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TRANSPIRATION AND OIL ACCUMULATION RATES FOR DEVELOPING OIL PALM FRUITS ELAEIS GUINEENSIS JACQ.

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SUMMARY

Transpiration rates from and oil content changes in developing oil palm fruits were measured. During fruit development, transpiration rates showed a monotonic increase. The rate of increase was most rapid in the last three weeks of fruit ripening during which practically all mesocarp oil formed. The rate of oil accumulation in the fruits exhibited an exponential followed by a steady increase phase. The phases are proposed to correspond to those for oil droplet precipitation and growth, respectively. The magnitude of the transpiration stream is significant after most of the fruit non-oily solid matter appears formed and before the appearance of oil. Later on, transpiration becomes high enough to account for all the water convected into the fruit with the sugar precursors for oil production. This suggests that xylem flow occurred initially into the fruit before the phloem becomes the primary source for transpired water as oil is produced.

1. INTRODUCTION

The oil palm fruit is richly provided with vascular bundles, many of which traverse the length of the drupe and are continuous into the subtending spikelet on the female inflorescence. Rapid formation of oils in the storage parenchyma tissue could therefore involve the flux into the fruit of large quantities of water, carrier for the sugar precursor for lipids from the leaves and other photosynthetic organs. On this convective flow, a concentration gradient of sugars (primarily sucrose) which is not eliminated by axial dispersion may be superposed. Concentration gradients have been noted in phloem tissues in the careful experiments of HUBER et al. (1937), ZIEGLER (1956) and ZIMMERMANN (1957) (see CANNY 1975). As was observed, sugar translocation rates into sinks exceeded the values attributable to diffusion alone by about five orders of magnitude. This would support the idea that convection of sap is most significant for solid matter transfer into a developing fruit (MÜNCH 1930).

Of the two different oils found in the endosperm (kernel) and in the mesocarp (soft outer tissue) of the oil palm fruit, the mesocarp oil which usually constitutes between 30 and 50 percent of whole ripe fruit weight ($\sim$ 3 to 10 grams) is formed within the 24 days preceding full maturity (YAMPOLSKY 1922; BLOM-

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MENDAAL 1925; CROMBIE & HARDMAN 1958; DE POERCK 1950; THOMAS et al. 1971). Given the facts that the sugar concentrations in sap translocated into the fruits, based on studies of exudates, most usually lie between 10 and 20% (VAN DIE & TAMMES 1975) and that the water initially present in the cytoplasm of the mesocarp parenchyma tissues would be gradually displaced as the oil accumulates (BLOMMENDAAL 1925; DESSASSIS 1955), a large amount of water must rapidly be transferred out of the developing fruit. ZIMMERMANN (1969) reviewed the controversy between MÜNCH (1930), DOEPP (1939) and ZIEGLER (1963) on this problem.

BLOMMENDAAL (1925) observed that the fruit epidermis is richly provided with stomata hereby suggesting that transpirational loss of water from the fruit surface may be significant. In this study we have endeavored to determine the diurnal transpiration rates from the fruits at different stages of the development and sought to establish the relationship between transpiration and mesocarp oil accumulation rates.

2. MATERIALS AND METHODS

Fruits of the "fertile" *Elaeis guineensis* Jacq., forma *pisifera* (shell-less) from 9-year old trees were used. Bunches on freely pollinated trees were selected according to the estimated age defined in terms of the number of weeks prior to the stage called ripening. This corresponds to the time when the fruits have the minimum available free fatty acids and maximum quantity of oil. The age determinations were made from visual inspection of many sectioned fruit samples from different bunches on the same tree, and studying the phyllotactic arrangement of the bunches in the leaf axils (HARTLEY 1967). With this technique one can confidently establish the age of a bunch with an accuracy of about one week. Given that the ripening process takes place over a 22 to 24 week period from pollination of the inflorescence, reckoning bunch age in terms of the number of weeks to ripening is considered sufficiently accurate in this work.

On selection of a representative spikelet with between 6 and 10 uninjured and healthy fruits attached, and about one-third the length of a bunch from its apex, spikelets in the immediate neighborhood were cut off to isolate test specimens and provide a working space for attaching a transparent polyethylene bag cuvette (*fig. 1*). The fruits reflected approximately the normal distribution between well developed exposed (or outer) fruits and etiolated, confined (inner) fruits. The bunch was usually allowed 12 to 24 hours to adjust to the injury. The 18.4 cm by 22.9 cm plastic bag cuvette was fitted over the spikelet and tied securely but without excessive pressure at the mouth around the base of the spikelet with a string. The bag has one inlet via a funnel sealed-in with the wide mouth covered with a fine-mesh screen gauze to keep out aphids, coccids and other insects. In the event it rained, the tilted funnel prevented liquid droplets entering the cuvette. Three outlets were provided via glass tubes sealed into the plastic bag at different locations around the spikelet so that transpired moisture would not have to travel far to reach the collecting line.

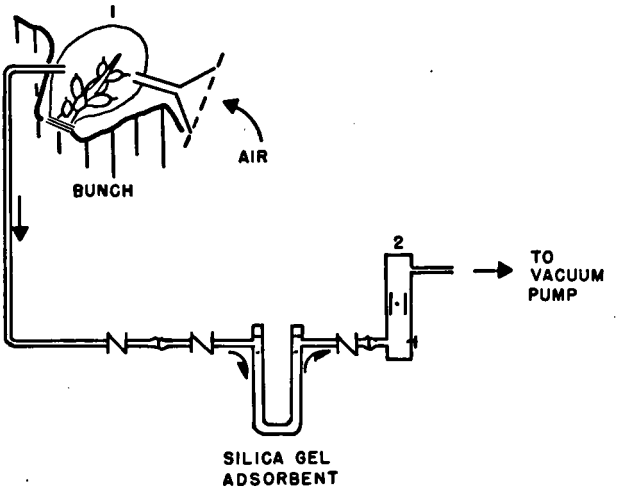

Fig. 1. Schematic diagram of apparatus set-up for transpiration measurement. Air flow rates through the cuvette (1) is measured with the rotameter (2).

The vertical 6-meter long, 1 cm internal-diameter glass collecting line with two stopcocks attached discharged into a U-tube filled with grade 03 commercial silica gel (with about 800 m^2 area/gram) which could absorb about 40% its own weight in moisture. The flowing gas stream traversed a distance of approximately 60 cm of adsorbent in the 2 cm internal-diameter tube. From here the dried air entered a rotameter (Matheson R-2-15-8/603) before it reached the vacuum pump which maintained the flow. The adsorbent tube was repacked with fresh silica gel before the last 15 cm of the bed had changed color from deep blue to the light pink indicative of high moisture content. The exit gas just before repacking had a dew point of about −20°C, i.e. 95 to 99% of moisture entering was effectively removed from the air stream.

In each experiment, the vacuum pump pulled ambient air from the atmosphere through the system at a rate preset with a needle-valve on the rotameter. Most of the pressure drop was downstream of the rotameter. Every two hours, flow was interrupted and the U-tube was disconnected for a maximum of about 2 minutes to determine the weight gain due to the water removed from the air on a top-loading Mettler Balance (Model P1200N) accurate to within 10 mg in draft-free area. Small drafts were obtained in our field station, hence the oscillations of the balance were watched for a minimum of 10 seconds before readings were recorded. About the same time, both the wet and dry bulb temperatures were recorded. Of the experiments performed, the shortest duration was for 12 hours and the longest almost 48 hours of continuous data collection.

The quantity of oil present in the fruit was determined the usual way by solvent extraction from digesting dried, crushed fruits with low boiling gasoline

fraction (b. pt. 40–65°C) or petroleum ether in a Soxhlet extractor (BLOMMENDAAL 1925; DESSASSIS 1955).

3. RESULTS

3.1. Transpiration from fruits

The data presented in *figs. 2* and *3* are typical of the results. *Fig. 2* (*a*, *b*, *c*) show the daily cycles of the wet and dry bulb temperatures. From these and a psychrometric chart, the relative humidity of the ambient, and the moisture content per unit weight of dry air needed to evaluate transpiration in this work were determined. The lowest percent saturation of air was 76% at a recorded dry bulb temperature of 28.7°C.

Fig. 3 shows the transpiration rates from the fruits on different spikelets (normalized with the total weight of fruits inside cuvette) as a function of the

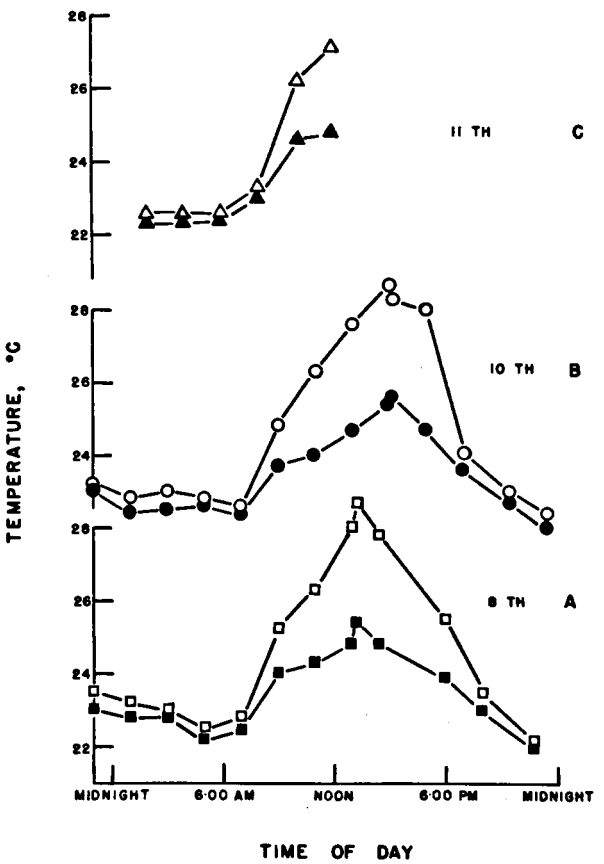

Fig. 2. Daily patterns of dry (△, ○, □) and wet bulb (▲, ●, ■) temperatures on the dates given in September, 1977.

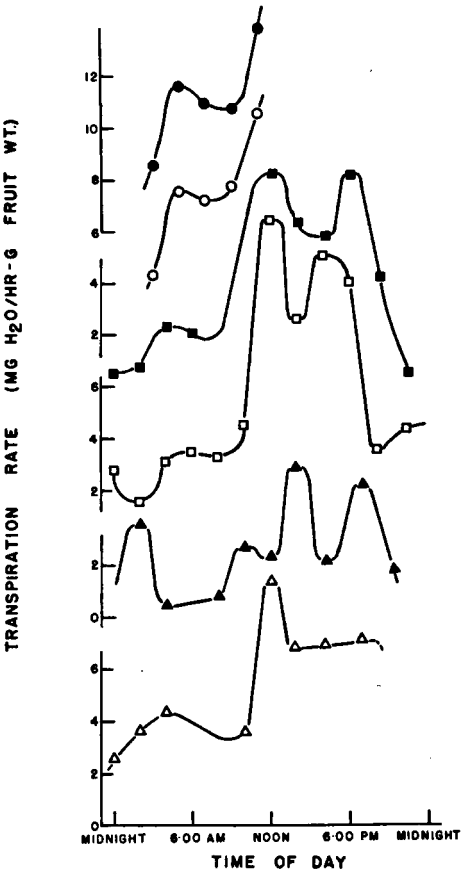

Fig. 3. Daily patterns of transpiration rates from oil palm fruits. Age given in number of weeks to maturity.

△——△ 1 week, 8 SEPT.
▲——▲ 3 (−) weeks, 8 SEPT.
□——□ 3 (+) weeks, 10 SEPT. TREE 9417
■——■ 13 weeks, 10 SEPT.
○——○ 13 weeks, 11 SEPT. TREE 9477
●——● 9 weeks, 11 SEPT.

time of the day. The plots show some significant features. In the early afternoon, transpiration rates were sharply reduced from peak values. Partial recovery of the rate of water loss was noted after a few hours when the weather conditions had not changed abruptly in the interval. Peaks in the different curves are usually out of phase with one another even when experimental conditions were almost identical, and there are variations in the general pattern of transpiration even from bunches on the same tree. The rate of nighttime moisture loss from the fruits oscillated slowly within 10 and 30% of values recorded during

daytime, and in each experiment, a small maximum in water loss rate was obtained in the pre-dawn hours.

Prior to discussing the results, it is in order to examine the conditions of the experiments and the factors which influence transpiration.

Fruit species. The selection of the homozygote *pisifera* (shell-less form of the oil palm fruit) minimizes the complication present with other forms, that is, earlier in its development, entering sugar precursors are diverted only in minute quantities to produce the endosperm oil. Most of the test specimens had no kernels and were sterile. When cavities were present, they were usually small (less than 1% of the fruit volume) and void, or they may have contained a watery sap containing approximately 2% sugars with or without a soft whitish gel lining the cavity space. Only one fruit in 25 to 50 contained a small, fully developed kernel with viable embryo. The choice of the fruit form thereby ensured that the formation of another oil did not create an additional internal factor which could interfere with a correlation between mesocarp oil formation and transpiration.

Cuvette climate. TRANQUILLINI (1964) discussed the "cuvette climate" noted in studies under field conditions. In the present work, the air volume of the free space inside the cuvette was replaced about 2 to 5 times a minute by air intake to ensure a negligible rise in temperature inside the plastic bag. The plastic bags had very thin walls for effective heat exchange with the ambient and the period of study was generally cool and partially cloudy. Higher air velocities were not used to control convective mass transfer at the fruit surface, especially cuticular transpiration from etiolated epidermis of inner fruits which ordinarily would have been unavailable for gas exchange because they were areas of pressure contact with adjacent fruits excised from the bunch cluster. (Most of the basal portions of individual fruits are normally shielded by overlapping calyx leaves provided with none or very poorly developed stomatal apparatus.)

External variables. Many variables influence the magnitude of transpiration. Atmospheric carbon dioxide concentration, air temperature, plant water status, light intensity and ambient relative humidity act directly on the stomata. Wind velocity reduces the resistance to diffusive mass transfer at the fruit surface. Literature on the response of stomata, primary sites for water exchange, to the various stimuli have been reviewed by MEIDNER & MANSFIELD (1968) and more recently by RASCHKE (1975). The observed diurnal changes of the transpiration rate are the result of the combined effect of environmental factors which are not completely independent of each other.

Gas exchange surface. The characteristics and magnitude of the exposed fruit areas determine total mass transfer. For individual fruits, the stomatal frequency index (ratio of the number of stomata and number of epidermal cells in a unit area) decreases from about 8.5 (10^{-3}) in the highly pigmented (dark purple coloration of anthocyanin) area near the apex to the order of 10^{-3} at the etiolated areas of pressure contact with adjacent fruits, and zero near the base of fruit covered with the calyx leaves (see *table 1*). The stomatal population frequency in the apical zone is of the same order of magnitude as in the adaxial

Table 1. Distribution of stomata on the oil palm fruit, *Elaeis guineensis*.

	Population Frequency		
	Epidermal parenchyma cells per mm²	Stomata per mm²	Stomatal Frequency Index (10^3)
Apical Zone (dark purple)	2129	18.2	8.5
	2237	16.7	7.5
	2143	13.3	6.2
Mid-Zone (light purple)	1857	8.1	4.4
	2172	9.1	4.1
	2000	8.0	4.0
	1964	4.5	2.3
Basal Zone (no pigments)	4401	5.4	1.2
	4558	1.8	0.4

(upper) surface of adult palm leaves, i.e. 10 to 20 per mm². This is about 15 to 20 times less than on the abaxial (lower) leaf surface in *Elaeis* (GHOSE & DAVIS 1973). Typical guard cells measure approximately 20 × 15 × 9 μm and wide open apertures about 15 × 6 μm. Between 5 and 95% of a fruit surface area may be exposed depending on its location on the spikelet. In most fruits, however, 20 to 40% of the apical zone is exposed and, presumably, major proportions of the transpiration occurs from this area. Gas exchange rate enhancement due to convection depends on the orientation of the surface areas to the flowing air stream as well as the relative velocity. All these factors combine to make normalization of transpiration data with total weight of fruits only approximate since the weight of fruits in the cuvette is not directly proportional to the surface area available for effective moisture transfer.

Other factors. Other factors may affect transpiration rates in developing fruits indirectly. These include individual bunch sizes, soil moisture status, number of leaves on the tree, number of bunches developing simultaneously sharing sap supply, even legend has it that rainfall the previous year is an important factor in current year's sap flow rate into inflorescence or bunch.

Experiment design. The study involved simple factorial design comparative experiments in which the overall effect of the various unregulated factors were observed. Two test specimens at different stages of ripening or maturity were examined under identical external conditions in each set. Specimens were selected to provide duplication on the same tree for fruits 3 weeks to maturity (different bunches) and on different trees at 13 weeks to ripening. Data on different specimens could then be related.

Given the wet and dry bulb temperatures, the psychrometric chart yields both the Humidity Ratio (g. water/g. dry air) for ambient air and the specific volume for dry air at any given temperature. Direct measurements yield the volumetric dry air flow rate (since rotameters are located after moisture

adsorbent), thus the rate of moisture intake from ambient into the system can be determined. Water extracted by silica gel from flowing gas stream is a combination of that input from ambient air, and transpiration from the fruits. Transpiration rate was determined from the difference and values were normalized with total weight of fruits enclosed in the cuvette.

3.2. Oil content changes

Representative data on oil content changes in fresh mesocarp of developing fruits are presented in *table 2*. Data from similar studies by BLOMMENDAAL (1925) are partly reproduced in *table 3*. There is little oil (~0.3%) at 13 weeks to ripening. By 3 weeks to ripening, the oil content was still of the order of 1% by weight in most samples. Within the following two weeks more than 10% of the fruit was accounted for by oil and in the final week, accumulated oil rose to about 30% of final fruit weight. Practically all mesocarp oil was formed within the last three weeks of fruit maturation. The data of CROMBIE & HARDMAN (1958) and THOMAS et al. (1971), although presented on the basis of dried fruit or dry mesocarp weight, support this observation. As noted by Blommendaal, variations were found in the quantity of oil produced in individual fruits and in the final rates of oil accumulation. The position of the fruit specimen – inner or outer fruit (denoting depth of embedding within bunch cluster), and basal or apical locations on the central stalk on which the spikelets were arranged, affected these factors. Position could partly account for the divergence of between 20 and 45% of fresh mesocarp weight attributed to oil in ripe (mature) fruits. Each bunch development would also reflect the external

Table 2. Relative quantity of oil, dry non-oily solid matter (SM) and water in oil palm fruits measured at different stages of development. These are average values for a minimum of 6 fruits representing the distribution on a bunch. Samples were enclosed in the cuvette and controls were selected from the same zone on the bunch. The percents (determined on the basis of initial total weight of fruits) always summed up less than 100%. This suggests the loss of some volatile material.

Weeks to ripening	Sample			Control		
	percent			percent		
	Oil	SM	Water	Oil	SM	Water
1	13.40	18.7	63.0	11.50	21.5	65.0
3	1.60	15.5	79.0	1.20	16.6	81.4
	0.70	13.2	83.9	0.54	13.7	84.2
9	0.57	13.8	84.3	0.41	13.8	83.7
13	0.27	13.1	84.9	0.40	13.2	85.2
	0.28	13.6	83.8	0.31	13.0	84.8

Table 3. Changes in oil content during ripening of *Elaeis*, forma deli-dura – BLOMMENDAAL'S (1925) data; partly reproduced from his tables VIII and IX.

	% Oil in mesocarp					
	Outer fruits					Inner fruits
Days to ripening	Tree 128 Bunch 1	Tree 152 Bunch 4	Tree 152 Bunch 5	Tree 152 Bunch 6	Tree 153 Bunch 2	Tree 153 Bunch 1A
0	26.3	36.4	41.6	38.9	32.6	31.9
1	26.9	–	–	37.0	–	31.3
2	25.8	35.1	–	34.9	32.3	–
3	24.7	33.5	40.8	–	31.1	–
4	–	–	39.6	–	30.6	29.3
5	22.0	–	–	29.4	30.2	–
6	–	29.4	36.4	–	29.2	28.1
7	20.2	28.0	–	–	–	–
8	–	–	–	24.0	–	–
9	19.2	22.6	–	–	–	–
10	–	20.0	27.5	–	28.1	–
12	–	–	22.3	–	25.3	–
14	–	–	20.0	14.0	22.0	–
19	–	–	–	–	15.8	–
21	0.0	0.0	–	–	13.7	–
28	–	–	0.0	0.0	0.0	–

conditions during the growth. Anatomical examination of ripening fruits by YAMPOLSKY (1922) and BLOMMENDAAL (1925) revealed that the first oil droplets appear in a zone near the base of the fruit. The zone gradually extends radially and apically. In *table 2* data are also presented for the percent weight of fruits which is water. Until about 3 weeks to ripeness, 83 to 85% of the fruit weight was accounted for by water. After this stage, the proportion of water dropped, at first rapidly to about 75% followed by a slower but constant rate as cellular water is displaced by accumulating oil. Similar results are found in DESSASSIS' (1955) data.

The oil content data, averaged for many bunches in a given period, can nonetheless be normalized as shown in *fig. 4(a)*. Here the percent of maximum quantity of oil formed in the mesocarp of individual fruits at maturity is presented versus the time to ripening. The extensive data fall within a 95% confidence limit on the well-defined sigmoid curve whose significance will be examined shortly.

4. DISCUSSION

Since transpiration is to be related to the stage of fruit development, it is considered necessary first to discuss in detail some of the physical processes possibly occurring in the mesocarp tissue during ripening. The physical processes, it is suggested, under normal conditions become the rate limiting

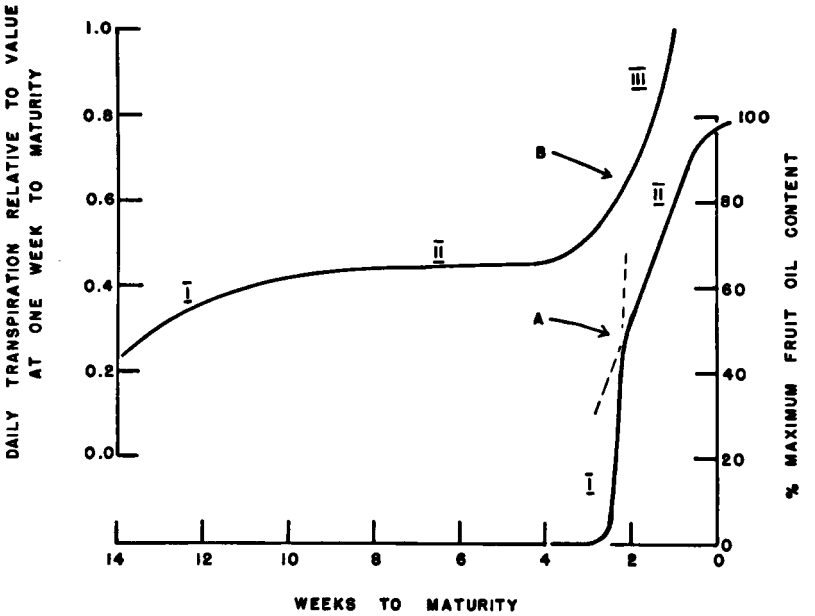

Fig. 4. (a) Percent of maximum oil produced in individual fruits plotted against age of fruits in number of weeks to maturity.
(b) Transpiration rates from fruits at different stages of development normalized to the value at 1 week to maturity.

steps for water transfer into the fruit as oil forms. The outlet for the excess water convected with sugars into the fruits is also of interest in view of the old controversy surrounding MÜNCH's (1930) hypothesis on the return flow of excess water from fruits back into the plant (see ZIMMERMANN 1969). No serious attention has been paid so far to the contribution of transpiration to water loss from developing fruits although VAN DIE (1974) suggested it may be significant during the ripening of *Cocos nucifera* and date fruits.

4.1. Fruit development

The sigmoid curve in the *figure 4 (a)* distinctly suggests that two oil accumulation rate-limiting steps are obtained when the percent of final quantity of oil produced in the mesocarp is plotted against stage of development. In the first part (I in *fig. 4a*) an exponential rate of oil accumulation is obtained. This suggests that primarily oil droplet nucleation (a physical process) and secondarily oil droplet growth (resulting from a complex series of enzymatic reactions) are controlling the events at this stage.

The origin and characteristics of oil droplets have been the subject of many studies and controversy (FREY-WYSSLING et al. 1963; NYMAN 1965; SOROKIN 1967; VIGIL 1970; MATILE 1975 and others). FREY-WYSSLING et al. (1963) hypothesized that oil droplets have spherosomes, minute vesicles detached

from strands of endoplasmic reticulum, as precursors. SOROKIN (1967) disagrees with this hypothesis. She suggests that spherosomes and oil globules (which are fat reserves) are distinct entities. What they have not resolved, however, is the question of how oil droplets originate and grow. These, together with the kinetics of reaction, are basic to how fast the sugars are converted into oil.

We propose that the active and prospective oil synthesis sites receive all the sugars (lipid precursors) needed and the quantity of oil formed in region I (*fig. 4a*) is determined strictly by the rates at which new oil nuclei form and enzymes catalyze the sugars to oil transformation. Excess sugars which enter the fruit are probably converted into starch simultaneously as the oil is formed. This may explain DESSASSIS' (1955) observation that starch and oil form at the same time. The rates are probably very different, oil formation being favored. Evidence exists that neutral fat may be dispersed in form of submicroscopic cytoplasmic emulsions (NYMAN 1965). These may be structured macromolecular clusters in the cytoplasm supersaturated with triglycerides. MULLIN & LECI (1969) found such clusters for organic citric acid in aqueous solutions. The triglyceride clusters in living cells probably gravitate towards special surfaces such as the endoplasmic reticulum where the energy barrier may be sufficiently lowered for oil globule precipitation homogeneously or heterogeneously around organelles or ergastic substances. The metastable condition is thereby relieved as clusters are inserted into the oil phase. Inorganic barium sulphate crystals presumably nucleated homogeneously in the cytoplasm of *Spirogyra* have been observed by KREGER & BOERE (1969). The weeks preceding the appearance of the first oil droplets may constitute an induction period during which the different parenchyma cells achieve various levels of triglyceride supersaturation. It is probably important to note that, even for hydrophilic substances, the solute concentrations which constitute supersaturation in ordinary water would be very different from those in the complex cytoplasmic fluids.

Theoretical considerations (see MULLIN 1972) suggest that the numerical rate of formation of the critical nuclei is given by the classical nucleation expression

$$J = A\exp\left[-B\left(\ln S\right)^{-2}\right]$$

where A is a weakly sensitive frequency factor and the exponent an activation energy related to the degree of supersaturation S. Slight variations in the exponent significantly affects the value of J once a critical level of supersaturation is exceeded. For the present, it suffices to note that the higher the supersaturation, the lower the activation energy, and the faster the rate at which new nuclei would be produced.

With the formation of nuclei, progressively more surface area (summed over all droplets) is made available for deposition of newly synthesized oil molecules even if, at a given temperature, the rate of enzymatic reactions remains unchanged. Ultimately, the maximum number of nuclei is formed and the

accumulation rate stabilizes. Between 40 and 50 percent of maximum oil content appears formed when this stage is attained.

Stage II probably depicts the zone of growth of individual oil droplets and their coalescence inside the parenchyma storage tissue. The kinetics of oil biosynthesis probably control the events over most of the range, and mass transfer of sugars by convection (in vascular tissue) and diffusion (out into the cells) become controlling near fruit maturity. The almost constant slope in this region is symbolic of a zero-order overall reaction and suggests that resistance to mass transfer (both passive and active) remains essentially stable until the space in which the oil accumulates nears exhaustion. The storage parenchyma cells, elaioplasts, then assume the round distended shape. One may conjecture that the oil synthesis apparatus thereafter becomes overwhelmed by its product as to diminish metabolic activity, that the porosity or permeability of the cell walls and membranes are lowered and the resistance to apoplastic mass transfer is increased by a raising of the tortuorsity factor. Oil accumulation rate slows down, although oil continues to be formed past the stage considered optimum for fruit harvesting.

4.2. Transpiration rates

In *fig. 3*, data are presented for the daily variation in transpiration rates for developing fruits. The averaged total water loss per unit fresh weight is obtained by integrating under the curves over the desired period. The factorial design experiment permits a comparative study of the transpiration data. This is presented in *fig. 4(b)*. In the plot the relative daily transpiration rates for developing fruits are normalized with the value at one week to maturity. Three regimes are apparent. Up to nine weeks to ripening, transpiration rate slowly increases. It is observed that since pollination of the inflorescence, the fruit has been growing in physical size, increasing the amount of solid matter and concomitantly increasing the exposed surface area for gas exchange with the ambient (De Poerck 1950). For the shell-less *pisifera* form (mostly sterile) the situation is apparently stable for the next five weeks in Region II (*fig. 4b*). In the last few weeks, activity increases and transpiration rate rises (III). Transpiration in the last week (not plotted) may be affected by the process of abscission which begins at the fruit base.

4.3. Relationship between transpiration and oil accumulation rates

On comparing *figs. 4(a)* and *(b)*, one notes the rapid increase in both transpiration and oil accumulation rates within the last 3 weeks of ripening; this suggests a correlation. The correlation is, however, not a simple one since the relative magnitudes of the two events prior to this stage are different. Between 9 and 3 weeks to fruit maturity, trannspiration is about 45% of the magnitude at 1 week while oil accumulation is negligible over the same period. If transpired water is partly or wholly obtained from phloem sap in this stage, the fate of the sugars entering with the water is not known. Neither oil nor appreciable

quantities of starch is yet formed and the dry (solid) matter of the fruit stays relatively constant at about 14%. DESSASSIS (1955) recorded 16% for dry solid weight in the mesocarp of the deli-dura species of the oil palm fruit. It is conceivable that the overall sugar concentration in the sap entering the fruit varies with the stage of development.

The xylem of the fruit probably supplies most of the water lost through transpiration at this stage, with the balance accounted for by the phloem sap in which sugars for respiration were conveyed. The presence of many calcium oxalate crystals (raphides or druses) in increasing numbers of specialized cells in this period seems to support this idea as calcium is poorly mobile in the phloem (ZIEGLER 1975).

The increased transpiration rate late in the ripening period appears to be in response to increased translocation of phloem sap into the fruits to meet the sugar supply requirements for oil formation. The curves in *figs. 4(a)* and *(b)* may not be expected to assume the same shape in the last 3 weeks because of additional water displaced from the cytoplasm of parenchyma tissue, varying quantities of water generated during biosynthesis and respiration, and other factors.

4.4. Excess water outlet from fruits

Measured daily transpiration ranges between 6 and 25% of the mesocarp weight depending on environmental conditions and stage of fruit development. We therefore select an example which permits the construction of the lower bound for the rate of water influx via phloem sap into maturing fruits, and the total amount of water that leaves. That is, late in the ripening period. In a specimen, 13.4% of fresh fruit weight was attributed to oil at 1 week to maturity. Between the nineth and third week to maturity, the dry non-oily solid matter of control samples on the bunch was almost steady at 13.5% of fresh fruit weight. At one week to maturity the value had risen to 23.6%. This increase is attributed primarily to cytoplasmic material and stored starch granules, although a small quantity of calcium oxalate is noted. The rate of dry solid matter increase is most significant at the initial stages of oil formation. Sugar concentrations in the phloem sap were not measured in the experiments, but during the wet seasons in the tropics, a concentration of 14% by weight is a reasonable value. The phloem is thus estimated to have supplied a minimum of 175 g water to 100 g fresh mesocarp between the third and the final week to maturity. (The basis is 100 g fresh mesocarp weight at 1 week to maturity.) Over the same period, the amount of water transpired is estimated (with the aid of *fig. 4(b)* and data that water equivalent to 13.8% of fruit weight was transpired in a day at 3 weeks to maturity) to be approximately 260 g. This is of the same order of magnitude as water supplied by the phloem after water displaced by oil from the cytoplasm and water generated by biochemical reactions have been taken into account. Contributions from the xylem may be involved as well. Ten to 25% variations in the measured amount of water transpired does not appear to alter the conclusion that the transpiration stream accounts for

water influx via the phloem, as the overall quantity of oil formed reflect the direction of the variation. That is, increased transpiration attended increased total oil formed and vice versa. Fruits embedded deep in the bunch transpire less than outer fruits and consequently form less oil. Inner fruits are smaller and generally have the same or less percent oil in the mesocarp as outer fruits. The fact that inner fruits ripening appears to lag behind the outer fruits (BLOMMENDAAL 1925) may be consistent with the fact that the driving potential for water loss is lower for inner fruits surrounded by an atmosphere that is almost saturated.

The events taking place may be described with the aid of *fig. 5 (a, b)*. In the early stages of ripening after formation of initial solid matter, it is suggested that water predominantly enters the fruit through the xylem, the flow actuated by transpiration pull (*fig. 5 (a)*). Small quantities of water may enter via the phloem with the food for respiration. No appreciable quantity of water is lost

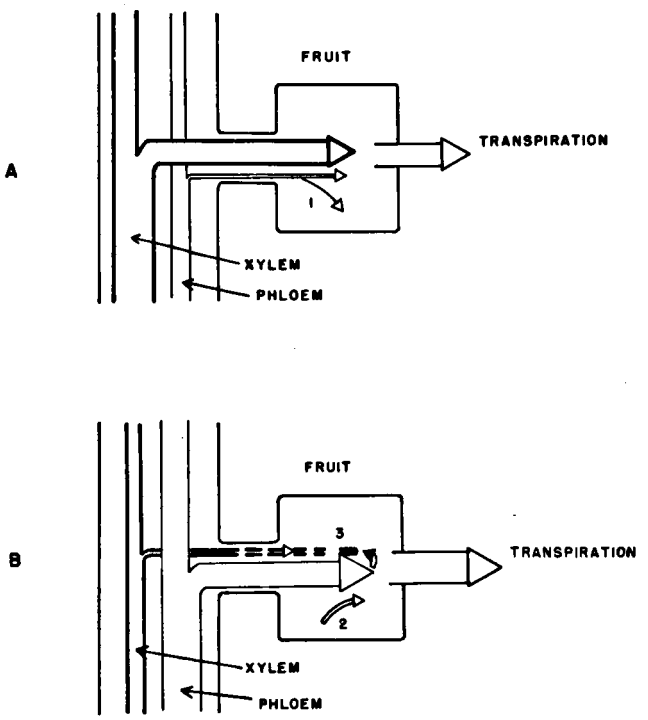

Fig. 5. Models for water flow in and out of developing oil palm fruits. Arrow width is drawn (not to scale) to reflect volumetric flow rates in vascular tissue, not the conduit size.
(a) Transpiration stream supplied primarily via the xylem of young fruits. Sugars are removed from the sieve tubes for local uses (1).
(b) Near maturity, transpired water is derived principally from the phloem. Water is also displaced from fruit parenchyma tissue (2). The xylem may supply or return small amount of water (3).

or gained by the fruit from the xylem stream. When oil formation starts (activated presumably by a hormone), a large quantity of water enters the fruit via the phloem (*fig. 5 (b)*). Estimates have shown this quantity to be comparable to the transpiration stream which apparently increased to handle the input. Under such conditions, the tension required to sustain inwards flow through the xylem would be much reduced. Obviously there would be an overlap period in which both phloem and xylem supply water to the fruit. Xylem flow into the fruit may ultimately stop or even be reversed depending on relative stream flow rates. The event depicted in *fig. 5 (b)* thus appears to be the basis of the controversy of MÜNCH (1930), DOEPP (1939) and ZIEGLER (1963). Different fruits may behave in different ways. For fruits "dry" at maturity, such as *Cocos nucifera* and *Phoenix dactylifera*, transpiration may at a late ripening stage exceed the influx rate of water as was postulated by VAN DIE (1974).

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REFERENCES

BLOMMENDAAL, H. N. (1925): Preliminary paper on the ripening of oil-palm fruits. *Comm. Gen. Expt. Sta. of A.V.R.O.S.* No. **20**. Medan, Sumatra.

CANNY, M. J. (1975): Mass Transfer. In: M. H. ZIMMERMANN and J. A. MILBURN (eds.), *Encyclopedia Plant Physiology* Vol. **1**, Chapter 5, pp. 139–153. Springer-Verlag, Berlin.

CROMBIE, W. M. & E. E. HARDMAN (1958): Fat Metabolism in the West African Oil Palm (Elaeis Guineensis), III. Fatty Acid Formation in Maturing Exocarp. *J. Expt. Bot.* **9** (26): 247–258.

DE POERCK, R. A. (1950): Contributions à l'étude du palmier a huile africain. *Oléagineaux* **5**, No. 11: 623–628.

DESSASSIS, A. (1955): La détermination de la teneur en huile de la pulpe de fruit D'Elaeis guineensis. *Oléagineaux* **10**, No. 12: 823–827.

DIE, J. VAN (1974): The developing fruits of Cocos nucifera and Phoenix dactylifera as physiological sinks importing and assimilating the mobile aqueous phase of the sieve tube system. *Acta Bot. Neerl.* **23** (4): 521–540.

—, & P. M. L. TAMMES (1975): Phloem exudation from Monocotyledonous axes. In: M. H. ZIMMERMANN and J. A. MILBURN, (eds.), *Encyclopedia Plant Physiology* Vol. **1**, Chapter 8, pp. 196–244. Springer-Verlag, Berlin.

DOEPP, W. (1939): Beiträge zur Frage der Stoffwanderung in den Siebröhren. *Jahrb. wiss. Bot.* **87**: 679–705.

FREY-WYSSLING, A., E. GRIESHABER & K. MÜHLETHALER (1963): Origin of Spherosomes in Plant Cells. *J. Utrastruct. Res.* **8**: 506–516.

GHOSE, M. & T. A. DAVIS (1973): Stomata and trichosomes in leaves of young and adult palms. *Phytomorphology* **23** (3/4): 216–229.

HARTLEY, C. W. S. (1967): *The Oil Palm*. Longmans, Green & Co., London.

HUBER, B., E. SCHMIDT & H. JAHNEL (1937): Untersuchungen über den Assimilatstrom. I. *Tharandt. Forstl. Jb.* **88**: 1017–1050.

KREGER, D. R. & H. BOERE (1969): Some Observations on Barium Sulphate in Spirogyra. *Acta Bot. Neerl.* **18** (1): 143–151.

MATILE, P. H. (1975): *The Lytic Compartment of Plant Cells.* Cell Biol. Mono., Vol. 1, Springer-Verlag, Berlin.

MEIDNER, H. and T. A. MANSFIELD (1968): *Physiology of Stomata.* McGraw-Hill. London.

MULLIN, J. W. (1972): *Crystallization.* Second Edition. Butterworths, London.

—, & C. L. LECI (1969): Evidence for molecular cluster formation in supersaturated solutions of citric acid. *Phil. Mag.* **19:** 1075.

MÜNCH, E. (1930): *Die Stoffbewegungen in der Pflanze.* Fischer, Jena.

NYMAN, B. (1965): Histochemical observations on the fatty reserve in Light- and Dark-germinated seeds of Scots Pine (Pinus silvestris L.). *Physiol. Plant.* **18:** 1095–1104.

RASCHKE, K. (1975): Stomatal Action. *Ann. Rev. Plant Physiol.* **26:** 309–340.

SOROKIN, H. P. (1967): The spherosomes and the reserve fat in plant cells. *Am. J. Bot.* **54** (8): 1008–1016.

THOMAS, R. L., P'HANG SEW, C. K. MOK, K. W. CHAN, P. T. EASAU and S. C. NG. (1971): Fruit Ripening in the Oil-palm Elaeis Guineensis. *Ann. Bot.* **35:** 1219–1225.

TRANQUILLINI, W. (1964): Photosynthesis and dry matter production of trees at high altitudes. In: *The Formation of Wood in Forest Trees*, M. H. ZIMMERMANN, ed. Academic Press.

VIGIL, E. L. (1970): Cytochemical and developmental changes in microbodies (glyoxysomes) and related organelles of castor bean endosperm. *J. Cell Biology* **46:** 435–454.

YAMPOLSKY, C. (1922). A contribution to the study of the African Oil Palm, Elaeis guineensis Jacq. *Bull. Jard. Bot. Buitenzorg*, Sér. 3, **5** (2): 107–174.

ZIEGLER, H. (1956): Untersuchungen über die Leitung und Sekretion der Assimilate. *Planta* **47:** 447–500.

—, (1963): Verwendung von ^{45}Calcium zur Analyse der Stoffversorgung wachsender Früchte. *Planta* **60:** 41–45.

ZIEGLER, H. (1975): Nature of substances in Phloem. In: M. H. ZIMMERMANN & J. A. MILBURN (eds.): *Encyclop. Plant Physiol.* **1**, chapter 2, 59–100. Springer, Berlin.

ZIMMERMANN, M. H. (1957): Translocation of organic substances in trees. II. On the translocation mechanism in the phloem of white ash (Fraxinus americana L.). *Plant Physiol.* **32:** 399–404.

—, (1969): Translocation of Nutrients. In: *Physiology of Plant Growth and Development.* M. B. WILKINS, ed. McGraw-Hill, London.