

THE DEVELOPING FRUITS OF *COCOS NUCIFERA* AND *PHOENIX DACTYLIFERA* AS PHYSIOLOGICAL SINKS IMPORTING AND ASSIMILATING THE MOBILE AQUEOUS PHASE OF THE SIEVE TUBE SYSTEM

J. VAN DIE

Botanisch laboratorium, Rijksuniversiteit, Utrecht

SUMMARY

Analyses of ripe fruits of *Cocos nucifera* and *Phoenix dactylifera* carried out at the author's laboratory, and data on the composition of the developing fruits of these palms derived from literature, have been used in a study which has shown that at any stage of its development the fruit may be regarded as being built up from a hypothetical fluid with an approximately constant composition. The composition of this assumed nutrient fluid, which could be postulated for its dry matter, total ash, K, Mg, Ca, P, and N contents, appeared to be very similar to that of the sieve tube exudates from severed inflorescences of *Cocos nucifera* and *Arenga saccharifera* (Palmae) and *Yucca flaccida* (Agavaceae). The only exception appeared to be the calcium content of the fruits, which was found to be at least 10 times higher than in an equivalent amount of sieve tube exudate. 90% or more of this calcium was localized in the vascular bundles of the husk and is assumed to have a xylem origin.

The total amounts of phloem exudate solutes, which are annually obtained by palm-sap collectors from the stumps of cut off inflorescences, are of the same order of magnitude as the amounts normally utilized for the production of fruits. Fruit production, and exudate production may therefore be regarded as alternatives in utilizing the mobile aqueous phase of the sieve tubes system, which carries the available photosynthates and ions to either developing fruits or bleeding site. Since during fruit development the assimilates flow simultaneously to about 10 bunches of growing fruits, while a bleeding *Cocos* tree produces its exudate from about 10 successive inflorescences, the rate of mass transfer through one inflorescence will be about 10 times higher during bleeding than during fruit production.

The data reported in this study are believed to deliver additional evidence for the view that mass flow is the way in which assimilates move through the sieve tubes into the growing fruits of *Cocos nucifera*, *Phoenix dactylifera*, and probably other palm species too.

2. INTRODUCTION

The phloem bleeding from palm inflorescences has much in common with that of an Agavacea like *Yucca flaccida*. Not only many details on the phenomenon of bleeding are very similar in both instances, but also the composition of the exudates hardly differ (VAN DIE 1968). With some exceptions (e.g. TAMMES 1933, 1952, 1958) only the bleeding from *Yucca flaccida* has so far been investigated in greater detail. Its exudate could be shown to represent the mobile aqueous phase of the sieve tube system, transporting labelled carbohydrates

without a change in specific activity from a pool of labelled photosynthates present in a leaf to the site of bleeding 30 cm or more away from it (VAN DIE, VONK & TAMMES 1973).

Removal of the labelled leaf of such a *Yucca* plant leads to a rapid fall in specific activity of the exudate sucrose (VAN DIE & TAMMES 1974) which indicates that outside the labelled leaf and the aqueous phase of the sieve tubes only traces of labelled compounds were available for translocation. Therefore, the suggestion of CANNY (1973) that in intact plants such an aqueous phase would be merely a stationary one in equilibrium with structural elements inside the sieve tubes, which would be actually involved in translocation, seems improbable. If such a situation would exist in the intact *Yucca* plant then the fall in specific activity of the exudate sucrose would probably be slower than actually observed, and cooling the translocation pathway would lead to a retardation of translocation. This was distinctly found not to be the case (TAMMES et al. 1969).

The *Yucca* plant as it grows in gardens in Western Europe unfortunately does not set fruit. A study on the change in composition of such fruits during their development would allow a comparison of the mechanism of the assumed flow to an artificial sink (the bleeding site) and to the natural sink (the fruits). Such an approach has recently been made for palm species with lateral inflorescences, such as *Cocos nucifera*, using literature data on their annual yields of fruits produced by intact inflorescences and of exudate produced from severed ones, and also in the case of palms with a terminal inflorescence such as *Corypha* species, with respect to their production of stem starch (sago), fruits, and exudate (VAN DIE & TAMMES 1974).

The present paper has found its origin in analyses of ripe *Cocos* and date fruits, carried out to compare their composition with that of *Cocos* and other palm exudates. Several reports have made it probable that the mineral nutrition of fruits of various plant species mainly occurs via the phloem (e.g. WIERSUM 1966, 1967; for more literature see FISCHER 1967, and BOLLARD 1970), with the possible exception of the calcium supply (cf. ANSIAUX 1958, 1959). Therefore, if the exudate composition of palm inflorescences actually reflects the composition of the normal assimilate flow, then the fruit will have the same mineral composition as the exudate.

The present study not only demonstrates this predicted relation between fruit and exudate composition, but it also shows that, with the apparent exception of calcium, the absolute amounts of both carbon compounds and minerals that can be collected in either exudate or fruits are of the same order of magnitude; consequently, that fruit and exudate production are alternatives in qualitative as well as in quantitative respect.

3. THE RELATIONS BETWEEN THE MOBILIZATION AND UTILIZATION OF CARBOHYDRATE RESOURCES OF THE PALM TREE AND THE PRODUCTION OF EITHER FRUITS OR BLEEDING SAP IN *METROXYLON*, *CORYPHA*, *COCOS*, AND *ARENGA*

The carbohydrate resources used or mobilized during bleeding from the stumps of cut off palm inflorescences may be brought together in three categories: (1) Mainly stored starch reserves, present in the pith of the trunk of trees like

Corypha and some *Metroxylon* species. These trees flower once in their lifetime and then die. Their terminal inflorescences are among the largest known in plant kingdom and may reach a size of 10 m height and 5 m diameter (DOUGLAS & BIMANTORO 1956). The quantity of starch which has gradually accumulated in the trunk during the lifetime of the tree may amount to several hundreds of kilograms (GIBBS 1911; HEYNE 1927, 1950; SPRECHER VON BERNEGG 1929). It becomes mobilized with the onset of flowering and is apparently utilized, together with the current products of photosynthesis, for the production of fruits. ZIMMERMANN (1973) reports the production of 600 kg of dry fruits from a single *Corypha elata* specimen. If a sago palm is to be used for starch production it should be cut down before it starts flowering (HEYNE 1927, 1950). *Corypha* species are usually not used for sago production but are tapped from the cut off stem apex just before the development of the inflorescence starts. Large amounts of exudate can be collected from such palms. They may contain several hundreds of kilograms of sucrose. During this exudation the amount of starch in the trunk gradually diminishes and has virtually completely disappeared when the exudation has come to an end (GIBBS 1911). From these data one may deduce that the carbohydrate resources of the trunk, which are mobilized at the time of flowering, subsequently move in soluble form to the inflorescence, either to the site of bleeding, or to the developing fruits (VAN DIE & TAMMES 1974). This deduction is not only of qualitative importance, but its quantitative aspects seem of even more significance, as they could point to the bleeding sap with its ca. 17% sugar to be the fluid that also in the normal intact inflorescence, supplies the growing fruits of carbon compounds and possibly mineral elements too.

(2) A second category of palms has lateral inflorescences, which, when the tree has reached a certain age, grow from buds present in the axils of the leaves. *Cocos nucifera* is a well-known example of which is also known that it does not accumulate starch in its trunk (REIJNE 1948). Apparently the fruits are made from the current production of photosynthates.

(3) A third group of palms seems more or less intermediate between the groups (1) and (2). *Arenga saccharifera* is a representative of it. The tree forms a number of lateral inflorescences a few years before the end of its life. Bleeding from *Arenga* inflorescences has been investigated in considerable detail by TAMMES (1933, 1952, 1958). The tree accumulates starch in its trunk, but compared with the trees of group (1) only a small amount (60 kg according to TAMMES 1933; 75–100 kg according to SPRECHER VON BERNEGG 1929), which

disappears when the tree is tapped from its inflorescences (TAMMES 1933). During the three to four years that this palm species makes inflorescences about 540 litres of exudate can annually be collected. This means that in all the tree may produce about 1900 l of sap with about 285 kg of sucrose (TAMMES 1933; SPRECHER VON BERNEGG 1929) during which about 80 kg of stored starch disappears. A rough calculation consequently shows that in the last 3½ years of its life the tree annually produces about 60 kg of photosynthates, which can be withdrawn from it by tapping. Normally this amount (together with the starch reserves) will be available for fruit production. A comparison with the annual fruit production of some commercially important palm-fruit producers with lateral inflorescences (group 2), such as the cocos, date, and oil palm shows that for these trees an annual production of about 60 kg of dry fruits will be near the average yields known for them (see *table 5* and page 538).

4. THE YIELDS OF EXUDATE FROM *COCOS NUCIFERA*

Since tapping the inflorescences of various palm species was – and often still is – of considerable local economic importance owing to the large amounts of sugar that can be obtained in this way, especially in the older tropical agricultural literature regular attention has been paid to this subject. The more physiological aspects of many of these investigations have recently been discussed in considerable detail elsewhere (VAN DIE & TAMMES 1974). In the present paper mainly the yields and composition of juice that can be obtained from a cocos tree will be dealt with.

According to PATEL (1938) there is a considerable variation in the yield of juice from day to day, season to season, spadix to spadix, and tree to tree. EATON (1917) has mentioned a total yield that could be obtained per spadix (inflorescence) of 16–34 litre (Ceylon).

PATEL (1938) has investigated two sets of cocos trees on which tapping had commenced in the months of November (5 trees) and April (4 trees) respectively (Madras, India). The average for the November group was 18.0 litre per spadix and for the April group 15.5 litre. NATHANAEL (1955) has reported for Ceylon an average yield of 1.5 litre per day per tree during a 12 months tapping period, or 547 litres per year. Such a total production has also been found by GIBBS (1911) for coconut trees of the Philippines. Trees in good condition, growing in good soil, produced about 400 l of sap annually and were in their prime when about 40 years old. Young trees often produced less than 300 l. A test with 100 average trees showed an average daily production (day flow + night flow) of 1.38 l per tree, or approximately 504 litres per year.

5. THE YIELD OF FRUITS

The annual yield of fruits depends on the number of bunches (spadices, inflorescences) formed, on the number of fruits each of them bears, and on the average size of the fruits.

a) *Cocos nucifera* – The fruits of the common variety of coconuts of the Malabar coast (India) were relatively small (SAMPSON 1923) and had an average dry weight of 500–600 g. Trees bearing 128 fruits per year (16 bunches with 8 fruits each) were not unusual (SAMPSON 1923), but plantations with an average yield of 60 nuts per tree were also nothing out of the usual. Consequently, the dry fruit production per year and per tree will have been about 30–75 kg. Also HEYNE (1927, 1950) has reported that a well-bearing palm has an annual production of 60–100 nuts, which may contain about 16–27 kg of dry copra. Keeping in mind that the other fruit parts occupy about 71% of the total dry matter of the fruits (*table 1*) then the annual production of dry fruits will have been about 55–93 kg per tree. An annual yield of 60–100 nuts per tree also appears to be a good average for Indochina and the French Polynesian islands (SPRECHER VON BERNEGG 1929; FRÉMOND et al. 1966).

b) *Phoenix dactylifera* – The cultivar Deglet Noor of the date palm sets more fruits than can be matured properly (HAAS & BLISS 1935) and therefore the bunches are naturally and artificially thinned. Approximately 90 kg of fruits are harvested annually from an average palm (10 bunches of about 900 fruits each). This amount corresponds to about 54 kg of dry fruit weight. Since dry substances have been lost in early stages of fruit development by thinning, the actual dry matter production of the date palm will be somewhat higher. From the data of HAAS & BLISS (1935) a total annual production per tree of 60 kg of fruit dry matter seems a fair estimate.

6. THE CHANGE IN COMPOSITION DURING THE DEVELOPMENT OF THE FRUITS

Since fruit growth is accompanied by an increase in amount of dry matter and water, a logical assumption seems that the various substances and water enter the developing fruits as an aqueous solution, at least as far as xylem solutes are concerned. As far as the substances are translocated through the phloem a constant ratio between all mineral elements in the developing fruits and their dry weights may be expected if also in the phloem a mass flow of assimilates takes place. A careful analysis of the developing fruit in all its stages of growth can therefore provide information about the amounts and the concentrations of the various materials that enter it, and consequently about the probability that these substances have been translocated *en masse*. Four processes should not be neglected in such considerations, i.e.

- (1) photosynthesis carried out by the fruit wall;
- (2) losses of dry matter due to respiration;
- (3) loss of water, e.g. due to transpiration during fruit development;
- (4) leaching of solutes from the fruits by rain.

In developing apricots, apples, and citrus fruits the rate of fruit photosynthesis is relatively low (BOLLARD 1970), and in citrus fruits the contribution of photosynthesis is no more than to supply enough matter to replace that used in respiration. No data are available on this subject with respect to palm fruits,

Table 1. *Cocos nucifera*. Composition of a whole ripe fruit. All weights are on a dry matter basis.

Fruit part	Mg		P		Ca		N		K		Ash		Dry Matter gr.
	mg/g	mg	mg/g	mg	mg/g	mg	mg/g	mg	mg/g	mg	mg/g	mg	
Husk	0.361	101	0.101	28.4	1.98	556	2.09	587	7.60	2135	27.0	7590	281
% of whole fruit	36.8		10.1		95.7		26.2		62.0		69.3		51.5
Nutshell	0.061	6.1	0.051	5.0	0.162	16	0.83	83	1.24	123	2.60	260	99.5
% of whole fruit	2.2		1.8		2.7		3.7		3.5		2.4		18.2
Endosperm	0.99	158	1.50	240	0.046	7.4	9.62	1539	6.78	1085	16.9	2700	160
% of whole fruit	57.7		85.2		1.3		68.8		31.5		24.6		29.3
"water"	1.66	9.4	1.46	8.2	0.336	1.9	4.78	27	18.0	102	71.9	405	5.65
% of whole fruit	3.4		2.9		0.3		1.2		3.0		3.7		1.0
Whole fruit	0.50	274	0.52	282	1.06	581	4.1	2236	6.3	3445	20.0	10955	546

therefore it is assumed in the present study that, as in *Citrus*, photosynthesis and respiration are in balance and may be neglected in comparison with the import of carbon compounds. Apart from that, an excess of photosynthesis over respiration, or its reverse, may become evident in fruit analyses as a rise in the dry matter-to-ash ratio, or as a fall in it.

a) *Cocos nucifera* – Results of analyses presented in the form of many tables by SAMPSON (1923) have been used for the construction of a number of graphs, which relate the dry weight of the fruits with the amounts of potassium, nitrogen, magnesium, calcium, and phosphorus present in them. A striking linear relation is shown (*fig. 1*) in particular between the amounts of K and P and the dry weights of the developing fruits. For each gram increase in dry matter the amounts of K and P rise with 6.9 mg and 0.62 mg respectively. For calcium this value proved to be 1.4 mg. For nitrogen such a linear relation appeared to exist for all but the last stages of fruit development, while during the first stages of growth the influx of magnesium seems considerably higher than in later stages. Leaving these irregularities out of consideration for a while, one may describe the growth of the cocos fruit during its entire period of development (12 – 14 months) as an import of 6.9 mg of K, 0.62 mg of P, 6.0 mg of N, 1.4 mg of Ca, and 1.1 – 0.6 mg of Mg per gram increase of fruit dry weight.

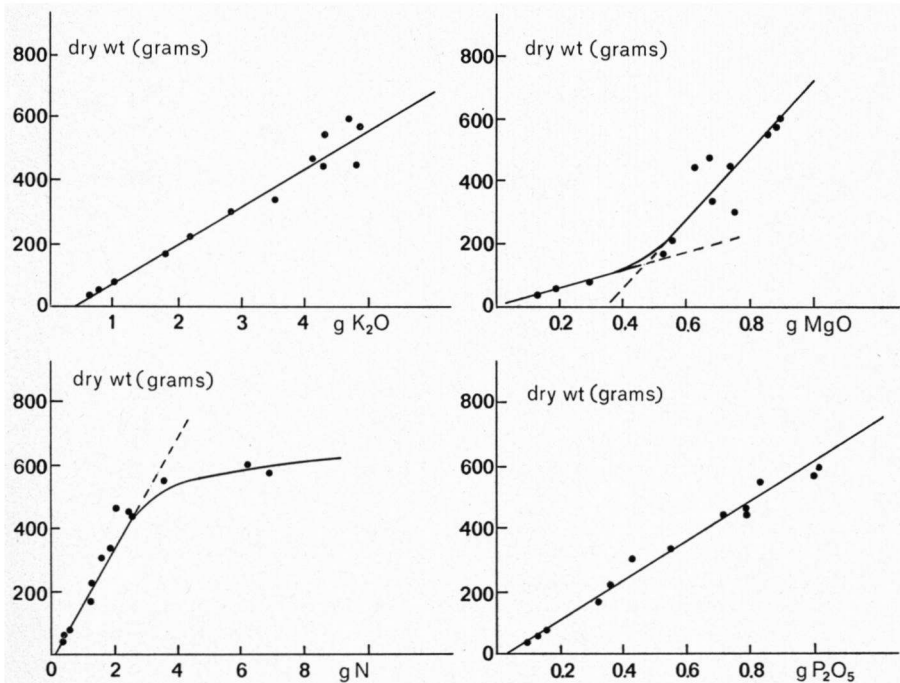


Fig. 1. The potassium, nitrogen, and phosphorus contents of developing cocos fruits in relation to the dry weights of these fruits. All data are derived from SAMPSON (1923).

These data could indicate that the various elements mentioned enter the fruit together with the bulk of dry matter in the form of an aqueous solution with more or less constant composition.

Fig. 2 gives the relations between fresh and dry weight of the developing cocos fruits as reported by SAMPSON (1923). From these data it can be inferred that up till their final volume (bunch 8 – 9) the dry matter content of the fruits is about 17 – 22%. A large part of the development of the cocos fruits can consequently be explained by the simple assumption of a gradual movement into it of a solution containing about 15-18% dry substances. During these growth stages loss of water by transpiration will be small. But also in later stages of development the hypothesis of this 15-18% solution appears to give a satisfactory explanation of the increase in fruit dry weight as is shown in Fig. 2. The rate of flow of this postulated solution into the fruit remains reasonably constant during almost the entire period of fruit growth, which may be considered a support for the

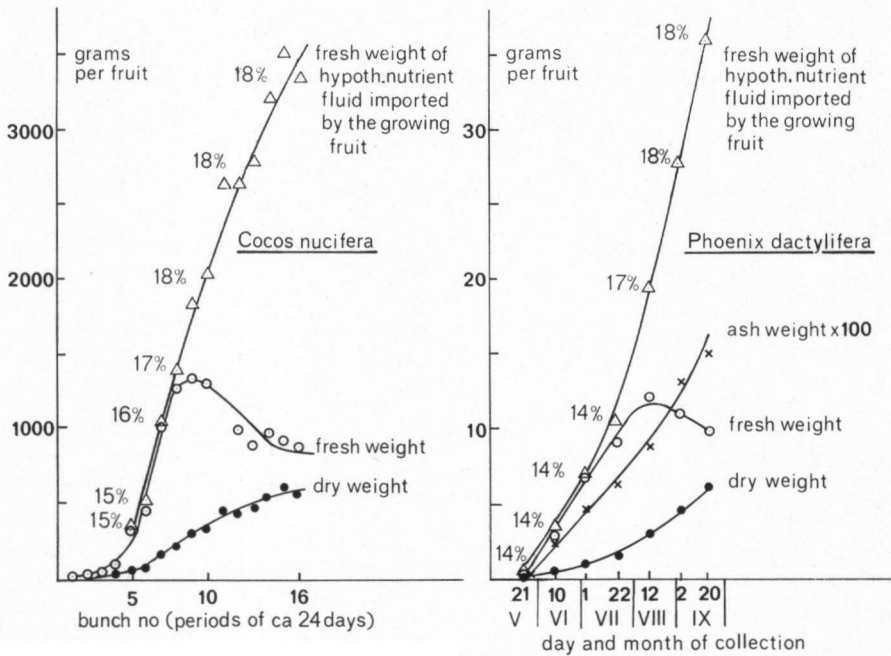


Fig. 2. The development of the fruits of successive bunches of a regular-bearing cocos tree. The difference in age between two successive bunches is about 24 days. Data on fresh and dry weights are derived from SAMPSON (1923).

Fig. 3. The development of the fruits of the date palm ('Deglet Noor'). Data on fresh weight, dry weight, and ash weight of the fruits (without seed) are derived from HAAS & BLISS (1935). Both figures also show the amounts of sieve tube fluid which are assumed to have entered the cocos and date fruits at any stage of development. The percentages beside these lines indicate the assumed dry matter content of the hypothetical fluids at the various stages of development.

correctness of the assumption. It also means that transpiration would become considerable after the fruit has obtained its final size. Again the tables presented by SAMPSON (1923) make clear that this half-way stage in fruit development is characterized by the onset of important biochemical processes within the fruit. It is at this stage that endosperm formation starts, that the volume of the so-called water inside the nut decreases, and – important for the assumption made – that the fresh weight of the husk starts to diminish. It is this latter process that points to a considerable decrease in resistance against transpiration, and consequently may explain its sudden increase predicted on the ground of the assumed constancy in composition of the postulated nutrient fluid.

Table 1 shows the results of an analysis of a mature cocos fruit carried out at the author's laboratory. They are in good agreement with the results reported by SAMPSON (1923) and are, therefore, considered to be a support for the correctness of the latter.

If one assumes a 15–18% nutrient solution with constant composition, then the development of a fruit with a dry weight of 600 g needs the import and utilization of about 3500 ml of this nutrient fluid (*fig. 2*). It has moved into the fruit with a rate of about 9.7 ml/24 hours during about 360 days. The number of fruits per bunch and the number of bunches per year differ considerably from tree to tree, but from literature one can take an average of 10 bunches of 10 fruits each, which at each time of the year will be present at the tree. 10 fruits per bunch means that per 24 hours 10 times an average of 9.7 ml of nutrient fluid has to enter the bunch, or about 97 ml/day. It also means that during the whole period of coconut development about 10 times 3500 ml of nutrient fluid, or 35 litres will flow into each bunch.

b) *Phoenix dactylifera* – The date palm shows a pattern of fruit development not essentially different from the one given for *Cocos nucifera* in *fig. 2*. Data reported by HAAS & BLISS (1935) have been used for the construction of *fig. 3*, in which just as in *fig. 2* a hypothetical curve represents the amount of nutrient fluid assumed to have entered the fruit at each time of its development (140–208 days from anthesis to complete ripeness). Here too, the assumed loss of transpiration water becomes apparent mainly after the fruits have reached their maximum size (in the period of 22.VII-12.VIII). HAAS & BLISS (1935) have determined the rate of water loss of detached freshly picked mature dates at temperatures between 70°F and 120°F (21° and 50°C), a range which covers the fluctuations in daily temperatures in the field (Riverside, California) during July and August. Under these circumstances an average date appears to lose 0.28–3.4 ml of water per 24 hours. Taking into consideration that within an average bunch of 900 fruits under natural conditions, owing to a relatively high humidity, considerably less transpiration will occur, the values of water loss per fruit predicted on the basis of the present hypothesis (0.21 ml/24h for the period of 22.VII-12.VIII, 0.45 ml/24h for the period of 12.VIII-2.IX, and 0.52 ml/24h for the period of 2.IX–20. IX; see *fig. 3*) seem to be in reasonable agreement with the rates of the actually occurring transpiration. Just as for the cocos fruit also for that of date palm graphs may be constructed for the amounts

of a number of elements present in the fruits at various stages of their development. Unfortunately, however, HAAS & BLISS (1935) have carried out their analyses with fruits from which the seeds had been removed. But since the seed occupies only about 9% of the fruit dry weight (*table 2*) the contribution of the seed to the mineral composition of the whole fruit is relatively small, especially since its ash content is only half that of the remainder of the fruit. *Table 3* presents data on the composition of the ash fraction of the fruits in relation to their age, and distinctly shows that this composition is remarkably constant. Just as for the cocos fruit, for the date fruit too one can postulate a hypothetical nutrient solution with constant composition from which the fruit will be built up during its development. For its composition the average values from those of Haas & Bliss have been taken (*table 3*). As has been found for the cocos fruit also for that of the date palm a reasonable degree of agreement appears to exist between the compositions reported in literature (SAMPSON 1923, HAAS & BLISS 1935) and those found by the author (*table 2* and *3*). The composition of the full-grown date fruit largely reflects the composition of the postulated nutrient fluid (*table 3*).

Table 2. The amounts of the four main elements in the ash of the two parts of the date fruit ('Deglet Noor'), expressed in mg/g ash.

		Fruit without seed	Seed
Dry weight (n = 15)		9.16 g (s = 0.94)	0.87 g (s = 0.08)
Ash weight (n = 15)		2.01% (s = 0.14)	0.90% (s = 0.054)
Potassium		428	475
		525	394
		426	282
		389	345
		361	422
	average	426	384
Magnesium		33	81
		37	80
		35	80
		31	84
		30	79
	average	33	81
Calcium		53	18
		37	10
		34	14
		33	25
		45	12
	average	40	16
Phosphorus		19	88
		17	84
		15	76
		19	102
		17	106
	average	18	91

Table 3. *Phoenix dactylifera*. The composition of the fruit (without seed) in various stages of its development (from 68 mg dry weight at 21. V to 5960 mg dry weight at 20. IX). The content of each element is expressed in mg/g ash. The data in the upper part of the table, except the average values are data reported by HAAS & BLISS (1935). The lower part of the table shows the composition of the ripe date fruit, as found by the author.

	Mg : P : Ca : N : K
21.V	30 : - : 48 : 232 : 414
10.VI	17 : 33 : 23 : 232 : 435
1.VII	28 : 35 : 32 : 198 : 382
22.VII	27 : 31 : 36 : 179 : 368
12.VIII	25 : 34 : 41 : 190 : 384
2.IX	24 : 27 : 37 : 158 : 403
20.IX	25 : 31 : 24 : 179 : 439
Average	25 : 32 : 34 : 195 : 404
	33 : 18 : 40 : 175 : 426

A difference of importance between the cocos and the date palm is that the latter produces its fruits only between March-April (pollination) and September-October (harvest). A regular-bearing coconut tree throughout the year, with intervals of about 24 days, forms new leaves, each with an inflorescence in its axil. The supply of photosynthates to these inflorescences will probably reflect this regularity: the leaf-to-fruit ratio remains more or less constant and the amounts of the nutrient fluid supplied to the fruits will not necessarily be subject to considerable changes, unless for example older leaves supply more photosynthates than younger ones. The date palm, however, develops six to eight new leaves in the summer, which increase the total leaf area about 6–12% (ALDRICH & CRAWFORD 1939). The increased supply of carbohydrates to the developing dates in late summer reported by both HAAS & BLISS (1935) and ALDRICH & CRAWFORD (1939) might partly be explained by this increased leaf-to-fruit ratio. In the present study this increased supply of solutes to the developing date has been accounted for in the hypothetical nutrient fluid by an increase in solute concentration from 14–18% together with an increased rate of influx from 0.15–0.41 ml/day (fig. 3).

The postulated increase in solute concentration of the hypothetical nutrient fluid for both cocos and date fruits (from ca. 14–18%) may also partly have been caused by a relatively high rate of respiration compared with photosynthesis in young fruits. In young date fruits the ash content is considerably higher than in mature ones (HAAS & BLISS 1935), which might indicate a loss of carbon compounds. On the other hand there are also indications that in early growth stages the supply of photosynthates or mobilized carbohydrates to the bunch is relatively low. In bleeding oil palms the first exudate collected has a low sugar content, and the tapper rejects it (SPRECHER VON BERNEGG 1929). During the following days a gradual increase of sugar occurs from 7½ to 13%. In *Corypha elata* the sugar content of the exudate increases gradually from an initial 11% to 14.4% at the 36th day of bleeding. Previous to the arrival of this "malorayat

stage" none of the sap is used for fermentation (GIBBS 1911). Also a bleeding *Arenga* inflorescence in the first days of bleeding produces a sap with a relatively low sugar content (TAMMES 1933). Its maximum concentration is also reached after about 35 days of bleeding.

7. THE HYPOTHETICAL NUTRIENT FLUID COMPARED WITH THE PHLOEM EXUDATE FROM PALM INFLORESCENCES

GIBBS (1911) has reported a striking resemblance in dry matter, sucrose, and ash contents of the bleeding sap from the palm species investigated by him (*Cocos nucifera*, *Arenga saccharifera*, *Nipa fruticans*, and *Corypha elata*). Only a few more detailed analyses of the exudates of the cocos and arenga palm can be found in literature. A compilation of the reported compositions of these exudates is presented in *table 4*, in which also the composition of the exudate from *Yucca flaccida*, and that of the hypothetical nutrient fluids of the cocos and date fruit are shown.

Table 4 clearly demonstrates the remarkable agreement in composition between all these fluids, with the apparent exception of the calcium contents, which are very low in the bleeding saps, but about 10 – 15 times higher in the assumed nutrient fluids of the date and cocos fruit.

The coconut tree fruits throughout the year, and the strain of providing assimilates, not only for the formation of fruits, but also for the development of other parts of the tree, is continual (apart from some seasonal influences). There is a distinct maximum in the amounts of assimilates available for movement into the fruiting inflorescences. If there are too many developing fruits on a bunch, some of them may be formed only partially, and bunches which follow (on the same orthostichy) usually carry a much smaller number of female flowers than the preceding well bearing ones (SAMPSON 1923). A similar situation exists for the date palms (cultivar Deglet Noor) investigated by HAAS & BLISS (1935), where natural thinning of the set fruits occurs in an early stage of development.

A similar reasoning can be made for tapping palm inflorescences. In order to keep the tree in a healthy, growing condition it cannot be tapped year after year. Trees deteriorate very rapidly if continuously tapped over long periods. In Ceylon (PATEL 1938) it has been found to be better in the long run to tap only for six months in a year. If tapping were to be continued further, there would be large variations in sap yield with frequently low yields. In Malaya (MARSDEN & SKILTON 1931) the palms are rested for about four months after tapping them for 18 months.

In the normal fruiting tree the withdrawal of assimilates for fruit production is apparently under metabolic control, while in the bleeding tree, provided care has been taken of regular wound renewal, such a control cannot be exerted by the plant. The bleeding inflorescence apparently is the dominating sink to which all available assimilates will move. As soon as the new inflorescence comes in production, however, the preceding one gradually stops its flow, so that in

Table 4. A comparison of the postulated composition of the hypothetical nutrient fluid of the fruits of *Phoenix dactylifera* ('Deglet Noor'), and of *Cocos nucifera*, with the compositions of the phloem exudates from the stumps of severed inflorescence of *Cocos nucifera*, *Arenga saccharifera*, and *Yucca flaccida*.

	Dry matter content	Per gram dry weight							K/Ca ratio
		N (mg)	P (mg)	K (mg)	Mg (mg)	Ca (mg)	Ash (mg)		
Hypothetical nutrient solution imported by growing fruits of									
a. <i>Phoenix dactylifera</i> - (based on data from HAAS & BLISS (1935)*	14-18%	3.9	0.64	8.1	0.50	0.68	*	11.9	
b. <i>Phoenix dactylifera</i> (author's data)		3.5	0.36	8.5	0.66	0.80	20.1	10.6	
<i>Cocos nucifera</i>									
c. (based on data from SAMPSON, 1923)	15-18%	6.0	0.62	6.9	0.6-1.1	1.4		5.0	
d. <i>Cocos nucifera</i> - (author's data)		4.1	0.52	6.3	0.50	1.06	20.0	6.0	
<i>Composition of phloem exudate</i>									
a. GIBBS (1911)	17-19%	5.5					22.8%		
b. BROWNING and SYMONS (1916)	15-20%	2.2-3.0							
c. LEONG (1953)***		1.8-2.1	0.36-0.61	6.6-9.4	0.20-0.28	0.027-0.086		77-136	
d. NATHANAEL (1955)		2.5	0.59	6.8	0.54	0.057	21.6	120	
<i>Arenga saccharifera</i> (Palmae)									
Composition of phloem exudate (1)	15-18%								
<i>Yucca flaccida</i> (Agavaceae)									
Composition of phloem exudate (2)	17-19%	6.8	1.0	8.4	0.54	0.068	24	123	

¹ Data derived from TAMMES (1933, 1958) and VAN DIE & TAMMES (1974).

² Data derived from TAMMES & VAN DIE (1964) and VAN DIE & TAMMES (1974).

* Based on the assumption of an ash content of 20.0 mg/g dry weight, which seems correct for the last two to three months of fruit development.

** Ash content derived from GIBBS (1911).

*** Quoted by CHILD (1964).

practice each inflorescence will only produce exudate for about one month. In comparing the amount of assimilates annually removed from a tree, either as dry fruits or as total exudate solutes, one has to keep in mind that the exudate originates from ten to twelve inflorescences, which have each produced for one month. Consequently an annual production of 350 litres sap from 10 inflorescences means that each inflorescence has produced 35 litres per month or 35×180 g dry weight = 6.3 kg dry weight per month and per inflorescence. An annual production of 100 nuts of 600 g dry weight each means that (10 bunches) each bunch has borne 6 kg dry weight, but this amount has entered the bunch over a period of about 12 months. Consequently, the rate of mass transfer from leaves to bunch was 0.5 kg/month and per bunch.

One may also express the difference between bleeding sap production and the supply of the postulated nutrient fluid to the developing fruits in terms of the demand the tree is making on its resources on account of either fruit development or bleeding sap production. A cocos tree with 10 bunches of 10 developing fruits each has to supply 100×9.7 ml per day (fig. 2) or approximately 1 litre of nutrient fluid with about 180 g dry substances per day. This amount will be determined by the photosynthetic capacity of the leaves. In case of bleeding a similar amount of exudate (and solutes) can be withdrawn from the tree without apparent damage to it. But this amount exudes from one inflorescence only, while in the case of fruit production the fluid enters 10 inflorescences simultaneously (see table 5). A similar reasoning has recently been made for *Corypha elata* (VAN DIE & TAMMES 1974) and it has been suggested that this aspect of mass transfer, which has been neglected in the past, might explain the astonishing high velocity of exudate flow (7 m/hr) through the phloem of the *Arenga* inflorescence stalk, as reported by TAMMES (1952). The anatomical consequences of these translocations are evident. Normally probably one row of leaves supplies the photosynthates to a particular bunch with developing fruits, but in the case of bleeding possibly all the available photosynthates move into the one inflorescence involved (for the anatomical basis of translocation in palms see e.g. TOMLINSON 1970 and ZIMMERMANN 1973).

8. THE CALCIUM SUPPLY OF THE FRUITS

Of several plant species the calcium content of the fruits is low compared with the potassium content (ANSIAUX 1959, FISCHER 1967, BOLLARD 1970). Of other fruits, however, the calcium content is considerably higher (e.g. CZAPEK 1920, ANSIAUX 1959). Apparently it is not a constant characteristic of a fruit type, as VAN SCHOOR (1957) demonstrated a linear relation between the calcium content of cotton seeds and that of the soil.

According to CANNY (1973) calcium occupies a special position among the ions in being non-translocatable by the phloem. On the other hand WIERSUM (1966) could not find an appreciable influx of ^{45}Ca moving in the xylem into developing apple and tomato fruits, which would mean that the low calcium contents of these fruits would be due to a low capability of the phloem to trans-

Table 5. A comparison of the annual production of two alternative crops that can be harvested from a Cocos tree, viz the fruits, or the exudate from the stumps of cut off inflorescences. For reasons of comparison also the annual production of the edible-date (*Phoenix dactylifera*, cv. 'Deglet Noor') and its constituents is presented.

	Volume of hypothetical nutrient fluid that enters one fruit during its development	Total volume of fluid that exudes, or is assumed to move into the fruits, per tree and per annum	Present in the fruits, or in the exudate produced per tree and per annum, expressed in grams or kilograms							
			Mg g	P g	Ca g	N g	K g	Ash g	dry matter kg	
<i>Phoenix dactylifera</i> (1)										
(+ 9% correction for the presence of seeds)										
43 ml										
9,000 fruits per year										
(without correction for fruit drop and artificial thinning)										
<i>Phoenix dactylifera</i> ²										
9,000 fruits per year										
<i>Cocos nucifera</i> ³										
128 fruits per year										
<i>Cocos nucifera</i> ²										
100 fruits per year										
<i>Cocos nucifera</i>										
Exudate										
12 months tapping:										
GIBBS (1911)										
NATHANAEL (1955)										
economic tapping:										
GIBBS (1911)										
EATON (1917) (10 inflor.)										
			36	44	35	262	640	1461	58	
		387 litres	65	40	65	270	720	1719	90	
			66	55	99	877	510		73	
	3500 ml	448 litres	27	28	58	224	344	1095	55	
<i>Cocos nucifera</i>										
Exudate										
12 months tapping:										
GIBBS (1911)										
NATHANAEL (1955)										
economic tapping:										
GIBBS (1911)										
EATON (1917) (10 inflor.)										
		504 litres	22	45	7	473	744	1961	86	
		547 litres				186			93	
		400 litres				374		1550	68	
		160-340 litres							27-58	

¹ analytical data derived from HAAS & BLISS (1935).

² data from the author. ³ Data derived from SAMPMON (1923).

locate this element. FAUST & SHEAR (1973) have also reported that calcium enters the apple fruit via the phloem. Possibly in fruits with a relatively high calcium content the xylem contributes more to fruit development than in fruits with a low calcium content. But apparently the phloem should not be excluded from calcium transport in plants, although the low calcium contents of the phloem exudates of palms and Agavaceae (TAMMES & VAN DIE 1964, VAN DIE & TAMMES 1974) very probably represent the highest possible ones in these alkaline, phosphate containing fluids.

The relatively high calcium content of the cocos fruit cannot be explained by the import of a phloem-exudate like fluid only. But from the author's data (table 1) as well as from those reported by SAMPSON (1923) it appears that 90–95% of this calcium occurs in the husk, and according to the present analyses, in the numerous fibrous vascular bundles of this fruit part.

A special feature of calcium transport is its ion-exchange type of movement in the xylem vessels (SHEAR & FAUST 1970), where lignin seems to be the compound providing the ion-exchange sites. Besides calcium, also magnesium and zinc have affinity for these charged groups. The present cocos fruit data may be explained, not by necessarily postulating a net uptake of appreciable amounts of xylem fluid by the fruits, but by simply assuming the existence of a fluid continuity in the xylem vessel system of the husk, that of the inflorescence stalk, and the vegetative parts of the tree. Depending on environmental conditions xylem water will regularly move in the direction of the fruits and probably even enter them, but after some time it will flow back again, taking with it most of the solutes of the xylem stream. But calcium, and perhaps some magnesium ions too, will stay behind, adsorbed by the lignin of the vascular bundles of the husk.

9. THE ROLE OF HORMONES IN PALM FRUIT DEVELOPMENT

The views developed in this study have as a consequence that the role of hormones in fruit development may be a more indirect one than usually supposed (e.g. NITSCH 1970, 1971). The flow of assimilates to the developing palm fruits is in essence largely similar to that which exudes from a stump of a severed inflorescence. There is even no need for the phloem bleeding to take place from an inflorescence with female buds. In *Arenga saccharifera* (TAMMES 1933) and *Elaeis guineensis* (SPRECHER VON BERNEGG 1929) it is the male inflorescence that is usually tapped for exudate. It means that the fruit, or the young or fertilized ovules, do not attract (by hormonal action) the assimilates from the leaves or stem, but simply receive them. The role of hormones in palm fruit and seed development may therefore be limited to creation of sink activity and the regulation of the biochemical and physiological processes which lead to the histological and chemical differentiation within these fruits.

Since phloem bleeding can only be obtained with palms and Agavaceae in which flowering starts, it might be possible that both the ability to bleed and the production of inflorescences have a common hormonal cause.

It would be interesting to investigate whether diphenylurea and zeatin riboside, both isolated from the liquid endosperm of the coconut (by SHANTZ & STEWARD 1955, and by LETHAM 1968, respectively, see NITSCH 1970), have been synthesized there or have been imported as such. In the latter case the presence of these cytokinins in phloem exudate of palm trees may be predicted.

10. DISCUSSION AND SOME CONCLUSIONS

The cultivar Deglet Noor of the date palm produces about 9000 fruits of about 10 g fresh weight each, the cocos palm about 100 fruits of about 1000 g fresh weight each. For this annual production they utilise roughly about 400 litres of a hypothetical nutrient fluid, the composition of which does not appreciably differ from that of the 400 litres of bleeding sap that, alternatively, by economic tapping can be obtained annually from *Cocos* trees (table 5). The data presented in this paper have led to the conclusion that the hypothetical nutrient fluid of the fruits, and the bleeding sap of *Cocos nucifera*, *Arenga saccharifera*, and probably some other palms too, may both be regarded as the mobile aqueous phase of the sieve tube system of these trees. As far as evidence is available palm exudates are very similar in composition, and do not differ much from those of *Yucca flaccida* (Agavaceae) and possibly *Agave* species either (VAN DIE & TAMMES 1974).

In the case of bleeding this mobile sieve tube fluid flows to an artificial sink (the bleeding site), in the case of fruiting the flow goes to the developing fruits. The rate of bleeding from a single inflorescence, however, is several times higher than the rate of assimilate flow into a single bunch during fruit formation. This throws some light on the high flow rate found for bleeding *Arenga* inflorescences (TAMMES 1952). Nevertheless the high flow velocity found in bleeding *Arenga* clearly shows that such a flow is theoretically possible in sieve tubes of this palm species.

With the water of the phloem sap stream the bulk of the inorganic ions, the nitrogenous substances, and the carbon compounds, together forming the raw materials from which the fruit substances are synthesized, move into the fruits. With the exception of calcium, (and possibly some magnesium), which presumably enters the fruits mainly via the xylem pathway.

During the growth of the cocos and date fruit about 3/4 of the water of the imported nutrient fluid again has to leave the fruit, very probably by means of transpiration. The experimentally determined rates of loss of transpiration water from detached date fruits (HAAS & BLISS 1935) appear to be in accordance with the rates calculated in the present study on the basis of the assumed imported nutrient fluid. The transpiration rates postulated for the last stages of growth of the cocos and date fruits exceed those for the influx of the sieve tube fluids. This leads to the drying up of these fruits, a phenomenon that accompanies fruit ripening.

From the sucrose which enters the date and cocos fruits, quite different fruit substances are synthesized. The date palm mainly produces starch and sugars,

which are stored in its pericarp. The cocos fruit also accumulates large amounts of carbohydrates in its pericarp (husk) in the form of cellulose, but it also produces the approximately 20% of lipids stored in the endosperm.

It would be interesting to investigate other palm fruits too, especially those of the oil palm (*Elaeis guineensis*), in connection with the views developed in this study. The quantitative information available on its bleeding sap composition and production, however, is very scanty (HARTLEY 1967, ZEVEN 1967), although this sap production seems of local importance in some African countries. SPRECHER VON BERNEGG (1929) and HARTLEY (1967) have reported an annual production of bleeding sap of 240 and 263 litres respectively, which according to the first mentioned author would be equivalent with about 31–34 kg of sucrose per tree.

Average data on the annual bunch yields (fruits + inflorescence stalk) from several oil palm varieties reported by GASCON & DE BERCHOU in 1964 (SPARNAAIJ 1969) range between 84 and 125kg. In general the fruit-to-bunch ratio varies from 35–85% (SPARNAAIJ 1969). Taking for this value an average of 60%, and assuming a dry matter content of 70%, an annual fruit production of 44 kg dry matter from the more or less improved present-day oil palm does not differ very much from the annual production of 31–34 kg of bleeding sap sucrose from the semi-wild oil palm.

11. FRUITS AND METHODS USED IN COMPLEMENTARY ANALYSES

Whole cocos fruits (the common coconut + the intact fibrous husk), probably of West African origin, could incidentally be bought in a local shop. Husk, shell, meat (endosperm), and "water" were separated and their dry weights determined.

Branches with date fruits ('Deglet Noor') of Algerian origin were also bought locally. The calyx was always removed prior to analysis. Drying was performed at 60–80°C, followed by storage above concentrated sulfuric acid, till constant weight.

For the mineral analyses samples of the various fruit parts were ashed at a temperature not exceeding 500°C, till the ash was virtually free of carbon. The ash was dissolved in 3N hydrochloric acid and diluted with distilled water (K, and Mg) or with a 0.5% lanthanum chloride solution (Ca). Calcium, potassium, and magnesium concentrations were determined by standard atomic absorption methods, using an Optica Densatomic (Milano) Atomic Absorption and Flame Emission Spectrophotometer (with air-acetylene flame). Series of standard concentrations of the three elements determined were always diluted in the same way as the sample solutions.

Phosphorus was determined (after dry ashing) by a colorimetric phosphomolybdate method. Nitrogen was determined by a standard Kjeldahl method, followed by titration. No special precautions were taken to convert possibly present nitrate to ammonium.

12. ACKNOWLEDGEMENTS

The author is much indebted to Dr. P. M. L. Tammes for many stimulating discussions and for drawing his attention to several valuable publications on coconuts. He also thanks Miss Netty Willemse for excellent technical assistance.

13. REFERENCES

- ALDRICH, W. W., & C. L. CRAWFORD (1939): The dry weight increase curves for date fruit. *Proc. Amer. Soc. Hort. Sci.* **37**: 187–190.
- ANSIAUX, J. R. (1958): Sur l'alimentation minérale des Phanérogames parasites. *Acad. Roy. Belgique Cl. Sci. Bull.* **44**: 787–793.
- (1959): La composition minérale des fruits et la voie de transport des ions alimentaires vers ceux-ci. *Ann. Physiol. végét. Université Bruxelles* **4**: 53–88.
- BOLLARD, E. G. (1970): The physiology and nutrition of developing fruits. In: *The biochemistry of fruits and their products* (ed. A. C. HULME) vol. I, pp. 387–425. Acad. Press, London-New York.
- BROWNING, K. C. & C. T. SYMONS (1916): Coconut toddy in Ceylon. *J. Soc. Chem. Ind.* **35**: 1128–1142.
- CANNY, M. J. (1973): *Phloem translocation*. Univ. Press., Cambridge.
- CHILD, R. (1964): *Coconuts*. Longmans, Green & Co., London.
- DIE, J. VAN (1968): The use of phloem exudates from *Yucca flaccida* Haw., in the study of translocation of assimilates. Symposium Stofftransport. Vorträge aus dem Gesamtgebiet der Botanik nF. **2**, 27–30. Fischer, Stuttgart.
- DIE, J. VAN & P. M. L. TAMMES (1974): Phloem exudation from Monocotyledonous axes. In: *Encyclopedia Plant Physiol.*, New Series (ed. A. PIERSON & M. H. ZIMMERMANN). Springer, Berlin-Heidelberg-New York. (in preparation).
- DIE, J. VAN, C. R. VONK & P. M. L. TAMMES (1973): Studies on phloem exudation from *Yucca flaccida* Haw. XII. Rate of flow of ¹⁴C-sucrose from a leaf to the wounded inflorescence top. Evidence for a primary origin of the major part of the exudate sucrose. *Acta Bot. Neerl.* **22**: 446–451.
- CZAPEK, F. (1920): *Biochemie der Pflanzen*. Vol. II. pp. 372–467. Fischer, Jena.
- DOUGLAS, J. & R. R. BIMANTORO (1956): Identification of the *Corypha* palms which flowered in the Hortus Bogoriensis during 1953–1955. *Ann. Bogor.* **2**: 137–146.
- EATON, B. J. (1917): Coconut toddy in Ceylon. *Agric. Bull. Fed. Malay States* **5**: 193–199.
- FAUST, M. & C. B. SHEAR (1973): Calcium translocation patterns in apples. *Transactions 3rd symposium on accumulation and translocation of nutrients and regulators in plant organisms*. Warszawa-Jablona-Skierniewice-Brzezna-Krakow, 14–18th May.
- FISCHER, H. (1967): Der Mineralstofftransport. In: *Encyclopedia Plant Physiol.* (ed. W. RUHLAND) vol. XIII. pp. 200–268. Springer, Berlin-Heidelberg-New York.
- FRÉMOND, Y., R. ZILLER & M. DE NUCÉ DE LAMOTHE (1966): *Le Cocotier*. Maison neuve et LaRose, Paris.
- GIBBS, H. D. (1911): The alcohol industry of the Philippine islands. *The Philip. J. Sci.: A. Chem. Geol. Sci. Ind.* **6**: 99–206.
- HAAS, A. R. C. & D. E. BLISS (1935): Growth and composition of Deglet Noor dates in relation to water injury. *Hilgardia* **9**: 295–344.
- HARTLEY, C. W. S. (1967): *The Oil Palm*. Longmans, Green & Co, London.
- HEYNE, K. (1927): *De nuttige planten van Nederlands Indië*. Ruygrok, Batavia.
- (1950): *De nuttige planten van Indonesië*. Veenman, Wageningen.
- MARSDEN, H. & F. L. SKILTON (1931): Yields of toddy from coconut palms. *Malayan agric. J.* **19**: 287–290.
- NATHANAEL, W. R. N. (1955): Toddy yields from coconut palms in Ceylon. *Ceylon Coconut Quarterly* **4**: 8–16.

- NITSCH, J. P. (1970): Hormonal factors in growth and development. In: *The Biochemistry of Fruits and their Products* (ed. A. C. HULME) vol. I, pp. 427–472. Acad. Press, London-New York.
- (1971): Perennation through seeds and other structures: Fruit development. In: *Plant Physiology* (ed. F. C. STEWARD) vol. VIA, pp. 413–501. Acad. Press, New York-London.
- PATEL, J. S. (1938): *The Coconut*. Madras.
- REIJNE, A. (1948): De Cocos palm. In: *De Landbouw in den Indischen Archipel* (eds. C. C. J. VAN HALL & C. VAN DE KOPPEL) vol. Ila, pp. 427–525. 's Gravenhage-Bandoeng: Van Hoeve.
- SAMPSON, H. C. (1923): *The Coconut Palm. The Science and Practice of Coconut Cultivation*. John Bale, Sons & Danielsson, London.
- SCHOOR, G. H. J. VAN (1957): Les relations entre la composition élémentaire de la plante et son alimentation. *Ann. Physiol. végét. Univ. Bruxelles* 2: 7–424.
- SHEAR, C. B. & M. FAUST (1970): Calcium transport in apple trees. *Plant Physiol.* 45: 670–674.
- SPARNAAIJ, L. D. (1969): Oil Palm. In: *Outlines of perennial Crop Breeding* (ed. F. P. FERWERDA & F. WIT) pp. 339–387. Veenman, Wageningen.
- SPRECHER VON BERNEGG, A. (1929): *Tropische und subtropische Weltwirtschaftspflanzen*. Ferdinand Enke Verlag, Stuttgart.
- TAMMES, P. M. L. (1933): Observations on the bleeding of palm trees. *Rec. Trav. bot. Néerl.* 30: 514–536.
- (1952): On the rate of translocation of bleeding sap in the fruitstalk of Arenga. *Proc. Kon. Nederl. Akad. Wetensch. Amsterdam* C55: 141–143.
- (1958): Micro and macro nutrients in sieve tube sap of palms. *Acta Bot. Neerl.* 7: 233–234.
- TAMMES, P. M. L. & J. VAN DIE (1964): Studies on phloem exudation from *Yucca flaccida* Haw. I. The phenomenon of bleeding and the composition of the exudate. *Acta Bot. Neerl.* 13: 76–83.
- TAMMES, P. M. L., C. R. VONK & J. VAN DIE (1969): Studies on phloem exudation from *Yucca flaccida* Haw. VII. The effect of cooling on exudation. *Acta Bot. Neerl.* 18: 224–229.
- TOMLINSON, P. B. (1970): Monocotyledons – Towards an understanding of their morphology and anatomy. In: *Advances in Botanical Research* (ed. R. D. PRESTON) vol. III, pp. 207–292. Acad. Press, London-New York.
- WIERSUM, L. K. (1966): Calcium content of fruits and storage tissues in relation to the mode of water supply. *Acta Bot. Neerl.* 15: 406–418.
- (1967): The mass-flow theory of phloem transport; a supporting calculation. *J. exp. Bot.* 18: 160–162.
- ZEVEN, A. C. (1967): *The semi-wild oil palm and its industry in Africa*. Centre for Agricultural Publications and Documentation; Agric. Res. Public. no. 689, Wageningen.
- ZIMMERMANN, M. H. (1973): The Monocotyledons: their evolution and comparative biology. IV. Transport problems in arborescent monocotyledons. *Quart. Rev. Biol.* 48: 314–321.