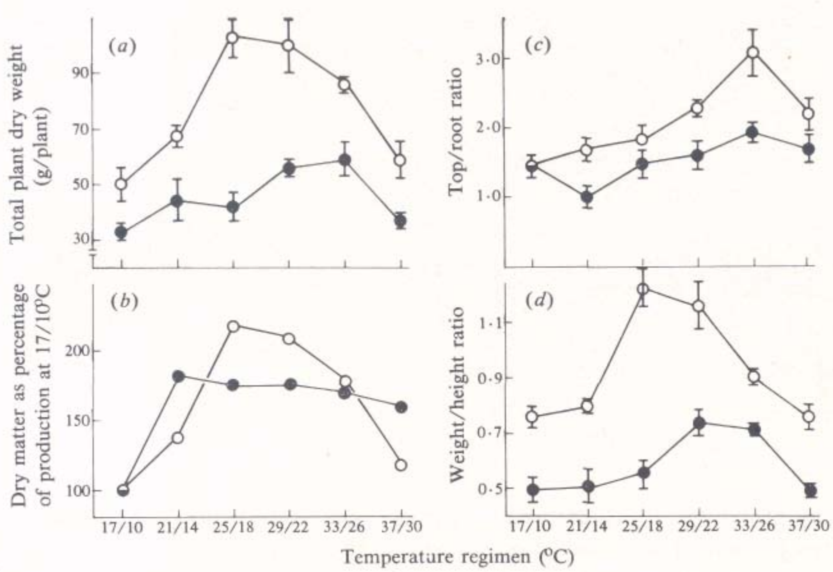

Fig. 4. The effect of ambient temperature on (*a*) total plant dry weight, (*b*) relative dry matter production, (*c*) top/root dry matter ratio, and (*d*) dry weight/height ratio at the end of the experiment. Data are means ± s.e. of three plants from each cultivar. ● Hass, ○ Fuerte.

Discussion

The results showed that the avocado can grow in a wide range of temperatures. Only the coldest (17/10°C) and the hottest (37/30°C) treatments were found to restrict growth and dry matter production.

In the two studies of the effect of temperature on avocado growth, Haas (1939) and Yusof *et al.* (1969) both used Mexican seedlings. The present report deals for the first time with grafted trees of the two most commonly grown avocado cultivars, Fuerte and Hass. Furthermore, the Mexican race is known to be the most resistant to cold, while the two cultivars tested are more sensitive. The Guatemalan race used as a rootstock is known to be more sensitive not only to cold but also to heat (Bower *et al.* 1978). Therefore, the vegetative material used in our experiment should have been influenced more by the extreme temperature regimens than was the material used in the previous experiments (Haas 1939; Yusof *et al.* 1969).

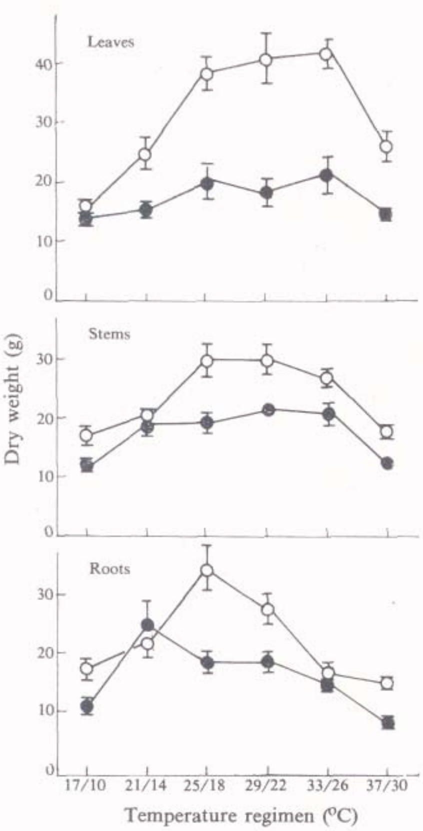

Fig. 5. The dry weights of avocado roots, stems and leaves after 81 days of growth, at the respective ambient temperature regimens. Data are means ± s.e. of three plants for each cultivar. ● Hass, ○ Fuerte.

The question of critical temperature for the growth of avocado roots has not been answered to date. The limited shoot growth in the early spring was always related to root senescence due to cold winter temperatures. The optimal temperature for the regrowth of roots in the early spring has never been investigated. The present research indicates that better root growth and more dry matter accumulation are achieved under low, as compared with high, temperatures. Furthermore, many more roots appeared to have died during the experiment in the high than in the low temperature treatments.

This leads to the assumption that root activity in the field could start relatively early in the spring. The optimal temperature for root growth was 21/14°C for the cv. Hass and 25/18°C for the cv. Fuerte. These temperatures prevail in the early spring in many avocado-growing areas in the world, including Australia and Israel.

High temperature was more advantageous in all parameters measured except for root dry matter production. Since the avocado roots were found to be active at a relatively low temperature, adequate supply of water and nutrients in the early spring may be expected to promote growth and flowering.

The main effect of high temperature was to reduce root growth. Shoots grew well in a wider range of temperatures, with the optimum at 33/26°C, whereas the optimum for the roots was at a much lower temperature: 25/18°C or even 21/14°C (Fig. 5). This corresponds with the results of Haas (1939), who reported the highest dry matter in roots grown at 24°C, and with those of Yusof *et al.* (1969) who reported it to be between 21 and 27°C. Thus the top/root balance was changed in favour of the shoots by the high and supraoptimal temperatures (Fig. 4*c*).

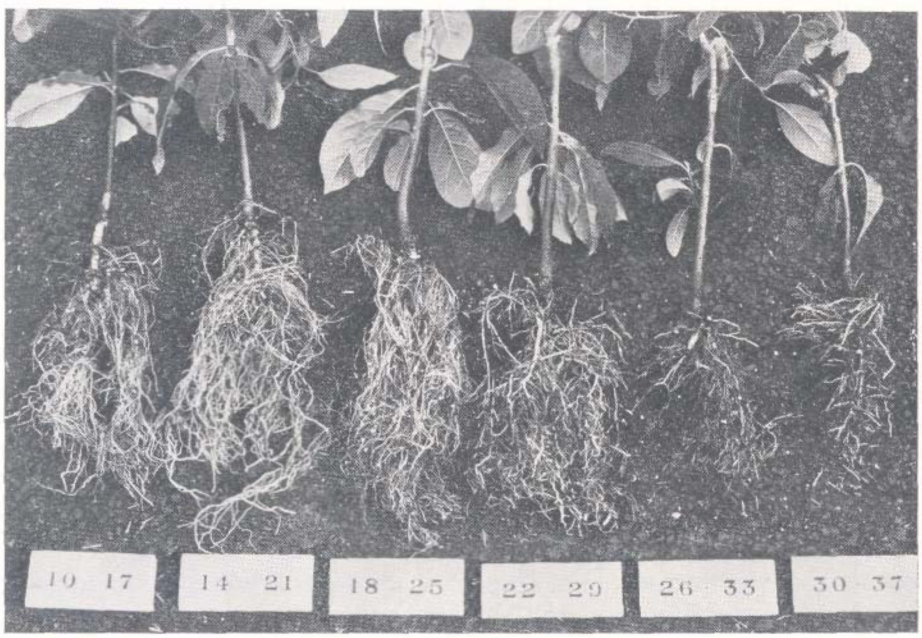

Fig. 6. Reduced root growth of avocado plants cv. Fuerte resulting from high ambient temperatures.

Avocados are known for their shallow root system (Oppenheimer 1978). Since clean cultivation is a common practice in many avocado areas, the temperatures in the upper soil layer, where most of the roots are found, may reach extreme values, especially in arid areas. Temperatures of up to 41 °C have been measured in the upper soil layer of an apple plantation under clean cultivation in Israel (Katznelson *et al.* 1967). Although soil temperature decreases with increasing depth, a temperature above 30°C which, according to the present study, may restrict growth of avocado roots, is quite common at a depth where most avocado roots are found.

The fact that avocado root growth is very restricted at high temperatures, could have many practical implications in the field. Since avocados are grown sometimes in areas with high summer temperatures, such as the Jordan Valley in Israel, every possible measure should be taken to cool the soil. Thus it should be recommended in such hot regions to mulch, grow cover crops, or shade the soil by intercropping. Intercropping of avocados with bananas has been found to benefit avocado growth and fruit production (Lahav and Zamet 1976). Whenever root rot is not a problem and soil aeration and drainage are good, frequent irrigation can be used as well for cooling the soil.

A temperature range of 20-25°C is optimal, not only for avocado root growth but also for floral behaviour, pollen tube growth, and embryo development. Under higher temperature regimens the temperature is not only supraoptimal for reproductive development but the tree is forced into a vegetative phase (Sedgley 1977). Vegetative growth is known to compete with fruit set (Biran 1979). Our measurements showed that under the high temperature regimen, leaf area was reduced much more than was the number of leaves (Fig. 3). It is therefore suggested that under high temperature conditions the growth/fruit-set competition might be much stronger than under normal temperatures.

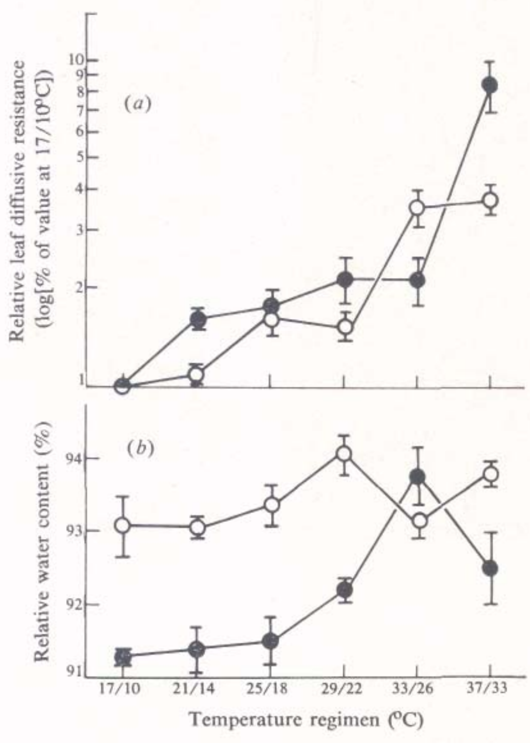

Fig. 7. The effect of ambient temperature on (*a*) the relative avocado leaf diffusive resistance (expressed as a percentage of the value at 17/10°C), and (*b*) the relative water content of the leaves. Data are means ± s.e. of three plants from each cultivar. ● Hass, ○ Fuerte.

The appearance of the red colour in the flush as a result of the cold temperature treatments has been reported in some crops but not in avocado. This effect was not obtained by Yusof *et al.* (1969), when the temperature range was not wide enough to reveal the differences, or by Haas (1939), who controlled only the root temperatures. In apples, high temperatures are known to accelerate anthocyanin degradation (Uota 1952). Avocado cultivars are sometimes characterized by the colour of the flush. It should be noted, therefore, that the colour of the avocado flush varies with temperature.

Although different potting mixes were used for the two cultivars, both produced strong and healthy trees. Since at the start of the experiment the Fuerte trees were larger than the Hass trees, only the relative growth indices such as relative increase in height, relative dry matter production, top/root ratio and weight/height ratio, enable us to make a true comparison between the two cultivars. The Fuerte plants were more affected by the extreme temperature treatments than were the Hass plants. The increase in temperature in the low range and the decrease in temperature in the high range resulted in sharp responses of most of the parameters measured for this cultivar.

Although the Hass cultivar has more Guatemalan ancestry and is known to be more sensitive to frost than Fuerte, it showed better adaptation in the low temperature range. This can be explained by its ability to accumulate dry matter in the roots and stems at 21/14°C, while maximum accumulation of the Fuerte cv. was at 25/18°C. Also, under low temperature conditions Fuerte plants produced small and thin leaves while Hass plants produced large and thick leaves (cf. Figs 3*c* and 3*d*).

The better adaptation of the cv. Hass in the high temperature range can be seen by its higher optimal temperatures (29/22-33/26°C) for total dry matter production and higher weight/height ratio at these temperatures, as compared with the cv. Fuerte (optimum 25/18-29/22°C) (Fig. 4). This could extend the growing season of the cv. Hass under marginal climatic conditions. It can therefore be concluded that Fuerte is more affected by extreme temperatures than is Hass, which has a broader optimum growth response. Similar conclusions were drawn by Sedgley and Annells (1981) after comparing the breeding cycles of Hass and Fuerte.

The higher top/root ratio under high temperatures (Fig. 4*c*), combined with the high evaporative demand, may have reduced the relative water content of the leaves and caused partial closure of the stomata (Fig. 7). The better adaptation of cv. Hass to high temperatures can be seen also by the increased leaf resistance, i.e. its ability to close its stomata under such conditions. In this respect it should be noted that Hass has been found to be more efficient than Fuerte in its growth and yield response to irrigation (Lahav and Kalmar 1977). The possibility of its low water demand in high temperature areas has still to be investigated.

With extreme water stress conditions, Bower *et al.* (1978) found that the leaf temperature rose up to 6°C above ambient temperature, thus reducing the heat load. We did not observe an increased leaf-air difference in temperature under the high temperature regimens, indicating that, since the plants were irrigated daily, no water stress existed.

The closure of the stomata as a response to the heat probably had an adverse effect on CO_2 uptake and photosynthesis. Air temperature for maximal CO_2 uptake was found to be 20-24°C (Bower *et al.* 1978), and decreased net photosynthesis because of increased stomatal resistance was proved to occur below 20° and above 30°C (Kimelmann 1979). Therefore, the rise in temperature under our conditions was probably paralleled by decreased dry matter production. As avocado fruits have a high oil content, their growth and development draw on a substantial proportion of the carbohydrate reserves. Thus, any stress-reducing photosynthesis will have a serious effect on dry matter accumulation (as we found) and probably on yield. Efforts should therefore be made to moderate temperature in avocado plantations during hot periods.

Acknowledgments

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References

Biran, D. (1979). [Fruitlet abscission and spring growth retardation—their influence on avocado productivity.] M.Sc. Thesis, The Hebrew Univ. Jerusalem. (In Hebrew, with English summary.)

Bower, J. P., Wolstenholme, B. N., and Jager, J. M. de (1978). Incoming solar radiation and internal water status as stress factors in avocado, *Persea americana* (Mill.) cv. Edranol. *Crop Prod.* 7, 129-33.

Haas, A. R. C. (1939). Root temperature effects on the growth of walnut and avocado seedlings. *Yearb. Calif. Avocado Soc.* 1939, 96-102.

Katznelson, I., Hoffman, M., and Sandowski, N. (1967). [Testing different methods of soil management in the apple orchard.] *Ktavim* 17, 289-301. (In Hebrew.)

Kimelmann, R. (1979). [The influence of different temperatures and light intensities on gas exchangeof avocado leaves *(Persea americana* Mill.).] M.Sc. Thesis, The Hebrew Univ. Jerusalem. (In Hebrew with English summary.)

Lahav, E., and Kalmar, D. (1977). Water requirements of avocado in Israel. II. Influence on yield, fruit growth and oil content, *Aust. J. Agric. Res.* 28, 869-77.

Lahav, E., and Zamet, D. (1976). [Comparison of growing avocados with or without bananas.] *Alón haNotea* 30, 464-73. (In Hebrew.)

Mearz, A., and Paul, R. M. (1963). 'A Dictionary of Color.' (McGraw-Hill Book Co.: New York.)

Oppenheimer, Ch. (1978). ['Subtropical Fruit Trees and Their Cultivation in Israel.'] (Am Oved: Tel-Aviv.) (In Hebrew.)

Sedgley, M. (1977). The effect of temperature on floral behaviour, pollen tube growth and fruit set in the avocado. *J. Hortic. Sci.* 52, 135-41.

Sedgley, M., and Annells, C. M. (1981). Flowering and fruit-set response to temperature in the avocado cultivar 'Hass'. *Sci. Hortic.* 14, 27-33.

Uota, M. (1952). Temperature studies in the development of anthocyanin in Mcintosh apples. *Proc. Am. Soc. Hortic. Sci. 59,* 231-7.

Yusof, I. M., Buchman, D. W., and Gerber, J. F. (1969). The response of avocado and mango to soil temperature. *J. Am. Soc. Hortic. Sci. 94,* 619-21.

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