

LEAF TEMPERATURE AND PHOTOSYNTHESIS OF A TROPICAL C₃ PLANT, *ELAEIS GUINEENSIS*

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RINGKASAN

Suhu optima untuk fotosintesis pada pokok kelapa sawit (*Elaeis guineensis* Jacq.) berhubung rapat dengan suhu maksima naungan (maximum shade temperature) dalam kawasan lembab tropik, tetapi daun-daun yang terdedah kepada matahari mungkin melebihi 10°C di atas suhu naungan. Fotosintesis oleh daun-daun misalnya mungkin hanya 50 peratus daripada kadarnya pada suhu optima, tetapi kepentingannya pada seluruh fotosintesis 'canopy' belum diketahui.

INTRODUCTION

Photosynthesis of C₃ species from the tropics and subtropics has not received much attention. Within the Graminae, a division is often made into 'temperate' species, with the C₃ photosynthetic pathway, and "tropical" species with the C₄ pathway. The C₄ species generally have higher temperature optima for photosynthesis (COOPER and TAINTON 1968), and TREHARNE and COOPER (1969) showed that the primary carboxylating enzymes for the two pathways also differed in their temperature optima. However, the division into tropical and temperate species is only valid to the extent that very few temperate C₄ species have been found (LONG *et al.*, 1975); in the tropics and subtropics there are probably numerous C₃ grass species. For example, of 96 genera occurring in Malaysia (GILLILAND 1971) only 41 are listed by DOWNTON (1975) as including C₄ species. Outside the Graminae, C₄ plants appear to be rare, and so far have only been identified in 12 other families. Thus the behaviour of C₃ species in environments with high ambient temperatures is of considerable importance.

PEARCY *et al.*, (1974) studied *Phragmites communis* growing in the very high temperatures of Death Valley, California, and found that leaf temperatures were always lower than air temperature (up to 8°C lower at midday). Thus even at air temperatures above 45°C, leaf temperature usually did not greatly exceed the optimum for photosynthesis of 30°C.

Ambient temperatures are not so high in the humid tropics (maximum shade temperatures of 30-35°C are common), but relative humidity is usually high; also air movement is often very low, so leaf boundary layer resistance will be high; thus both transpirational and convectional cooling of the leaf will be limited. We observed leaf temperatures in the oil palm (*Elaeis guineensis* Jacq) considerably above air temperature; since the oil palm appears to be a C₃ species (on the basis of leaf anatomy), we investigated the effect of leaf temperature on photosynthesis.

MATERIALS AND METHODS

All measurements were made on palms of the *tenera* (thin shelled) fruit type, in South Johore, Malaysia. Seedlings were grown out of doors in polythene bags of soil, watered daily and fertilized monthly.

Leaf temperatures were measured with copper constantan thermocouples, pressed against the lower surface of the leaf by the spring action of the lead wires, so that there was little interference with air movement around the point of measurement.

CO₂ uptake was measured with an infra red gas analyser in an open system, using an air sealed leaf chamber (WOLF *et al.*, 1969). The chamber was water jacketed for control of leaf temperature. We were not able to calibrate the system accurately in absolute terms, but conditions were maintained as constant as possible throughout each series of readings and results expressed in arbitrary units. A 500 W incandescent lamp was used as light source, and photosynthetically active radiation (PhAR) was measured at chamber height with a Lambda quantum sensor.

The temperature optimum for photosynthesis was determined from a series of measurements on one leaflet of leaf two (where leaf 1 is the most recently opened leaf) at a range of leaf temperatures, made over a period of 2 or 3 hours. Rate of CO₂ uptake was plotted against leaf temperature, a quadratic curve was fitted to each set of data by least squares, and the temperature giving maximum CO₂ uptake was estimated from the curve by differentiation.

Wind speeds were measured over half minute intervals with a sensitive cup anemometer. Total solar radiation was measured with a Lambda pyranometer sensor.

Stomatal diffusion resistance was measured with a Lambda LI-15S porometer.

RESULTS

Temperature optima were determined for nine one-year old seedlings. At a PhAR level of 800 μ einstein $m^{-2} s^{-1}$, the mean optimal temperature was 29.1°C (11 sets of measurements, standard error $\pm 1.2^\circ$). *Figure 1* shows typical sets of results for two seedlings. Although quadratic curves gave a statistically good fit to the data (generally accounting for nearly 90 percent of the variation in rate of CO₂ uptake), it appears from *Figure 1* that the relationship is not truly quadratic. Rather, photosynthesis reaches a plateau level, extending as much as 5°C above the "optimum" of the curve, and then decreases, often very abruptly (e.g. palm 2 in *Figure 1*). Rates of over 90 percent of the maximum were generally obtained up to at least 33°C. Above about 40°C, CO₂ uptake was very much reduced, often to zero or negative levels.

Measurements of leaf temperature in seedling palms showed large fluctuations over periods of a few minutes. The major factor affecting leaf temperature was solar radiation, and to a lesser extent wind speed. Regressions of the leaf/air temperature difference (Δt , in °C) on radiation (I , $W m^{-2}$) and wind speed (V , $m s^{-1}$) accounted for nearly 80 percent of the variation in Δt for most seedlings studied. A typical example, combining data from three seedlings, was:-

$$\Delta t = 0.4 + 0.0088 I - 1.6 V \quad (R^2 = 0.78, 131 \text{ d.f.})$$

Wind speeds did not exceed 2.5 $m s^{-1}$, and leaf temperature was always higher than air temperature unless incident radiation was below about 350 $W m^{-2}$. In full sunshine (800-1100 $W m^{-2}$) leaf temperature was at least 3°C above air temperature. The highest leaf temperature recorded was 42.6°C, 12°C above air temperature, and Δt commonly exceeded +8°C. The seedlings studied here were irrigated daily by a sprinkler system, and it is unlikely that they were suffering from water stress. Measurements of stomatal resistance made on other occasions showed that the stomata remained fully open throughout the day.

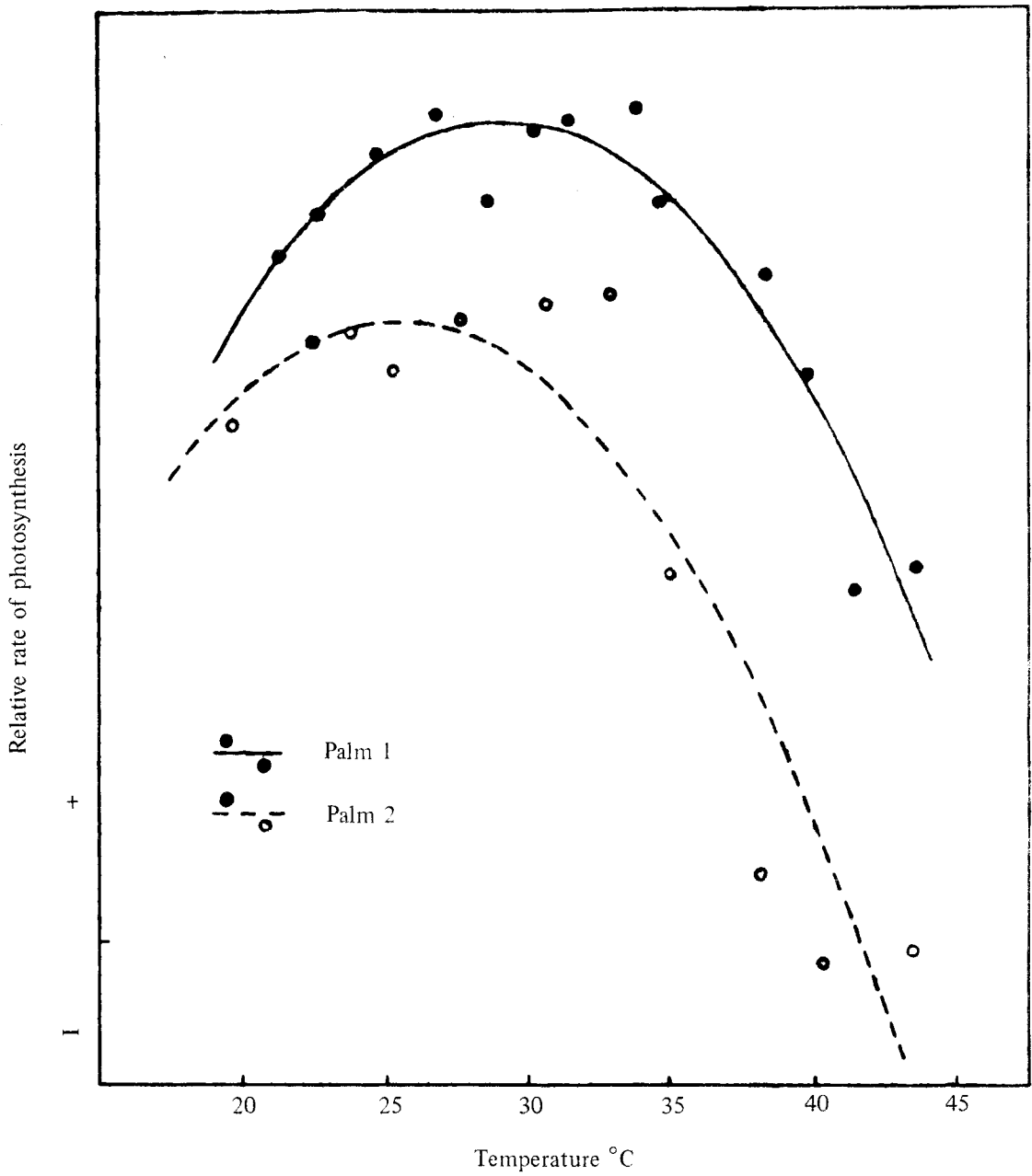


Figure 1. Photosynthetic rates (arbitrary units) of two oil palm seedlings plotted against leaf temperature. The points represent individual measurements, the lines fitted curves.

Measurements on the upper, fully exposed, leaves of 6 year old palms gave similar results. Leaf temperatures of up to 38°C were recorded, and Δt commonly exceeded 6°C. Here also there was no reason to believe that the palms were suffering from water stress, since heavy rain had fallen on several days immediately before the measurements were made.

DISCUSSION

The optimal temperature for oil palm photosynthesis is appreciably higher than optima reported for C₃ species from temperate climates, and is close to normal maximum shade temperatures in the humid tropics. However, leaves exposed to the sun may be over 10°C hotter than shade temperature. These high temperatures can be attributed partly to low wind speeds (rarely more than 1 m s⁻¹ in Malaysia, which only reduces leaf temperature by about 2°C compared to still air) and also probably to the xeromorphic nature of the oil palm leaf. Stomatal resistance to diffusion of water vapour is rarely lower than 2.5 s cm⁻¹, and usually averages about 3.5 s cm⁻¹ in well watered palms; cuticular resistance normally exceeds 100 s cm⁻¹. Thus it is likely that transpirational cooling of the leaf is relatively inefficient. In addition, stomatal closure occurs at air temperatures above about 32°C (REES 1961, CORLEY 1973), at least in palms under some degree of water stress. There was no evidence for such closure in this study, but even higher leaf temperatures could be expected where such closure does occur.

At a leaf temperature of 40°C, photosynthesis is probably reduced on average to about 50 percent of the maximum rate (CO₂ uptake at 40°C by different seedlings ranged from zero, or negative values, up to 90 percent of the maximum). However, the importance of this under field conditions is difficult to assess. A mature stand of oil palms has a leaf area index of about 5, and leaflet angle distribution is probably plagiotrophile (CORLEY in press). Thus it can be expected that the majority of leaflets will not be exposed to direct sunlight. Further, in the humid tropics the sky is often overcast during wet seasons, while during dry seasons photosynthesis may anyway be restricted by water stress and stomatal closure (REES 1961).

Stomatal closure during the dry season can be prevented by irrigation (DESMAREST 1967), but our results with seedlings indicate that irrigated palms will still develop high leaf temperatures. Thus under irrigation leaf temperature might have a significant limiting effect on oil palm productivity. Various possibilities for overcoming this could be considered.

With some plantation crops shade trees are planted; one of the main functions of the shade is to reduce leaf temperatures in the crop (e.g. HADFIELD 1968). REES (1963) showed that relative growth rate and net assimilation rate of oil palm seedlings were not reduced by quite heavy shading, but mature oil palms generally fail to produce fruit under the heavy shade of either older palms or forest, and shading has not been considered for the crop beyond the nursery (seedling) stage.

An alternative would be to try to select for palms with a less xeromorphic leaf structure; but in a preliminary trial we found little evidence for heritable variation in stomatal resistance (CORLEY and TAN G.Y., unpublished). Before further such work is undertaken, a detailed study of leaf temperature throughout the canopy of both irrigated and unirrigated palms would appear worthwhile.

SUMMARY

The optimal temperature for photosynthesis of the oil palm (*Elaeis guineensis* Jacq) is close to normal maximum shade temperatures in the humid tropics, but leaves exposed to the sun may be over 10°C above shade temperature. Photosynthesis by such leaves is probably only 50 percent of the rate at the optimal temperature, but the importance of this in terms of whole canopy photosynthesis is not known.

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