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Role of Pressure in Xylem Transport of Coconut and Other Palms

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Abstract

The significance of root pressure in the transport of xylem sap has been investigated in *Cocos nucifera* L. and a few other palms. Despite the fact that excised palm roots can generate considerable pressures *in situ*, the quantity of water transported is only a small fraction of the demand resulting from transpiration. Most water transport is induced by negative pressure gradients, as in other higher plants. The development of considerable negative pressures has been demonstrated both directly and indirectly.

Acoustic detection was used for the first time to monitor cavitation in water-stressed Cocos leaves. Its detection implies the ready disruption of xylem sap under these tensions. We suggest that root pressure might serve to refill cavitated xylem conduits when water is abundantly available and transpiration practically zero. However, little or no positive pressure could be demonstrated in intact palms subjected to low water stress experimentally.

Introduction

One of us (Davis 1961) reported many experimental measurements illustrating the fact that whilst detached palm roots can generate considerable root pressure over extensive periods, the suction exerted by the corresponding root stumps still attached to the palm was insignificant. Thus for Cocos a positive pressure of 1240 cm of water was recorded from detached roots whereas the greatest negative pressure generated by attached root stumps was only 20.1 cm of water.

The observation that high root pressures can be generated by detached palm roots does not necessarily imply their occurrence in normal intact palms but rather that positive pressures may develop under appropriate conditions. These conditions have been examined. Secondly the extremely low negative pressures recorded contravene the widely accepted cohesion mechanism for the ascent of sap, seeming to imply that palms behave differently from other terrestrial plants (Davis 1961, Corner 1966). Attempts have been made to reconcile these observations with accepted theory. Since Cocos was reported to exhibit the phenomenon described above most clearly, it was preferred for experimentation.

Materials and Methods

Plant material. All palms used for experiments grew in the campus of the Indian Statistical Institute in Calcutta. Though the top-soil was quite dry, the water table stood only one to two metres below the ground. All experiments were conducted in November–December 1972, a dry, cool season for Calcutta.

Palms used were *Cocos nucifera* L. from two to four metres tall, *Phoenix sylvestris* Roxb. six metres tall, and *Borassus flabellifera* L. over twelve metres tall. Trenches were dug to expose the almost-horizontal roots.

Potometry. Newly exposed roots were washed free from superficial soil. The light brown exodermis and inner cortex were stripped away by hand to expose several centimetres of almost undamaged stele. Laterals were trimmed with a razor blade. The stele was pressed into a dish of water and severed obliquely. Graduated 1 ml pipettes were connected by latex tubing and filled or recharged with a syringe fitted with a fine plastic extension. Thread ligatures were made over latex connections if required. Whole root diameters varied 5–7 mm: steles were 2–3 mm.

Manometry. Roots were prepared and severed as described above. Attached root stumps were connected to a water filled siphon positioned above the stump to restrict air entry. Ligatured latex tubing formed a sleeve over transparent plastic tubing through which the cut stump could be examined for bubbles. Stripped stele and latex connections were painted with hot gelatine which rapidly solidified. Then the vertical siphon tube in water (see Figure 2 inset) was slid more deeply into the beaker which contained both water and mercury. The vertical ascent of mercury was timed up a metre scale using a stopwatch. Water was distilled but not boiled to remove gases from solution.

Water potentials by refractometry. Palm leaves were sealed in plastic bags for one to three hours to allow xylem and leaf water potentials to equilibrate before sampling. Discs, 8 mm in diameter, were cut from mature leaves with minimum exposure to air. Eighteen or twenty formed a single sample. Each replicate contained five such samples placed in miniature test tubes for one hour in 0.2 ml of sucrose solutions ranging from 50–250 g per litre of water. The discs were deliberately injected by partial evacuation of air using a 25 ml syringe, pressed on a neoprene seal applied to the tubes, pulled for about 15 seconds soon after setting up, then again before final readings were made. Tubes were shaken at intervals three times during the one hour exposure period to mix the solutions. A hand refractometer (0–50 % sucrose, Bellingham and Stanley) was used for readings each of which was duplicated, and compared with the original solutions at the end of each experiment.

Xylem exudation experiments. A clear plastic envelope of 500 gauge polythene prevented transpiration. Observations on exudation were made at midnight, sunrise, mid-day and sunset.

Cavitation experiments. The acoustic probe, fitted on an acoustically insulated retort stand, drove a pre-amplifier as described by Milburn (1973), then a battery power-amplifier with speaker, which was kept in a separate room to prevent feedback. A length of palm frond, about 15–40 cm long, cut from the middle of a frond with scissors, was transported in either a plastic bag or with a water supply. It was suspended on the probe by impaling the midrib (see inset Figure 4). A 100-watt tungsten lamp 30 cm from the leaf provided radiation to enhance transpiration. Water was restored to a leaf segment by raising or removing a beaker of water to a cut surface from below. Clicks were monitored manually by means of a stopwatch.

Light and temperature measurements. Sunlight was monitored on a photographic meter (Boots P.R.75) calibrated in sunlight against a Megatron lightmeter reading in lux. Air temperatures were taken on a thermometer bound within and shaded by palm foliage at a height of two metres.

Results

Experiments to measure uptake by attached and detached roots

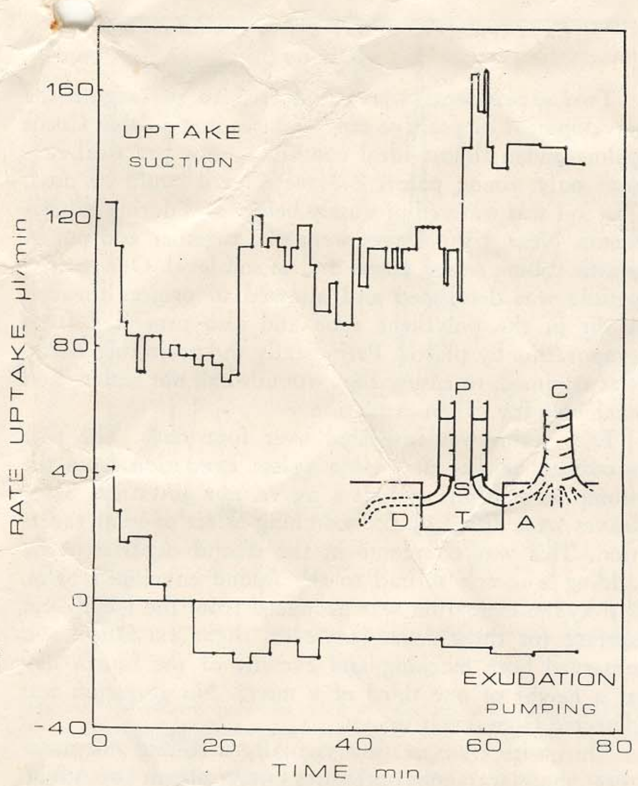
In several preliminary experiments and in eight detailed replicates, the root stumps still attached to palm trees were found to absorb water rapidly from potometers for extended periods (many days). In contrast, detached roots, isolated but still mainly embedded in soil (Figure 1 inset) were found to absorb water rapidly at first but uptake declined gradually. In some experiments it changed from absorption to exudation as a result of root pressure. However, the rate at which detached roots were able to exude sap was at best a small fraction of the absorptive capacity of attached root stumps, see Figure 1. Thus, since demand exceeded supply, a sap tension in the system was implied, rather than a positive pressure; this despite the fact that isolated roots could produce positive pressures after excision. In the short-term pattern of uptake by attached stumps the rate of uptake usually decreased, followed by an increase irrespective of the time of day.

Some potometric experiments were continued for several days. Uptake gradually tended to decline as the root stump attached to the palm became sealed or blocked. After the transitory effects shown in Figure 1, a diurnal pattern of uptake was clearly established (Figure 2). These experiments implied considerable sap tensions in attached root stumps throughout the diurnal cycle.

Direct demonstration of negative pressures generated by attached root-stumps

Davis (1961) used both corticated and decorticated roots for his manometric experiments and obtained comparable results. However, on account of the large air-filled lacunae in the cortex we adopted the latter method. Negative pressures were measured on a mercury manometer (Figure 2 inset). It was possible to observe through the transparent connecting sleeve that as tension increased air bubbles emerged from the cut stele; air seemed to enter the system via damaged conduits. The maximum suction generated using latex rubber seals was equivalent to 130 cm of water, a considerable improvement on Davis' 20 cm but well below the technical limit around 1017 cm (atmospheric pressure).

More successful experiments were then conducted on steles sealed with a coating of gelatine to prevent air influx. A rise equivalent to 894 cm of water was achieved. Results from this sequence of experiments on the same palm are summarised in Table 1. There can be no possible doubt that attached roots are capable of generating considerable tensions if precautions are taken to control embolism. That such tensions were widespread in other palms was confirmed by injection experiments. When vascular tissue was punctured through a superimposed drop of ink, the ink was always drawn into the xylem at considerable speed confirming the general operation of tensions. However neither the injection method nor the direct manometric method would permit



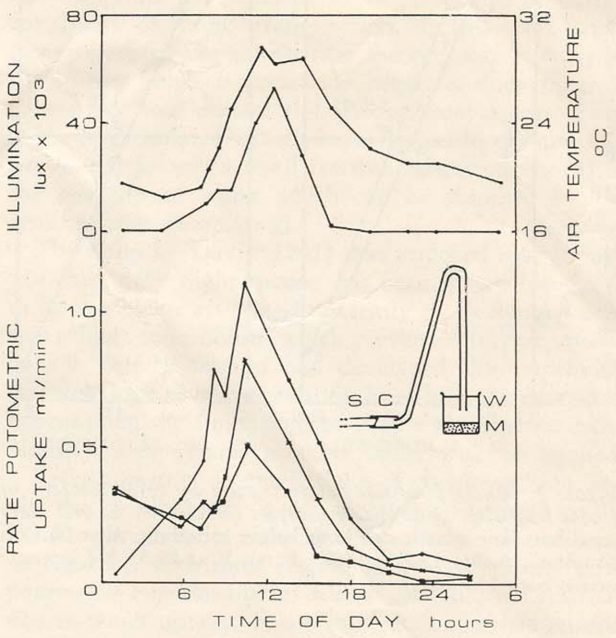


Figure 1. *Short-term potometric uptake of water by palm root stumps S from trench T, started 10.45 h.* Both absorbed water initially then the detached stump D (lower curve) exuded sap whilst uptake by the attached root stump A (upper curve) increased. *Inset*: Diagram illustrating potometer connections.

Figure 2. *Long-term simultaneous potometric uptake of water by three Cocos roots attached to the same palm* (lower curves). Uptake is plotted as rate per mean time, as in histograms. Upper curve is air temperature with illumination below during the diurnal cycle. *Inset*: Siphon arrangement for potometer attachment to a stump S without air locks. After connections C were sealed a potometer was substituted for the siphon. Alternatively the vertical tube was lowered through water W into mercury M to measure suction manometrically. Note: The rate of potometric uptake is ten times smaller per individual root than actually shown.

Table 1. *Suction developed by attached root-stumps of Cocos.* Mercury manometers were attached to decorticated roots of the same palm.

Sequence of experiments	Mercury column Max. value, cm	Suction developed, bar	Sealing system utilised
1	9.0	0.12	Latex tubing only
2	9.7	0.13	,, ,, ,,
3	13.7	0.18	,, and some gelatine
4	61.3[1]	0.81	,, ,, more ,,

[1] This value was reached in less than three minutes. It quickly fell as bubbles emerged from water throughout the glass and transparent-plastic tubing.

accurate estimations of suction, hence indirect techniques were employed.

Estimation of water potentials in xylem by refractometry

A pressure bomb was not available so the refractometric method described by Ashby and Wolf (1949) was selected for measurements on palm leaf tissue. Discs were punched from leaves equilibrated with xylem tensions in the absence of transpiration and submerged in sucrose solutions of known concentration with minimum exposure to evaporation. Water was absorbed or released from the bathing solutions changing their concentration. The null (isopiestic) point was found by refractometry.

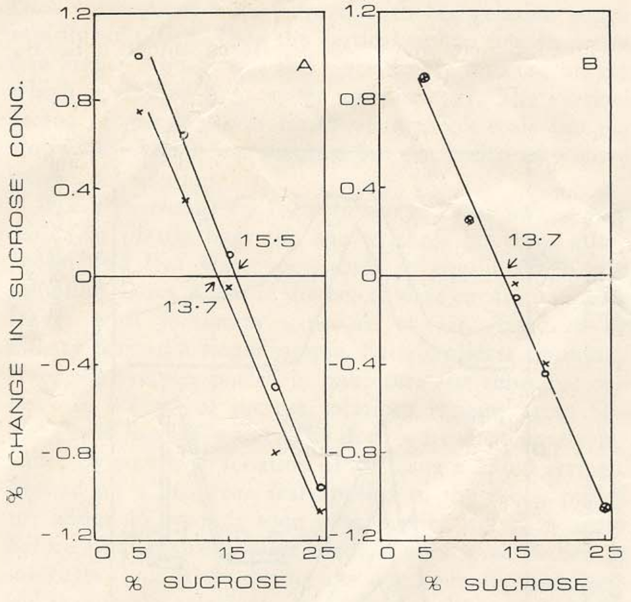


Figure 3. *Water potential determination by refractometry of Cocos leaf discs as duplicate samples* (× and ○). Leaves were equilibrated in plastic one hour before sampling, A at 00.15 h (isopiestic points 13.7 and 15.5 bars), B at 09.35 h (isopiestic points both 13.7 bars).

The method gave little variation between samples (Figure 3). Leaf water potentials at the isopiestic point were determined from osmotic pressure tables. Xylem sap had a refractive index close to pure water indicating an insignificant osmotic pressure, so these values should correspond to palm xylem sap tensions. Data for several palms is presented in Table 2. Considerable sap tensions were implied throughout both night and day. Differences between leaves in plastic bags and exposed leaves were negligible.

Experiments to induce xylem exudation and guttation

Two experiments were conducted to investigate the development of positive sap pressures in available Cocos palms under almost ideal conditions. For practical reasons only young palms 2–3 metres tall could be used. The soil was watered profusely before and during experiments. Next, palm leaves were tied together and put in plastic tubing sealed above and at soil level. One mature petiole was defoliated and allowed to project through a slit in the polythene tube and also protected from evaporation by plastic. Periodically the projecting stump was trimmed, to ensure that wounds had not sealed, and examined for xylem exudation.

Each palm was inspected over four days. The first produced neither detectable xylem exudation from the stump at a height of half a metre, nor guttation. Some leaves were killed by the scorching effect of solar radiation. This was overcome in the second experiment by adding a cotton shroud to the second enveloped palm. No xylem exudation was produced from the freshly-cut surface for three days. However, slight exudation was observed both morning and evening of the fourth day at a height of one third of a metre. No guttation was detected from intact tissues.

Thus with transpiration virtually zero and soil moisture abundant, root pressures were absent or slight. Seemingly the demonstration of positive sap pressures in intact palms requires an extremely favourable water balance.

Study of cavitation in leaf vascular tissue

A possible advantage to palms from the development of positive sap pressures might be the restoration of sap continuity in xylem embolised after cavitation. Accordingly preliminary investigations were performed to see if cavitation could indeed be detected in isolated palm leaves stressed by progressive water loss. An acoustic

Table 2. *Water potential determination of palm leaves.* Discs were submerged in sucrose solutions and the isopiestic point was found by refractometry. 3 replications.

Palm sampled	Time of sampling in sequence shown, h	Null point as % sucrose			Mean value %	Water potential of mean, bar
		1	2	3		
Cocos 1	12.15	15.5	14.5	—	15.0	-11.5
,, ...	21.30	14.0	14.0	—	14.0	-10.7
,, ...	10.15	13.5	13.5	—	13.5	-10.4
Cocos 2[1]	15.15	16.2	—	—	16.2	-12.5
Borassus	15.30	12.0	—	—	12.0	-9.2
,, ...	15.30	7.5	7.5	7.5	7.5	-5.9
Phoenix	11.15	20.0	—	—	20.0	-15.4

[1] Leaf not sealed in plastic envelope prior to sampling.

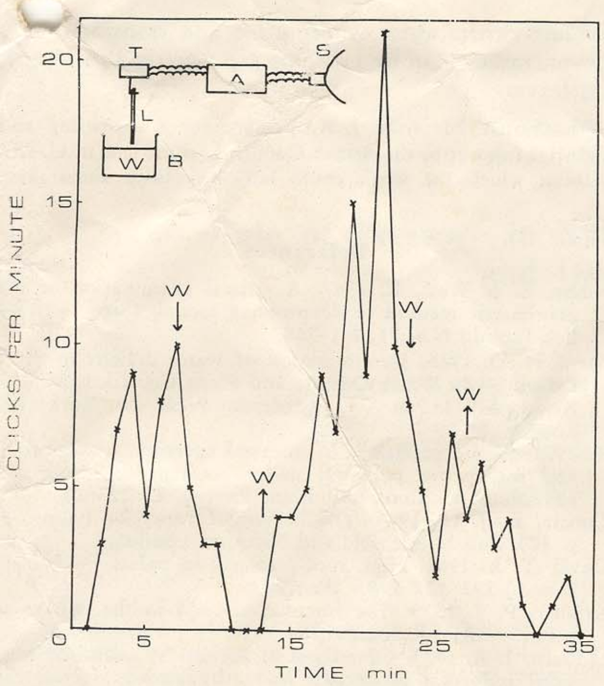


Figure 4. *Relation between click production and water supply to a transpiring Cocos leaf segment.* The lower cut surface was given several short incisions to facilitate uptake. Water W supplied at ↓, removed at ↑. *Inset:* Diagram of cavitation detector omitting illumination system and timer. The leaf L was suspended from a magnetic transducer T which fed an amplifier chain A with output to speaker S. Water supply W was controlled by beaker B position.

detector was used as described by Milburn (1973). Palms have large xylem conduits which might be expected to produce energetic vibrations, detected as clicks, when cavitation releases tensions which distort the conduit walls.

Click production was detected as described by Milburn and Johnson (1966) for *Ricinus* leaves. Clicking began almost immediately when freshly collected leaf material was impaled on the probe. Click production increased in frequency then gradually decreased as water loss continued. It could be objected that clicks are produced by causes other than cavitation. These objections are difficult to refute completely, however renewal of water supply suppressed click production (Figure 4) as is the case with *Ricinus* leaves. This response was less marked as click production proceeded presumably due to a progressive loss of xylem conduction.

Discussion

Our investigations into the role of root pressure in palms have confirmed its development as described by Davis (1961). There seems no reason to doubt the magnitude of the root pressures reported, but it seems very significant that they were measured under abnormal conditions, the roots having been isolated from the palms for several days. Development of static pressure does not imply its development in the intact palm during conditions of rapid transpiration. Indeed potometric measurements have shown that the pressure in roots of transpiring palms is invariably negative, since water is drawn into both excised and attached root stumps. Even when roots isolated in situ begin to exude, the production of sap is only a small fraction (about one-tenth) of the quantity of water which can be absorbed by the attached root stump.

The claim by Davis (1961) that attached root stumps can exert only slight suction has been shown for Cocos to be due to an artifact. Apparently the technique used was subject to embolism which prevented further uptake once a certain tension had developed. By improving this technique negative pressures have been demonstrated approaching the limitations of simple manometric techniques. Much greater tensions could well be implied.

Refractometric determinations of xylem tension imply the development of considerable tensions (5 to 16 bars) in three species examined. The determinations must be regarded with some reserve however for long term potometric experiments revealed a clear diurnal fluctuation in water uptake. This would result if xylem tension were greater around mid-day, and much less during the night. Despite the apparent consistency of the refractometry results, such a diurnal cycle of tension was not detected. Further work, preferably a comparison with pressure-bomb techniques, is needed to elucidate this discrepancy. However, the results seem sufficiently valid to support the indications from potometry and injection experiments, that palms fit the accepted pattern of water transport in higher plants, by negative pressure. Root pressure plays, at most, a minor role. Similar observations were made on *Lycopersicum* by Kramer (1939). This view conforms with other experiments on palms, *e.g.* by Rees (1961) from relative water content measurements on the oil palm (*Elaeis guineensis*), by Scholander *et al.* (1961) from potometric experiments on the 'climbing palms' the rattan (*Calamus* sp.), and by Zimmermann (1966) for palms generally. The notion expressed by Davis (1961) and Corner (1966) that root pressure may play an important role in the ascent of sap in palms seems no longer justified.

The pattern of uptake in short-term potometric experiments is interesting. An initial fall in uptake, followed by a steady increase, might suggest an initial reduction in leaf water deficit followed by adjustment to a diurnal tension cycle. This cannot be the case however, since the same pattern is produced in both the morning when tensions are probably increasing and the late afternoon when sap tensions are probably falling (see Figure 2). Probably the initial rapid influx of water induces transitory stomatal closure through the temporary imbalance of turgor between subsidiary and guard cells. This is a familiar response when water is supplied to water deficient plants or leaves (Barrs 1971). It is followed by stomatal recovery and re-opening as turgor equilibrium is restored. Slight stomatal closure also probably accounts for the fact that the maxima of diurnal uptake (Figure 2) precede those of temperature and illumination. Such 'mid-day closure' is well established for many plants including the oil-palms (Rees 1961).

The observation by Corner (1966) that "palms do not show guttation", is interesting considering the ability of palm roots to develop positive pressures. In two experiments on well-watered palms, enveloped in plastic to stop transpiration, guttation could not be detected. In one case a pressure corresponding to one metre of sap ascent (about one-tenth of a bar) was demonstrated. Possibly greater positive pressures may develop during monsoon seasons when the ideal time to detect the escape of guttation sap from intact leaves would be around midnight. However, growth itself may create sufficient demand in an intact plant to render root pressure insignificant (Potter and Milburn 1970).

Cavitation was detected in palms acoustically for the first time, a view supported by the observation that click production is suppressed by re-supplying water which must reduce the sap tension despite continuing transpiration. The ease with which cavitation seems to occur in palms subjected to water stress suggests that positive sap pressures might serve a role in restoring conduction. Cavitated conduits become gas filled and can be refilled only by forcing the gas back into solution under pressure. Hence we suggest that root pressures developed in intact palms may play a minor role in restoring cavitated conduits when water is abundant and transpiration is absent, rather than by pumping sap directly to transpiring leaves.

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