

A STUDY ON THE RESPIRATORY ORGANS OF *COCOS NUCIFERA* Linn.

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SUMMARY

In this report, a brief account of the morphology, anatomy and physiology of the pneumatophores or respiratory roots of *Cocos nucifera* is given. Coconut pneumatophores are further compared briefly with the respiratory organs found in a few other species of palms such as *Areca catechu*, *Borassus flabellifer*, *Phoenix sylvestris*, *Raphia hookeri*, *Caryota urens*, *Chrysalidocarpus lutescens* and *Ptychosperma macarthurii*.

Apart from the primary roots (main roots) which radiate from the bole and the root-lets of various orders produced from the roots, the coconut palm has a third kind of small, whitish, pointed outgrowths on the main roots and rootlets. These are called the pneumatophores or respiratory roots. They are neither branched nor negatively geotropic, but their size varies considerably. Those developing from the main roots are the biggest, measuring about 8 mm long and about 4 mm broad at the base. The production of respiratory roots of palms growing in clayey soils is very poor compared to that for trees standing in porous or aerated soils. The first few respiratory roots are formed on the first root of a young coconut sprout within a month of its germination.

Even under fairly uniform soil texture, the roots spreading horizontally have a greater number of breathing roots than the deep-going ones. Moreover, in the deep-going vertical roots, a greater number of the respiratory organs are found towards their base, that is, near the stem. Data on the distribution of pneumatophores at various depths of about 2,000 roots from 24 trees are presented. It was observed that a great majority of the respiratory organs were distributed within one metre from the soil surface.

Production of respiratory roots in young coconut palms growing in sandy soil under conditions prevailing in the West Coast of India was estimated for two groups. In one, seedlings of age from three months after sowing upto one-year were examined at monthly intervals. A 3-month old seedling on an average produced 5 respiratory roots, and this number reached 305 for a year old seedling. These seedlings also produced more or less equal numbers of root-lets of the first order. The second set of 8 palms examined were of ages ranging from 2 to 10 years. The respiratory roots in these palms outnumbered the first order root-lets, the proportion being 1 : 1.3.

The respiratory root has an endogenous origin and emanates from the endodermis of the root (or root-let) from which it originates, and this is exactly how an ordinary root-let originates. The linear expansion of the pneumatophore is arrested very early and its distal end starts bulging due to the multiplication and enlargement of the cortical cells. The hypodermis, not being able to cope up with the expansion of the cortex, ruptures at many points, and eventually peels off, exposing the highly perforated and hardened cortex which has a farinaceous appearance. With age, the cortical cushion gradually withers away, and eventually the stele (the harder core), which is left out, acts as a spine. A dark brown gummy secretion is deposited in time at the starting place of the pneumatophore which prevents the possible entry of water into the cortex, lest the latter should rot.

The respiratory roots and the root-lets sometimes seem to exchange functions. By examining the roots of palms growing under different environments, it was observed that some respiratory roots have their stele prolonged into regular root-lets which may produce further orders of root-lets. Also, occasionally a root-let, after growing to some length, may be transformed into a respiratory organ. By simple experiments, the interchangeability of functions of respiratory roots and root-lets has been demonstrated.

Production of respiratory roots can be accelerated by flooding, by cultural practices and by burying coconut husks near the stem. One of the experimental *Phoenix sylvestris* palms produced pneumatophores on the stem about two metres above the ground as a result of continued flooding. However, no positive results were obtained on a similar treatment with the coconut and areca palms.

Respiratory roots are of great importance to the coconut. Being primarily organs for the exchange of gases, these modifications enable the coconut palm increase its area of distribution, extending even to the otherwise unsuitable water-logged and marshy regions. The presence of pneumatophores is clearly a hydrophytic (or halophytic) adaptation even though the coconut has several undisputable xerophytic characteristics.

INTRODUCTION

While water and salts are usually absorbed from the soil, it is common knowledge that plants get their important gaseous food materials such as oxygen and carbon dioxide, so vital for their existence, from the atmosphere. Submerged water plants adapted to such a condition, however, obtain these from water. The air partly enters the epidermal cells and more through the stomata from where it reaches the internal tissues and traverses freely through the intercellular spaces. In roots where stomata are usually wanting, the air enters either through the epidermis or passes through the aerial parts along the air passages provided by certain tissues. Some plants living in water-logged or marshy conditions which are not able to obtain fresh air through the roots have certain special organs known as pneumatophores or respiratory roots which enable the submerged root to be communicated with the atmosphere.

In certain hydrophytes and swampy plants such as *Rhizophora*, *Avicennia*, *Jussiaea*, the respiratory roots grow erect and protrude above the marshy soil to obtain the atmospheric air for transmission through their aerenchyma to the subterranean parts, especially to the actively growing tips. Respiratory roots occur among members of many families which are very remote from each other such as Rhizophoraceae, Combretaceae, Lythraceae, Meliaceae, Verbenaceae and Palmae. These pneumatophores vary greatly in form and structure. They may resemble the well-defined pneumatophores or look like knee-roots or compound knee-roots as in *Mitragyna ciliata* or *Symphonia globulifera* (Jenik, 1967). Some look like horizontal surface roots, and others may be aerotropic as in *Raphia* and *Phoenix*. Also stilt pneumatophores occur as in *Xylocopa standtii*.

PIONEERING INVESTIGATIONS ON PNEUMATOPHORES

The problem of breathing roots engaged the attention of scientists as early as in 1886 when Gobel made a report of his studies on *Sonneratia* and *Avicennia* and threw much light on the constitution of the bark and the peripheral tissue. Gobel called these roots 'Luftwurzeln' (respiratory roots) by which he expressed that these organs draw air from outside and pass them to the underground roots. Jost (1887) observed these peculiar root-formations from the base of *Livistona australis* persisting throughout the year at the Strasbourg Botanical garden. These roots grew vertically upwards above the soil and Jost gave them the name pneumathodes. These organs were generally found to be swollen, and in certain parts they had whitish powdery or mealy markings which were in contrast with the brown surface of the exodermis. These formations were provided with caps, visible to the naked eye, and they showed endogenous ramifications. An almost similar condition may be seen in some roots of *Borassus flabellifer* (Fig. 1). However, in *Borassus*, the breathing roots, seldom appear above the soil except in very old palms where aerial breathing roots are produced. Jost also described some root structures of *Phoenix dactylifera*. Schenck reported in 1889 his work on *Avicennia tomentosa* which almost resembled Gobel's *A. officinalis*. In addition, he studied *Laguncularia racemosa* of Combretaceae which also showed a very loose bark. Soon after, Schimper (1891) studied the Indo-Malayan mangroves such as *Capra obovata*, *Bruguiera caryophylloides*, *Lumnitzera coccinea*, *Avicennia officinalis* and *Sonneratia acida*. From the point of view of the organs that communicate with air, Karsten (1893) compared the respiratory organs of several species of *Bruguiera*. He also pointed out that the elbowed-roots (arched-roots) of *Lumnitzera* and *Bruguiera* differ in their morphology and function. By submerging the base of the plant in water, Wieler (1898) stimulated the production of erect roots bearing pneumathodes in *Phoenix reclinata* but not in other palms. Gage (1901) described pneumathodes in *Phoenix paludosa* which in some parts of India is subjected to flooding at certain seasons of the year. Gatin in 1907 on the basis of his own observations answered Jost, that pneumathodes are found not only on palms grown in botanical gardens, but also on those growing in their natural habitat. The respiratory roots of *Pandanus australiana* was first studied by Schoute (1910). In this species, pneumatophores were observed on the roots as well as the shoot. He pointed out that the pneumathodes found in the respiratory roots of *Pandanus australiana* were similar to those described by Jost in the case of palms. Ernould (1921) studied the respiratory roots in *Bruguiera gymnorhiza*, *Avicennia officinalis*, *Sonneratia acida*, *Metroxylon sagu* and *Raphia laurenti*. In *Elaeis guineensis*, Yampolsky (1924) observed modified branch-roots functioning as pneumathodes, but they were not negatively geotropic.

Thus, it is clear that the respiratory roots of some species of palms also received the attention of early investigators. Among palms, one or more species of the following genera possess pneumathodes—*Phoenix*, *Hyphoene*, *Livistona*, *Metroxylon*, *Raphia*, *Cocos*, *Areca*, *Borassus* *Elaeis* and presumably some others. Mahabale and Parthasarathy (1963) include the stilt roots of *Verschaffeltia splendia* also into the category of Pneumatophores. The breathing organs of *Cocos nucifera* described in the following pages are very minute structures differing greatly from its other kinds of roots as well as from the pneumatophores of many other species. However, as these outgrowths function as organs for the exchange of gases, they have to be regarded as respiratory roots.

THE DIFFERENT KINDS OF ROOTS IN THE COCONUT

Coconut, being a monocot, produces numerous fairly uniform roots from the base of the stem, termed the bole. These roots, known as the main roots or primary roots, radiate from all sides of the bole and are generally disposed to keep the direction in which they start. Usually they go as deep as the permanent water table. In sandy soils where the rainfall is high, it is not uncommon to trace out roots spreading over a length of 25 metres. The number of main roots vary from tree to tree and from tract to tract. A mature robust palm (over 50 years) on the West Coast of India may possess 4,000 to 7,000 main roots. A palm at the Central Coconut Research Station, Kayangulam, South India produced as many as 11,360 main roots (Menon and Pandalal, 1958).

The main roots give rise to several lateral branches which subsequently branch and re-branch. These are the root-lets which are popularly known as the feeding roots. While most of the main roots are capable of living for over 20 years, the root-lets are short-lived, a majority of the thinner ones dying every year during the dry summer months. These roots concentrate around the bole and help in the absorption of nutrients (vide Fig. 2).

The small, whitish, pointed outgrowths developing from the main roots as well as root-lets is yet another kind of root which is called the respiratory root or pneumatophore. Because of their perforated surface, these roots enable the atmospheric air to reach the growing tips of roots immersed in water or marshy places deprived of adequate aeration. Earlier workers on the coconut, (Copeland, 1913 ; Sampson, 1923 ; Patel, 1938 ; Child, 1964 ; Menon and Pandalal, 1958) briefly reported these roots as possible organs for the exchange of gases. A review on the respiratory roots of palms in general was given by Tomlinson (1961).

Some old palms or those living under partial water-logged conditions produce roots from the aerial stem in the form of a root-cushion which is usually contiguous with the roots developing from the bole (Menon et al, 1955). Cook (1941) named such a root-cushion formed of slender erect roots common among the members of *Thrinacaceae* as 'rhizotyle'. The rhizotyle absorbs moisture and accumulates humus. Erect roots are also produced at the base of many palms under specific conditions. In *Cryosophylla nana* (*Acanthorhiza aculeata*), numerous erect branch-roots are produced which grow much above the soil (Fig. 3). These roots with their hardened ends are perhaps meant to protect the stem. According to Chandler (1912), *Cryosophylla* produces such erect protective spines at all heights on the stem.

COCONUT PNEUMATOPHORES

The main roots as well as the root-lets of different orders of the coconut often bear numerous whitish, jasmine bud-like outgrowths which serve as breathing organs. Of the two enlarged views of coconut respiratory roots shown in Fig. 4, the one on the left (A) is younger and about to get rid of its fragmentary hypodermis. The size of these organs varies considerably, those developing on the main roots being the biggest. It measures about 8 mm lengthwise with a maximum width of about 4 mm towards the base. But those developing from the root-lets are smaller, their size becoming smaller as the root becomes thinner. A breathing root has a

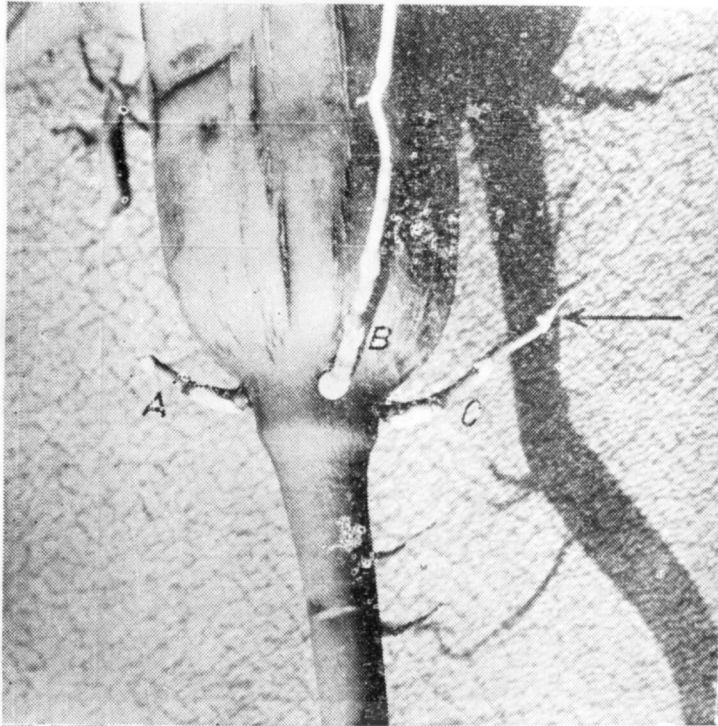


Fig. 1

A young *Borassus flabellifer* seedling having white, mealy markings on the root-lets (A, B, C) which function as respiratory organs.

Fig. 2

View of a root-matting concentrated at the base of a coconut palm.

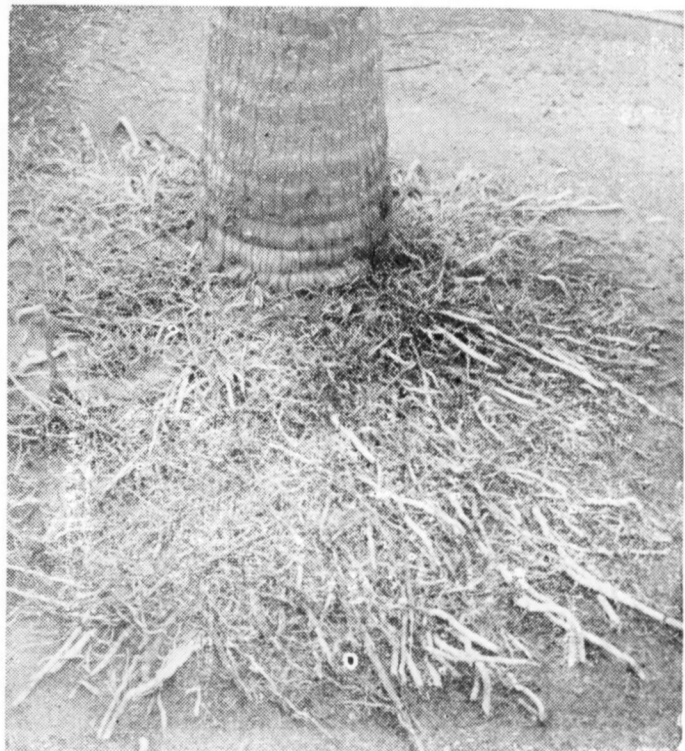




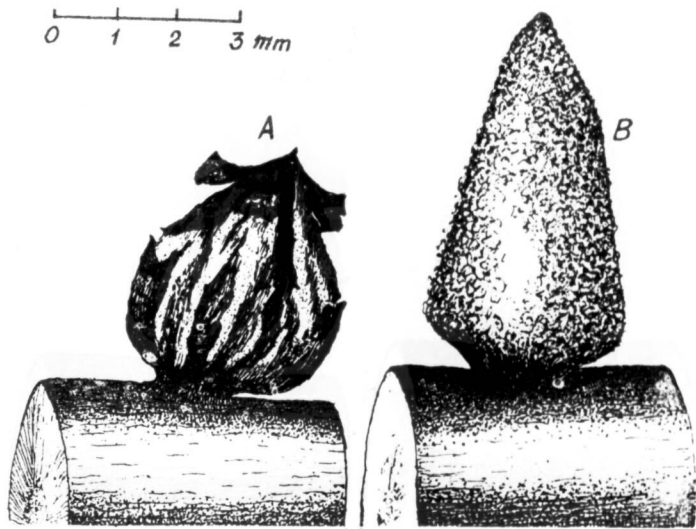
Fig. 3

Negatively geotropic roots in *Cryosophylla nana* (*Acanthorhiza aculeata*) clustering at the base of the stem. (Photo from the Botanical Garden, Brussels).

0 1 2 3 mm

Fig. 4

Magnified view of coconut respiratory organs. In A, the hypodermis is in the process of being peeled off. In B, the hard covering is shed completely.



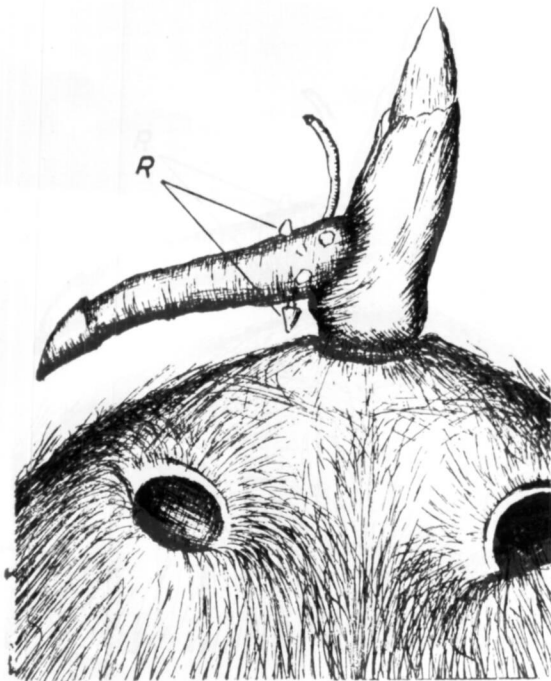
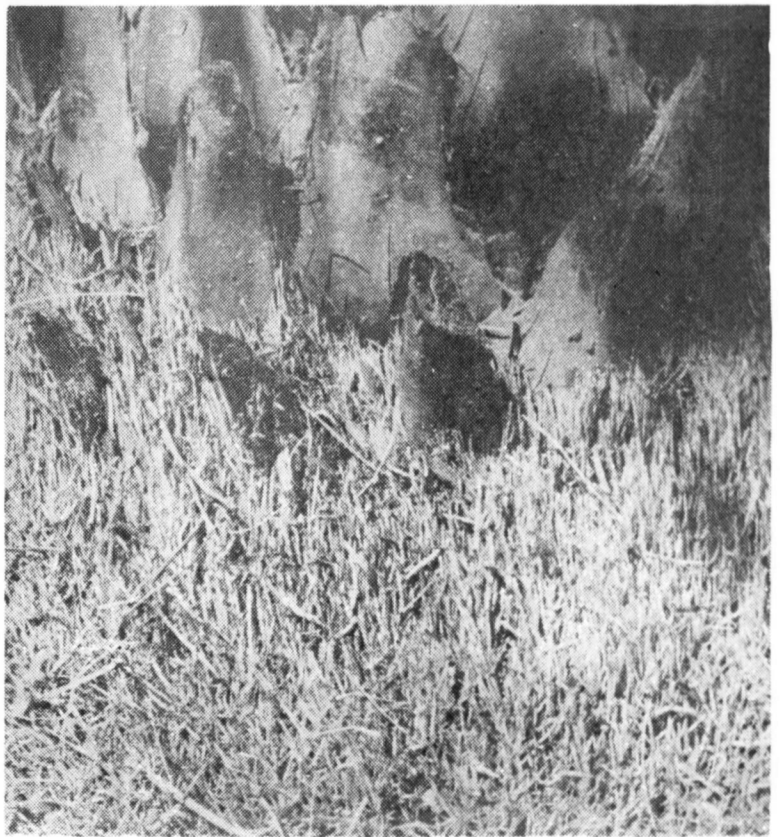


Fig. 5

A coconut sprout bearing respiratory roots (R) on its first-root.

Fig. 6

Innumerable vertical pneumatophores developing at the base of *Phoenix sylvestris*.



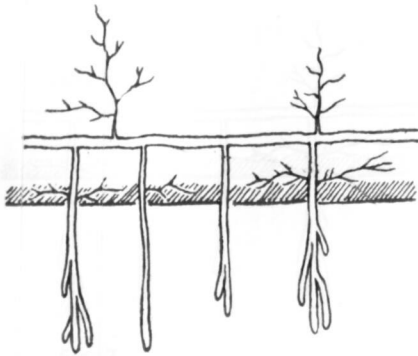


Fig. 7

Branched and simple, erect pneumatophores in *Raphia hookeri*. (After Jan Jenik, 1967).

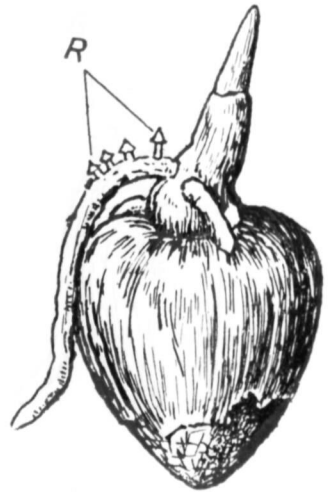


Fig. 8

Respiratory roots (R) on the first-root of *Areca catechu*.

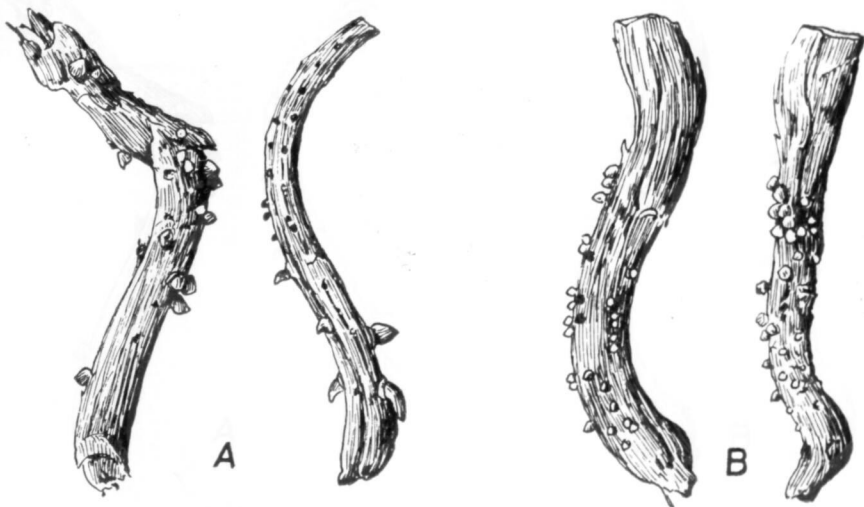


Fig. 9

Pneumatophores on the main roots of *Chrysalidocarpus lutescens* (A) and *Ptychosperma macarthurii* (B). The size of the respiratory organs on the same root varies considerably.

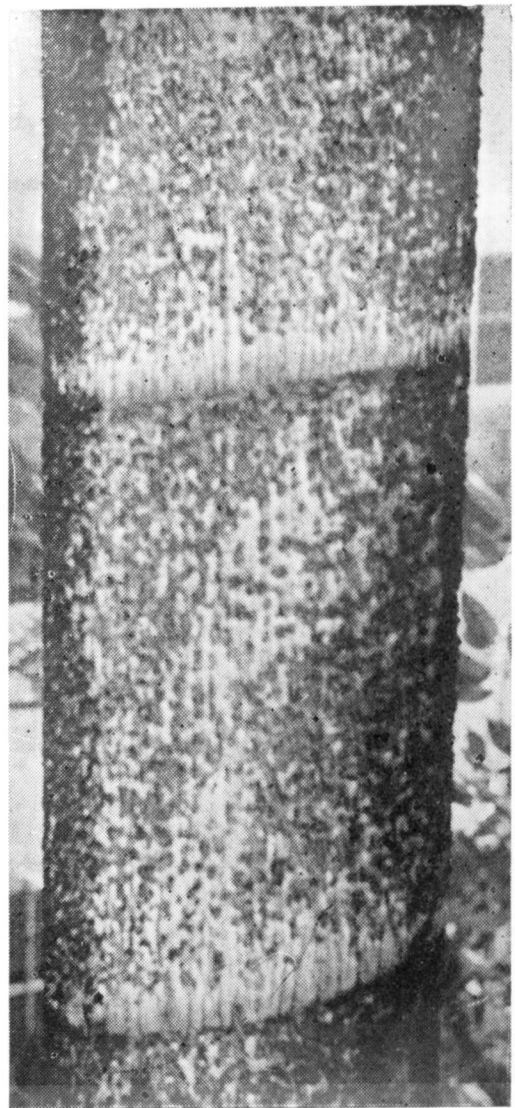


Fig. 10

A main root of *Areca catechu* having many pneumatophores. These out-growths are often distributed in lines.

Fig. 12

Numerous lenticel-like openings on the mature stem of *Caryota urens*.



narrow stalk that fixes the pneumathode with the stele of its parent root. The intensity of production of respiratory roots depends on many factors. Under totally water-logged conditions or in clayey soil, the formation is much less while in porous and aerated soils, coconut roots produce numerous breathing roots before they penetrate the poorly aerated soils. The portion of the roots which remain above the water level (of palms growing in water-logged areas) has been observed to have numerous pneumatophores. Roots entering loosely-filled organic matter also produce profuse breathing roots.

The first respiratory root in a coconut seedling is formed according to Davis and Anandan (1957) within six weeks after the germination has commenced. At this stage, the seedling will have produced three main roots and a few root-lets. However, the seedling in Fig. 5 which is only four weeks old has eight respiratory roots on the first root itself. Since the first few roots are covered to a great extent by the loose fibres of the husk, they produce a good number of respiratory roots distributed on all sides of the root as is the case with the production of root-lets.

An important distinguishing feature of the coconut respiratory roots is that, they do not grow above the soil if they are not already formed from an exposed root. Moreover, these roots are neither negatively geotropic like those of *Phoenix sylvestris* (Fig. 6), or *Raphia hookeri* (Fig. 7) nor branched like those of *Raphia*. Among the respiratory organs examined on other palm species, those on *Areca catechu*, *Chrysalidocarpus lutescens* and *Ptychosperma macarthurii* come closer to that of *Cocos nucifera*. Even the very first root of a germinating *Areca* produces several almost uniform respiratory roots (Fig. 8). Davis (1961), and Bavappa and Murthy (1961) reported on the respiratory roots of *Areca catechu*. The breathing roots of *Chrysalidocarpus lutescens* and *Ptychosperma macarthurii* do not differ very much from each other. In these two species, the size of the breathing roots on a single root varies considerably (Fig. 9) unlike those of the coconut which are uniform for each root. Further, the former two species seem to produce more respiratory roots per unit area compared to *Cocos nucifera*. Though according to Yampolsky (1924), the pneumathodes of *Elaeis guineensis* are modified branch-roots, several root-lets are also transformed into respiratory roots. d'Almeida and Correa (1949), Haberlandt (1914) and Gillain (1890) also discussed the pneumathodes of some species.

Even under uniform soil texture, roots which are distributed horizontally have a greater number of breathing roots than the deep-going ones. In the deep-going vertical roots, more respiratory roots are distributed towards their base, i.e. towards the bole of the palm, and sparsely towards their tips. In order to study the frequency distribution of these breathing roots at various depths of the soil, about 2,000 roots of 24 trees were examined at Kayangulam where the soil is sandy, with the permanent water table not lower than three metres. The data are summarised in Table I.

TABLE I
Distribution of coconut respiratory roots
at different soil depths

Depth (from surface)	% distribution of breathing roots	No. of roots examined
Upto 0.4 m	28.8	377
0.5 — 0.8 m	27.7	493
0.9 — 1.2 m	19.4	456
1.3 — 1.6 m	12.2	290
1.7 — 2.0 m	8.8	222
2.0 — above	3.1	147
	100.0	1,985

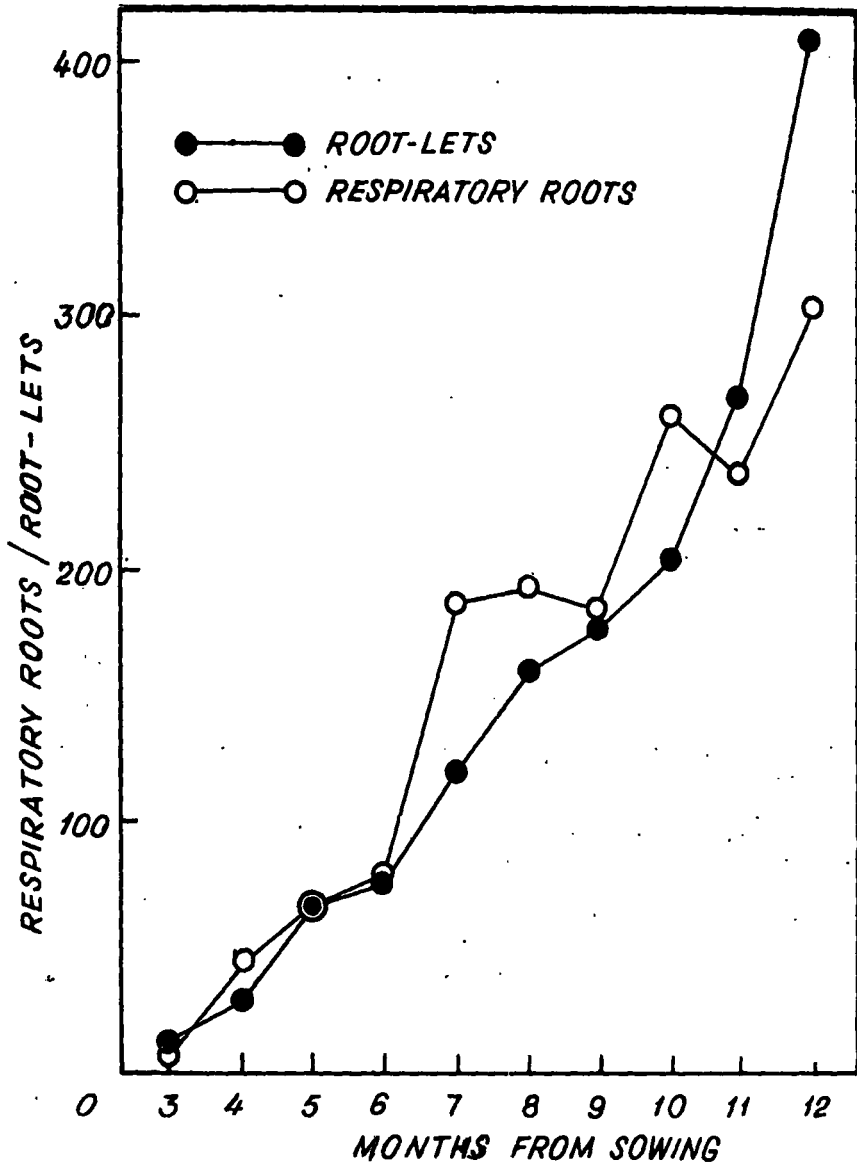


Fig. 11 Production of respiratory roots and first order root-lets in young coconut seedlings compared.

As seen from Table 1, the majority of the breathing roots was distributed within a metre from ground level, and most of them were shared by the horizontal roots.

An attempt was also made to assess the frequency of respiratory roots on the horizontally spread and deep-going main roots of trees growing in sandy soil with deep water table (4 metres) and clayey soil with very high water table (1 metre). Roots of only three trees in the water-logged category could be studied. It was found that the overall number of breathing roots as well as root-lets was greater in the case of trees growing in sandy soils. But the number of breathing roots (per unit length) on the 'aerial roots' of trees growing in water-logged areas is much greater. However, the distribution of the same was found to be reduced in the lower layers in both the categories, especially for trees growing under water-logged conditions. Abundant breathing roots are also produced at the base of the main roots of *Areca* palms growing under marshy conditions (Fig. 10). They are seen arranged in rows.

Pneumatophores and root-lets of young coconut seedlings :

In a special nursery, 100 seed nuts obtained from a single palm of the Tall variety were sown at Kayangulam to study the root-development. The soil was sandy and the water table during the summer months was about 4 m below ground level but it rose to within a metre during the monsoon. A set of six seedlings was uprooted carefully every month commencing from the 90th day of sowing. The husk of the nuts was carefully stripped off in bits, and the numbers of all respiratory roots, first order root-lets as well as the primary roots were estimated. Data were also obtained on the lengths of primary roots, the number of leaves and the thickness of the collar. In Fig. 11 are represented the mean numbers of respiratory roots and the first order root-lets for ten continuous months. The graph relating to the root-lets shows a steady and steep increase. But that on the breathing roots is not so steady. Especially during the last two months there is a clear decline from the usual rate of production. The reason is not known, but it is presumed that the six-seedling sample per month is very small especially in view of the fact that the crop is highly cross-pollinated and heterozygous. In spite of this, it may be concluded that young coconut seedlings in sandy soils produce almost equal numbers of breathing roots and first order root-lets. For a rough comparison, the total numbers of the two kinds of roots estimated on different seedlings during the ten monthly intervals are 1556 breathing roots and 1516 root-lets. Data similar to these given above were obtained also on the seedlings of *Borassus flabellifer* from a larger population. The numbers of respiratory roots and root-lets (first order) on two sets of 9-month old seedlings are given in Table 2.

TABLE 2

Borassus flabellifer : Production of respiratory roots and root-lets under two soil conditions

Soil	Seedlings :		Total :		: Per seedling :	
	No.	Age	Resp. roots	Root-lets	Resp. roots.	Root-lets
Clayey	10	Nine months	170	543	17.0	54.3
Loose alluvial	10		1378	73	137.8	7.3
Total	20		1548	616	154.8	61.6

It is very obvious that in alluvial soil a very great number of root-lets are formed. The upper strata of roots in clayey soil produced more breathing roots.

Breathing roots on young coconut palms :

The root system of a set of young palms whose ages ranged from two to ten years was partially exposed and the numbers of primary roots, first order root-lets and the respiratory roots were counted. The entire data are shown in Table 3.

TABLE 3
Distribution of respiratory roots, main roots and first order root-lets
in young coconut palms

Age from transplanting (years)	No. of main roots	No. of root-lets	No. of respiratory roots	Respiratory roots/ root-lets	
2	...	6	271	447	1.65
3	...	9	892	922	1.03
5	...	182	4359	5252	1.20
6	...	191	8132	7233	0.89
7	...	276	10777	16586	1.54
8	...	164	12874	14275	1.11
9	...	512	6785	11335	1.67
10	...	824	32696	43497	1.33
Total	...	2164	76786	99547	1.30

N.B.—The figures on roots for each palm are the absolute numbers relating to one-fourth the root sector. Multiplying a figure by 4, therefore, gives the total number of roots of that kind for that palm.

Since exposing the delicate roots, especially the deep-going ones was very laborious, only one young palm under each age group was experimented with. The redeeming feature for this venture was the advantage of the soil being sandy. Moreover, the digging was conducted at a time when the water table was very low.

As expected, the data show great variation. Since the palms were transplanted ones, the two and three-year old palms bore relatively smaller numbers of primary roots, and presumably the other two kinds of roots as well. All the palms (except the six-year old) bore more breathing roots than the first order root-lets, the ratio reaching as high as 1 : 1.65 and 1 : 1.67 for the two-year and nine-year old palms respectively. When the roots of all the palms are considered collectively, the root-lets and breathing roots occur in a 1 : 1.3 proportion.

ORIGIN OF THE PNEUMATOPHORE

The pneumatophore originates from the endodermis of the main root or root-let, and until it emerges from the hypodermis and in some cases even sometimes later, grows like a root-let. After emerging from the mother root and growing to a few mm, it stops growing when its entire exposed region excepting a very narrow stalk, swells considerably, eventually attaining the shape of a jasmine bud or sometimes much compressed, vide Fig. 4A. The breathing roots develop invariably from a little behind the tip of the root and before the hypodermis

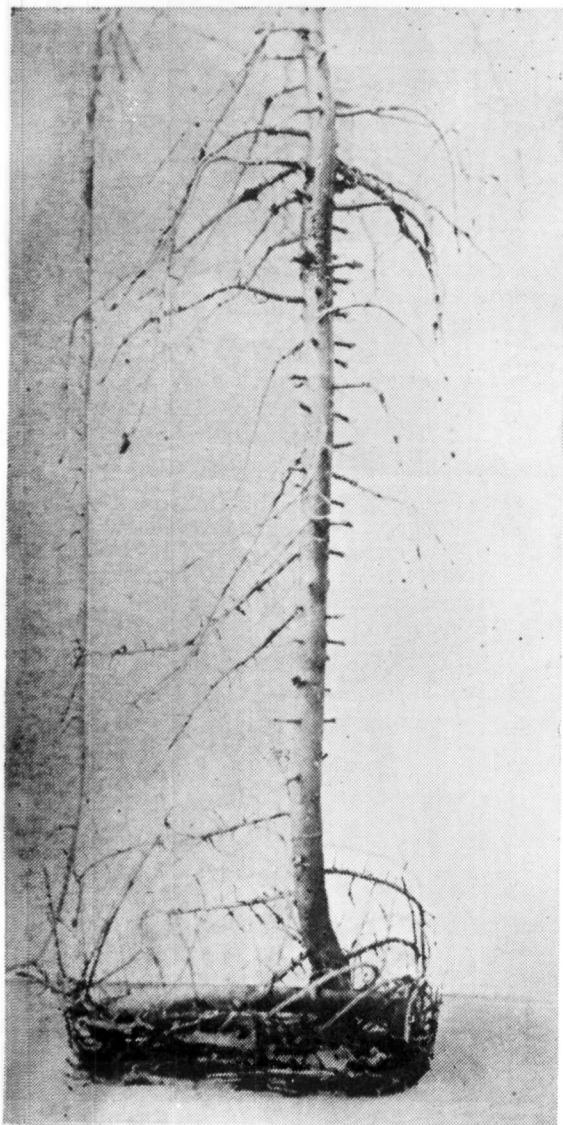
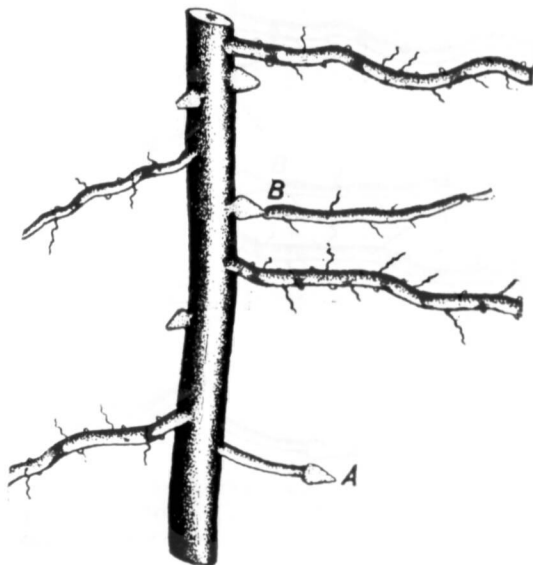


Fig. 14

Of the five breathing roots visible, one has a long stalk (A) ; another produces a root-let from its tip (B).

Fig. 13

A coconut main root producing pneumathodes at the tips of short root-lets in response to a treatment.



of that region hardens. However, sometimes fresh breathing roots develop on old roots also. Being a root, the breathing organ when young possesses a root cap. The activities of the calyp-trogen stop soon after the root ceases to elongate and till this stage, the hypodermal layer remains fairly thin. The breathing root then bulges as a result of the lateral expansion and loosening of the cortical parenchyma. Presumably new parenchymatous cells are also added. During this process, the epidermis and the hypodermis which attain a degree of hardness, ruptures at various points and peel off as scales. The remnants of such scales can be seen in Fig. 4A. The root cap also meets with a similar fate. In the meanwhile, the stele hardens and serves as a strong central pillar on which the porous, farinaceous cortical structure rests. The tip of the respira-tory root is generally hard and pointed due to the mucronate ending of the stele. When the epidermal and hypodermal tissues peel off, the remaining structure gets a white, globular or conical and much perforated appearance. The cortical cells thus exposed get thickened and be-come stiff. In their function, these breathing roots resemble the lenticels present in the phel- loderm of certain other species, or the pneumathodes of some hydrophytes (halophytes).

The lenticel-like openings on the stem of *Caryota urens* can be seen in Fig. 12.

Fig. 4B represents a typical breathing root whose outer tissues have peeled off completely. However, a narrow slanting ring of the hard hypodermal region of the breathing root may be seen at its base. This region can be much elongated in some cases.

RELATIONSHIP BETWEEN BREATHING ROOTS AND ROOT-LETS

No pneumatophore has been seen directly developing from the bole of the palm that would represent a modified primary root. From the size also, it is possible, to judge whether the breathing root is transformed from a main root or a root-let. From its reduced size and origin, the breathing root has to be considered homologous with a root-let. Accordingly, breathing roots of various sizes which represent the different orders of root-lets are available. Some of them appear as though they exchange functions with the rootlets. For instance, a root-let may suddenly turn into a respiratory root (Figs. 13 and 14A). In this case, the usual short stalk is replaced by a fairly long stalk of a root-let, provided with well-developed hypodermis. Figure 14B depicts a breathing root which from its distal end develops a root-let. A few more similar roots can be seen in Fig. 13. Therefore, the conversion of a root-let into a respiratory root, or vice versa is a secondary phenomenon influenced greatly by environmental factors, but having little to do with the conditions prevailing at the time when the root-let or the breathing root originated. This has been further substantiated by the following experiment.

Experimental evidence :

1. The different main roots of a coconut seedling grown in a special container were care-fully drawn out and each of them let into a long, 8 cm wide jar filled with one of the following media : saw dust, sand, clay and water. While the root introduced into the jar containing only water did not register appreciable growth, all the others developed normally. Though the roots grown in clay and sand media produced several root-lets, the production of respiratory roots in them was very poor, the few ones formed were seen only at the upper region of the main roots. The root grown in the jar containing moist saw dust continued to grow well producing many root-lets. Due to excessive growth, the tip of this root coiled at the bottom of the jar as it could not penetrate it (Fig. 13). At this stage, water was poured into the jar as to immerse the coiled portion of the root. The glass jar was handy for making certain observations, as for instance, to mark the height of the water level. Within a couple of days, innumerable breath-ing roots were produced from the upper portion of the main root. Most of the young root-lets which would have otherwise continued to grow as root-lets transformed into breathing roots. Even many of the early formed root-lets produced small breathing roots at their tips (Fig. 13). The abnormal lengths of the stalks of the pneumathodes explain strikingly the reversed function of such roots. The humid and aerated saw dust was obviously conducive to better root-growth.

2. The above experiment was further repeated with slight modification. One of the main roots of a seedling grown in a pot was drawn out through a single hole at the bottom. The pot was made to rest on burnt mud bricks arranged so as to provide a long vertical enclosure within which the root was allowed to grow. The bricks were constantly soaked with water and the soil below was kept almost water-logged. The root developed quickly through the humid and dark enclosure producing a few root-lets. But as soon as its tip pierced the water-logged soil, numerous breathing roots were simultaneously produced. These breathing roots would have otherwise continued as root-lets. It is, therefore, apparent that according to necessity, a root-let can modify itself into a respiratory root. From Fig. 14, it is also clear that a respiratory root, evidently under changed conditions, can transform and function as a root-let.

Accelerating the production of respiratory roots :

Subjecting a palm to water-logging accelerates the production of pneumatophores in some species including the coconut as evidenced by the experiment described above. This was further established with *Phoenix sylvestris*. At Calcutta, adult palms of three species (*Cocos nucifera*, *Areca catechu* and *Phoenix sylvestris*) were subjected to flooding for short periods during four years from 1963. Constant flooding for two months did not have any obvious effect on the coconut. A few of the areca palms showed clear chlorotic symptoms during the treatment which lasted for an equal period. However, this did not stimulate the production of either breathing roots or aerial roots. But the wild date behaved differently. All the palms of this species subjected to flooding produced vertical pneumatophores, not only from the underground stem, but also from some of the lower leaf axils. One of them produced over a million pneumatophores (Fig. 6). This particular palm was subjected to heavy flooding so as to submerge all the vertical pneumatophores including those at the lower part of the stem. Within 15 days, about one hundred pneumatophores appeared on the stem at a spot which was 2 m above ground level (Fig. 15). However, no root was formed on the stem between this spot and the original rooted region.

Cultural operations and production of breathing roots :

On the basis of long-term experiments, Patel (1938) recommended cultural operations such as ploughing, raking, piling and levelling of mounds, making trenches and basins for the coconut garden, as they have a great beneficial effect on fruit-production. Results of experiments even established that cultural practices alone enable the palms to produce more fruits than adequately manuring without cultivation. By cultivation, along with breaking the soil-clot, a few roots are damaged and this stimulates the formation of branch roots or large root-lets which are provided with active breathing roots. These 'Ventilators' further ensure the deep-going roots of adequate air supply. When a trench between rows of coconuts where coconut husk had been buried earlier as is one of the recommended practices, is partially exposed, one can see root-mattings penetrating the husk. These roots are provided with innumerable breathing roots.

Roots of 16 coconut palms of which 4 were diseased were pruned at different distances and depths from the bole. In addition, some roots each of many trees were pruned for the collection of root exudations. The pits made to expose the roots were refilled with loosened soil. Some pits were filled with coarse river sand. After a couple of months, these pits were partially opened and the condition of the pruned roots examined. Almost all the roots of healthy palms produced one or rarely more thick branch-roots at the cut-end which continued growth like primary roots giving rise to several root-lets and breathing roots. In Fig. 18 is seen one of the cut roots producing three branch-roots which are provided with a number of breathing roots near their places of origin, and many root-lets towards the distal end. It is emphasized that the original primary root at the region where it was cut did not produce many breathing roots as the soil around it was rather hard. But subsequently after loosening the soil, several breathing roots were produced on the newly formed branch-roots. It is interesting to find that one branch root has been transformed into a breathing root (Fig. 18A). Trees which were affected by a Root (wilt) disease, as evidenced by the results of the experiment were not so vigorous in producing branch-roots, breathing roots or root-lets as the healthy palms.



Fig. 15

Pneumatophores developing from the stem of *Phoenix sylvestris* about 2 m above ground.

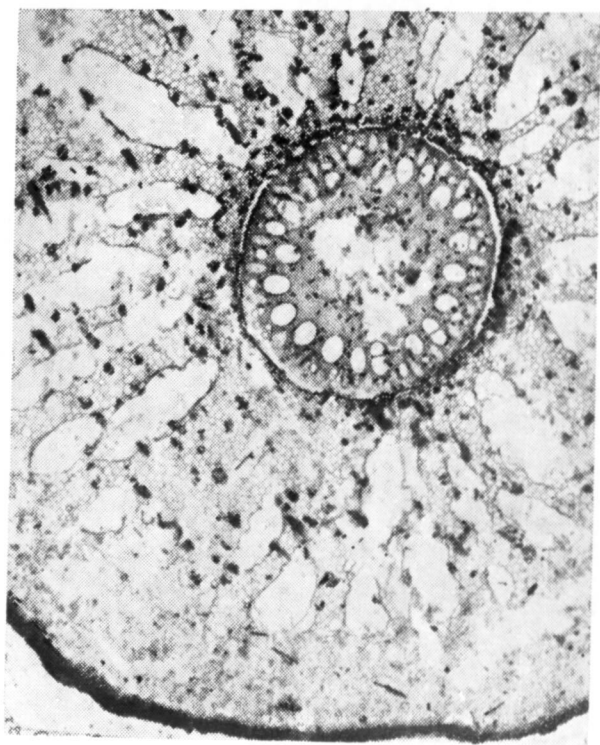


Fig. 16

View of a transverse section through a second order root-let of coconut.

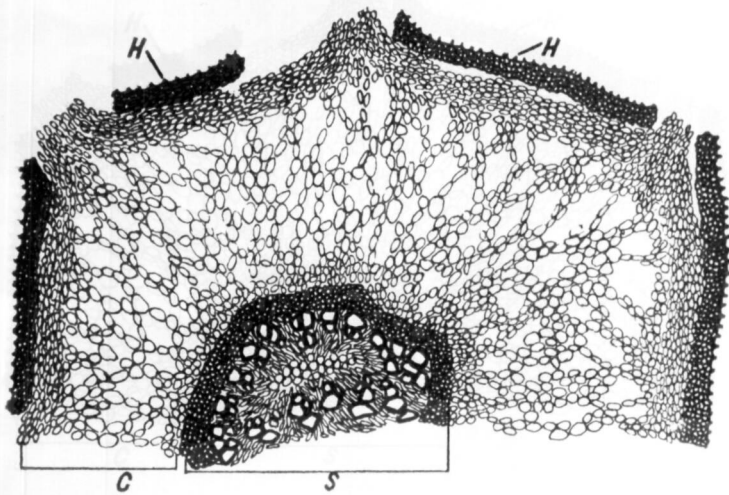


Fig. 17

Structure of a coconut respiratory organ. C-cortex ; S-stele ; H-hypodermis.

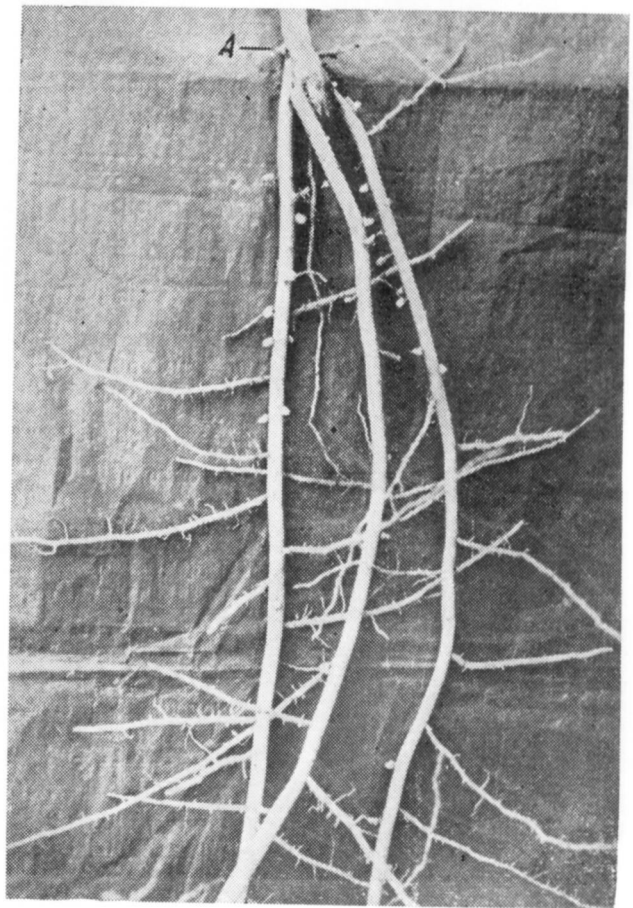


Fig. 18

Three branch-roots developing from the cut-end of a root. The respiratory organ, A, represents a branch-root.

STRUCTURE OF THE BREATHING ROOT

The breathing roots resemble root-lets externally during the early stage of development. Therefore, they are presumed to have many common anatomical features. They have a similar origin at the endodermal tissue of a primary root or a root-let. However, the stele, endodermis, cortex, hypodermis and epidermis show considerable variations between the two kinds of roots. Brief accounts of the structures of respiratory roots and root-lets of the second order are given below.

As briefly mentioned, a breathing root can be a transformed root-let of any order. Therefore, though its size varies considerably, its essential structure does not differ with the size although a bigger respiratory root has more well-defined tissues.

Fig. 17 is a camera lucida drawing of the transverse section of a fairly young breathing root developing from second order root-let. The breathing root consists of a prominent cortex (C) which is still to enlarge and ramify fully. This tissue envelops the stele (S) in the centre which in the present case is compressed. The outermost layer of cells forming the epidermis is wanting. Usually the epidermis of the coconut root consists of very large but thin-walled cells which function as root-hairs for the absorption of moisture. Like the root-hairs, this tissue is short-lived, but their places of attachment can be made out from the impressions left on the hypodermal tissue. The epidermal cells are normally at least four times as big as the ones that can be guessed from the impressions. Being a breathing root and not having any need to absorb moisture from the soil, these epidermal cells remained under-developed and withered away very early.

The hypodermal layer (H), though many cell thick, is thinner in the breathing root compared to that of a normal root. The cells which constitute the hypodermis are initially collenchymatous which in the ordinary root get more and more thickened and form the hard hypodermis, impervious to water and perhaps also to air. As the hypodermis cannot expand peripherally, it ruptures as the cortex enlarges. At the points where the hypodermis is broken, the cortex is exposed to the atmosphere. These openings on the hard hypodermis thus simulate the lenticels seen in many plants. With further expansion of the cortex, the hypodermis gets more and more detached and is blown off in bits. The pneumatophore in Fig. 4 A shows such a stage of the hypodermis. Therefore, it is easy to make out whether a breathing root is young or old by the presence or absence of the hypodermis.

The cortex is obviously the most important layer of the respiratory root. Here the cells which are parenchymatous finally become ruberised/lignified and remain hard though brittle. The cortical cells are well packed towards the periphery and near the stele enclosing very narrow intercellular spaces between them. But the mesodermis encloses plenty of more disorderly air spaces than the mesodermis of a normal root (Fig. 16). With age, the cortex becomes more compact and reticulate. The air spaces of the porous pneumathode are in direct link with the aerechymatous layer of the root on which the breathing root has grown. The larger intercellular spaces of the cortex extend almost upto the very tip of the growing root. Thus, even if the root tip is immersed in water or in poorly aerated marshy soil, even a single respiratory root located on the main root or on one of its root-lets and exposed to the atmosphere can enable the root to communicate with the atmospheric air. As the root becomes old, the hardened cortex gradually gets worn out and finally leaves the barren stele which acts as a spine. In the event of mechanical injury, lumps of the cortical tissue may get detached making the rest of the root uneven.

Though the endodermis and the pericycle cannot be clearly demarcated, a thick sclerenchymatous continuous band borders the vascular bundles. The stele in general is poorly developed with small or deformed conducting tissues. The xylem vessels remain under-developed, and the phloem is hardly distinguishable. The sclerenchymatous sheath extends beyond the

bundles towards the centre of the root in the form of rapidly elongated cells. There is a narrow pith in the centre composed of parenchymatous cells. The stele provided with extra-mechanical tissues offers the maximum turgidity and protection to the delicate cortex. In very old respiratory roots, even the central spine of the stele may get worn out or broken.

Anatomy of a root-let :

A general view of the transverse section through a coconut root-let would highlight the extent to which a breathing root has undergone modification. As already mentioned, the breathing root originates as a root-let, and in some cases the breathing root has the long stalk of a root-let. One such stalk of a second order root-let, was sectioned with the help of a microtome and a transverse view is shown in Fig. 16.

The hypodermal layer is quite thick, compact and unbroken. The thick cortex shows prominent parenchyma which are rather uniform and radially disposed (Fig. 16). However, the cortical region just near the hypodermis is devoid of large air spaces. The stele is round and uniform with prominent vascular bundles. The xylem vessels are very large and well organised. Large phloem patches are also visible between the prominent xylem vessels. A sclerenchymatous sheath surrounds the vascular bundles and a relatively larger pith is located at the centre. Thus, the long stalk of a breathing organ has the normal anatomical features of any root.

Coconut pneumathodes impervious to water :

As the respiratory roots remain undamaged even during prolonged submersion in water, they have to be regarded as having structural adaptations, which make them impervious to water. The exposed surface of a breathing organ encloses air in its numerous tiny pores which act as barriers to prevent the water from entering into the system. Since these organs are distributed nearer the soil surface, during ordinary floods the shallow water columns may not develop enough pressure to overpower the air bubbles. The hypodermis is impervious to water. However, when coconut palms are subjected to severe water-logging or when the submerged respiratory organs are injured, water enters the root system and causes the rotting of the inner softer tissues and eventually the root dies. When many roots are thus killed, the crown turns yellow and wilts.

However, normally even when the cushion of the respiratory organ gradually disappears, water cannot enter the root since a gummy deposit is accumulated at the base of the outgrowth. Examination of such regions of many roots suggested that by the time the pneumathodes becomes nonfunctional, the palm takes preventive measures. A few layers of cells at the junction die and turn brown and with the sticky deposit the passage is effectively blocked. It is possible to see several depressions on very old roots through which once breathing roots functioned. Such cavities are blocked by a similar process.

Respiratory roots are of great importance to the coconut. They primarily act as organs for the exchange of gases. If coconut can grow in water-logged or marshy areas, it is solely due to the efficient functioning of these respiratory organs. Though the coconut has many undisputable xerophytic adaptations, it is able to thrive along the tropical coast on account of its peculiar hydrophytic adaptations, one of which is the pneumatophore.

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REFERENCES

1. BAVAPPA, K. V. A. and MURTHY, K. N. (1961). Morphology of arecanut palm—the root. *Arecanut J.*, 12 : 65-71.
2. CHANDLER, B. (1912). Aerial roots of *Acanthorhiza aculeata*. *Trans. Roy. Soc. Edinb.* 24 : 20-24.

3. CHILD, R. (1964). *Coconuts*, Longmans, London.
4. COOK, O. F. (1941). A Haitian cactus palm adapted to Florida. *Nat. Hort. Mag.*, **20** : 21-52.
5. COPELAND, E. B. (1931). *The coconut*. Macmillan & Co., London.
6. DAVIS, T. A. (1961). Aerial roots in the areca palm (*Areca catechu* L.) *Arecanut J.*, **12** : 72-78.
7. DAVIS, T. A. and ANANDAN, A. P. (1957). The first root of the coconut. *Indian Coconut J.*, **10** : 9-14.
8. d'ALMEIDA, J. P. (1949). A contribution to the study of the root habits and anatomy of Indian plants. *J. Univ. Bombay*, **17** : 42-44.
9. ERNOULD, M. (1921). Rescherches anatomiques et physioloziques sur les racines respiratoires. *Mem. Acad. Roy. Belgique cl. Sci. 2 ser* **5** : 52.
10. GAGE, A. T. (1901). On the anatomy of the roots of *Phoenix paludosa* Roxb. *Sci. Mem. Med. Sanit. Dep. India.*, **12** : 102-103.
11. GATIN, C. L. (1907). Observations sur l'appareil respiratoire des organes souterrains des palmiers. *Revue Generale de Botanique*, **19** : 193-207.
12. GILLAIN, F. (1890). Beitrage zur anatomic der Palmen und Pandaneen Wurzeln. *Bot. Centralbl.*, **83** : 11-13.
13. GOBEL, K. (1886). Uber die Luftwurzeln von *Sonneratia*. *Revue Generale de Botanique*, **4**, 6.
14. HABERLANDT, H. (1914). *Physiological plant anatomy*. Macmillan & Co., London.
15. JENIK, J. (1967). Root adaptations in West African trees. *J. Linn. Soc. (Bot.)*, **60** (381) : 25-29.
16. JOST, L. (1887). Ein Beitrag zur Kenntniss der Athmungsorgane de Pflanzen. *Bot. Ztg.*, **45** : 600-606 ; 617-628 ; 634-643.
17. KARSTEN (1893). Uber dei Mangrovevegetation des Malayischen Archipels. *Bibliotheca Botanica*.
18. MAHABALE, T. S. and PARTHASARATHY, M. V. (1963). The genus *Phoenix* Linn in India. *J. Bombay Nat. Hist. Soc.*, **60** : 371-387.
19. MENON, K. P. V. and PANDALAI, K. M. (1958). *The coconut palm, a monograph*. Indian Centr. Coconut Cttee., Ernakulam.
20. MENON, K. P. V., DAVIS, T. A., ANANDAN, A. P. and PILLAI, N. G. (1955). Aeria roots in the coconut palm. *Indian Coconut J.*, **8**, 79-91.
21. PATEL, J. S. (1938). *The Coconut, a monograph*. Govt. Press, Madras.
22. SAMPSON, H. C. (1923). *The coconut palm*. Bale, Sons and Danielsson, London.
23. SCHENCK (1889). Uber die Luftwurzeln von *Avicennia tomentosa* und *Laguncularia racemosa*. *Flora*.

24. SCHIMPER (1891). *Die Indo-malaysche Strandflora. Iena.*
25. SCHOUTE, J. C. (1910). Pneumatophoren von Pandanus. *Annales Jardin Bot. Buitenzorg*, 3rd Supplement. Paris.
26. TOMLINSON, P. B. (1961). *Anatomy of the Monocotyledons. II/Palmae.* Clarendon Press, Oxford.
27. WIELER, A. (1898). Die Function der Pneumathoden und des Aerenchyma. *Jb. Wiss. Bot.*, 32 : 503-524.
28. YAMPOLSKY, C. (1924). The pneumathodes on the roots of the oil palm (*Elaeis guineensis* Jacq.). *Amer. J. Bot.*, 11 : 502-512.