



PRINCIPES

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JOURNAL OF THE PALM SOCIETY

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Cover Picture

Washingtonia robusta planted at 20-foot intervals on the margin of an orange grove, Redlands, California. Photo by Dennis Johnson.

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JOURNAL OF THE PALM SOCIETY

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Palm Sugar in East Madura

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The island of Madura lies off the northeast coast of Java, Indonesia. It has a relatively dry climate and scarcely any remaining natural vegetation, most of the island being covered in small holdings planted with rice (where irrigated), coconuts, tobacco, vegetables, bamboo, and fruit trees, perhaps the most famous of the last being the Madurese *salak* (a variety of *Salacca edulis*). Areas of higher ground along watersheds are covered with a scrub wilderness and are not cultivated, presumably because of the lack of water and the proximity of the limestone rock to the surface; these areas serve as a source of fodder for animals and fuel. Throughout the eastern and

drier part of the island, *Borassus sundai-*
cus is the most conspicuous palm, occurring on sand dunes, field margins and in the stony scrub wilderness. It is almost certainly planted or subspontaneous near villages but could be native in the sand dunes in the north of the island and in the scrub wilderness.

Beccari (1924) considered that collections of *Borassus* from East Java eastwards differed sufficiently from *Borassus flabellifer* L., the lontar of India, Ceylon, the Bay of Bengal, and Indochina, to constitute a separate species, *Borassus sundaiacus* Becc. The differences are slight, being found in details of the fruiting corolla, absence of scales



1. A stand of *Borassus sundaiacus* near Gapura, East Madura.



2. A sugar tapper, squeezer in his left hand, two curved knives in holder on his belt, a coconut holder for *laro* hanging from a holder on his belt, and a climbing-loop held in his right hand.



3. A closer view of the squeezer. The rachillae are squeezed in the curved part of the squeezer.

on the lamina, stomatal distribution, and degree of branching of the male inflorescence. As far as I know, nowhere are the two taxa in cultivation side by side and certainly herbarium specimens are al-

most all inadequate for assessing the relationships of the two taxa. At this stage it is not intended to discuss further the specific delimitation within *Borassus* and for the purposes of this ac-



4. A tapper at work in the crown, a bucket and some covering baskets just visible.

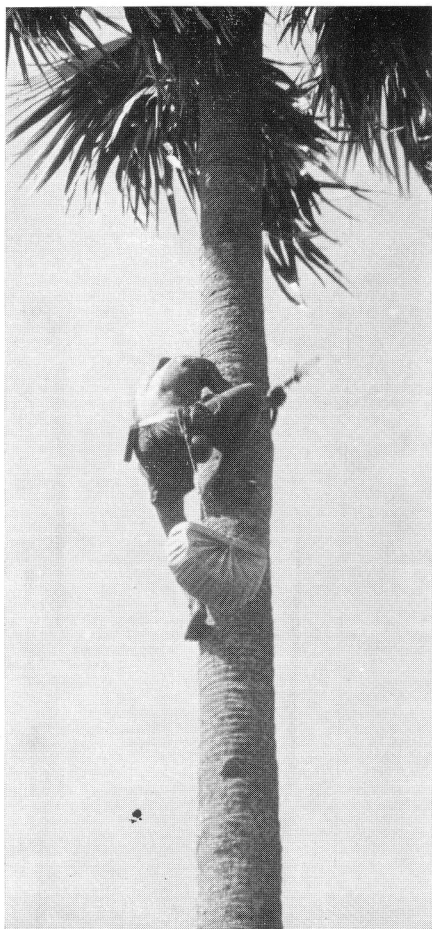
count the Madurese taxon will be referred to as *Borassus sundaicus*.

Occurring in thousands of individuals, *Borassus sundaicus* must be one of the most important economic plants of Madura. Every part of the plant is used in some way by the Madurese villagers, even if only as a source of fuel.

The major use of *Borassus* in the east of the island is as a source of sugar, this being an important village cash crop. The palm is known as *tarebung* in Maduraese and *siwalan* in Javanese. Though the method of sugar production may vary slightly from place to place, the method used in Gapura, a small village near the south coast, is probably representative. In the area around the village, both male and female trees of *tarebung* are tapped, though it is more usual for the male trees to be used. The sugar-

making process is usually a family business with the men of the family tapping the palms and the women extracting sugar from the sap. In one day a man taps about 30 trees; the tapper mostly owns his own trees but he will also hire himself out for tapping.

The equipment used for tapping in Madura is very specific, each piece of the equipment having its own Madurese name. One tapper recalled how he had bought his tapping equipment from another tapper and had not made it himself, though parts are of relatively simple construction and appear to be easy to make. The equipment consists of 1) buckets (*temba*) made from folded *Borassus* leaves often smoked to make them more durable, 2) a climbing-loop (*salampar*) made from *Borassus* petiole fiber, sometimes reinforced by rawhide, held at each



5. The tapper climbs down the palm, full bucket of sap hanging from the holder on his belt.



6. Freshly collected sap is strained through a coconut leaf-sheath sieve into a clean bucket, thus removing *laro* and debris.

end in two hands behind the trunk to gain frictional support, 3) a curved knife (*pangerat*) for slicing the rachillae of the inflorescence and splitting the bracts (occasionally two knives are used, one for each job), 4) a wooden holder for the knife (*camplak*), 5) *laro*—a mixture of the powdered bark of *Lannaea coromandelica* and the crushed dried leaves of *Anacardium occidentale*, or the leaves of *Schleichera oleosa* only; this mixture is added to the bucket collecting the sap, 6) a container for *laro* (*tambut*) made

from a polished coconut shell, with a loop made from *Borassus* petiole string, 7) a holder (*balajut*) for the climbing-loop and *laro* container—this can be made of wood or horn, 8) a squeezer (*pangape*) made from two polished pieces of wood tied with *Borassus* fiber at one end, used for squeezing the rachillae, 9) baskets (*bajut*) made from loosely woven *Borassus* leaflets, used for putting over the inflorescences, 10) a sieve (*tapes*) made from coconut leaf sheath, and 11) rope (*tale*) made from *Borassus* petiole fiber.

Tapping begins when the inflorescences reach a stage just before anthesis—"five days after the inflorescences are ripe" is the term used by the Madurese tapper—and four or five inflorescences on the tree may be tapped at the same time. The male inflorescence is massive, almost 2 m. long, consisting of about



7. The tapper returns to his village with the morning's tapings.

eight partial inflorescences of three rachillae each. There are hence at least 24 potential sources of sap in each inflorescence, but in practice only a limited number of rachillae (normally 12) is tapped at any one time. The first stage in the tapping of an inflorescence is the squeezing of the rachillae by means of the *pan-gape*, the rachillae being gently but firmly squeezed in the ends of the *pan-gape*. This squeezing process is known as *ngaremo*. After a preliminary period of squeezing (twice a day for three days), the rachillae, when cut, will begin to produce sap. This preliminary squeezing apparently induces wound activity

and is comparable to the beating with sticks or burning used to stimulate secretion in *Arenga pinnata* sugar-tapping. When the inflorescence has begun to produce sap, the tapper climbs the tree twice a day every day. In the early morning he climbs, removes the *bajut*, the basket covering the inflorescence, pours the sap accumulated in the collecting bucket into another bucket hanging from his belt, slices off a section about 3 mm. thick from the rachillae to be tapped, and squeezes the rachillae in the *pan-gape*. He then puts a collecting bucket under the freshly cut rachillae, which may have to be tied with twine to keep them dripping into the bucket, adds the *laro*, covers up the inflorescence and the bucket with the basket, and works on to the next inflorescence. When he has finished collecting from all the inflorescences on one tree and has made fresh cuts on the rachillae, the tapper climbs down the tree. He then strains the collected sap through the coconut leaf-sheath sieve to remove debris and *laro*, the strained sap collecting in a clean bucket below.

The function of the *laro* has not been clarified but it is suggested that it has a bactericidal and/or fungicidal action, preventing fermentation of the sugars in the sap. When asked what happened if *laro* was not included in the sap, the tapper said that the sap would spoil and become sour.

One inflorescence can produce up to two and one-half liters in one day including the morning and evening collection. Usually a single climb of the tree gives about a bucket full of sap—about five liters. The freshly collected sap is delicious, cool, very sweet, and slightly soporific. It is rarely drunk neat, usually being taken home directly for sugar-making. Most tappers agree that the morning collection of sugar is greater than the evening collection and that although the palms may be tapped throughout the



8. The kitchen used for making sugar. Note the crenellated oven mouths.



9. The final stages of sugar-making when the thick syrup is beaten as it fudges.

year, the yield of sugar is much greater during the dry season. Tapping is also reduced somewhat during the wet season, probably due to pressure of other agricultural work and inclement climbing weather. Generally about 30 trees can be climbed and tapped each day, and the inflorescences, once begun, will go on yielding sap for about three months as long as the squeezing and slicing continues. Furthermore, slicing in any partial inflorescence alternates from rachilla to rachilla to give best results.

When the tapper has filled as many buckets as he can carry on a yoke over his shoulder, he returns to the sugar-making hut, usually a separate hut next to the kitchen of the house. Inside the hut on the hard earth floor is a series of hard clay hearths, built into each other, with lateral mouths for feeding the fires and crenellated openings in the upper part to hold cooking pots. The whole



10. The crystallized sugar on the left, a pot of clean water with two coconut-shell scoops in the middle, and a bucket containing the *Borassus* leaflet molds on the right.

composite hearth can hold four or more clay or iron cooking pots of various sizes, and in the huts visited about seven bucketsful of sap can be processed each day. It takes about two hours to boil down the sugar from about one and one-half buckets and the output of the hut varies from three and one-half to five kilos of sugar a day.

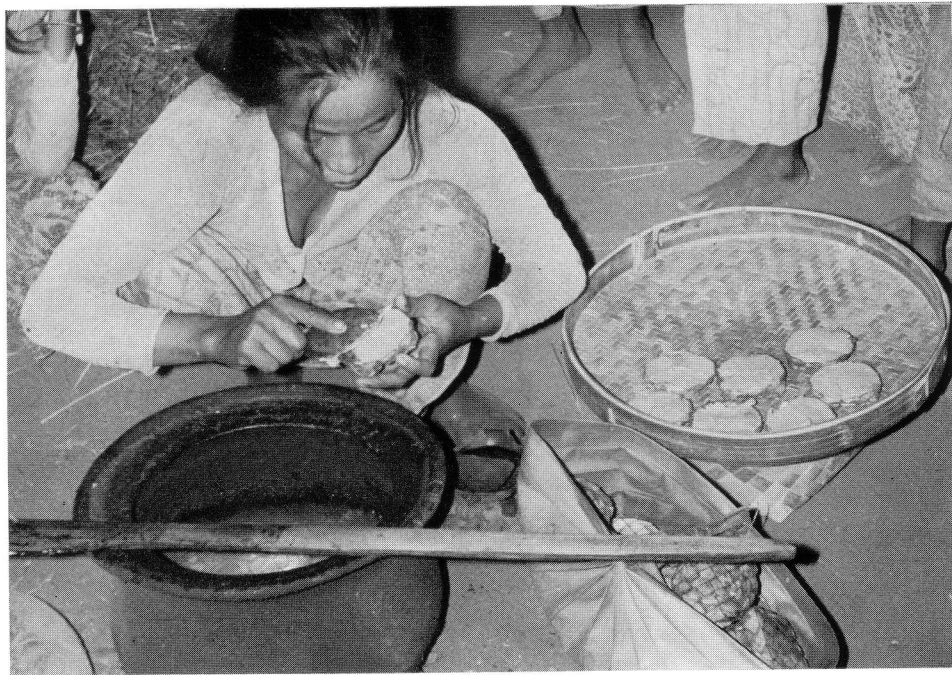
Sap is sieved again through a coconut leaf-sheath sieve and into the first and smallest of the cooking pots, where it is boiled down, and more sap is added several times. When it is beginning to thicken, it is transferred to the next largest pot and so on until a thick syrup is produced, when it is transferred to the largest pot and stirred constantly. When the syrup has the consistency of cream, the pot is removed from the fire and the syrup is stirred and beaten constantly until it crystallizes. As it crystallizes, beating is continued and then the fudge-like sugar is removed from the pot with a scoop made from a piece of coconut

shell and pressed firmly into neat little molds made from woven *Borassus* leaflets. The molds filled with sugar are then placed on a tray made of woven bamboo and allowed to cool.

Finally, the hardened sugar is eased out of the molds and wrapped in elegant boxes made of *Borassus* leaflets or in more ordinary packs of plaited leaflets. In the relatively dry climate of Madura the sugar can be stored like this indefinitely, but in a moister climate it has a tendency to deliquesce.

To obtain really pale-colored sugar, egg white is sometimes added to the syrup, but of course such pale sugar will be much more expensive than the normal pale brown product. The sugar is quite delicious eaten by itself, being reminiscent of maple candy or fine fudge.

The owner of the sugar-making concern sells the sugar to middlemen or women who collect the sugar from week to week and sell in the local markets to further dealers who may eventually ex-



11. The sugar is scooped out and pressed into the mold, then placed on a split bamboo woven tray.

port the sugar from Madura to Java. It is generally recognized that the fine pale palm sugar from Madura is superior to that made from *Arenga* in West Java, and the Madurese sugar commands a favorable price in Javanese markets, supply rarely meeting the demand. Prices of the sugar vary but a sugar tapper and his family can live off the proceeds of sugar tapping alone if the tapping is carried out intensively full time.

Acknowledgements

I should like to thank Dr. Mien A. Rifai, Keeper of Herbarium Bogoriense, Bogor, and his mother, of the village of Gapura in Madura, for helping to explain the sugar-making process and for entertaining me in Madura.

Reference

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Rare Axillary Shoots in Phoenix

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The monocotyledons exhibit many interesting types of branching. Some are quite normal to a species, but others are of occasional occurrence and are considered abnormal (Tomlinson, 1973). Among the palms, there are records of unusual branching in species which normally do not produce branches (Davis, 1973). The genus *Phoenix* includes unbranched species and others which form suckers (Tomlinson, 1961). In the latter, activation of axillary buds is usually the cause of branching. The present contribution deals with the origin, development, and morphology of axillary shoots in some abnormal specimens.

This study is based on field observation in Madurai and Ramnad districts of Tamil Nadu aimed at locating specimens showing activation of axillary primordia to form vegetative buds. The survey covers three species, *Phoenix sylvestris* (L.) Roxb., *P. farinifera* Roxb., and *P. loureirii* Kunth (*P. humilis* of authors, not Cav.). Among the specimens collected, the following types of axillary growths were recorded:

(i) Highly compressed axillary shoots enclosed by persistent leaf sheaths as in *P. sylvestris*.

(ii) Bulbil-like growths occurring in leaf axils in *P. loureirii*.

(iii) Numerous bulbils with secondary bulbils in *P. farinifera*.

Morphology of normally produced suckers

Phoenix loureirii and *P. farinifera* normally produce suckers or lateral branches at ground level. These struc-

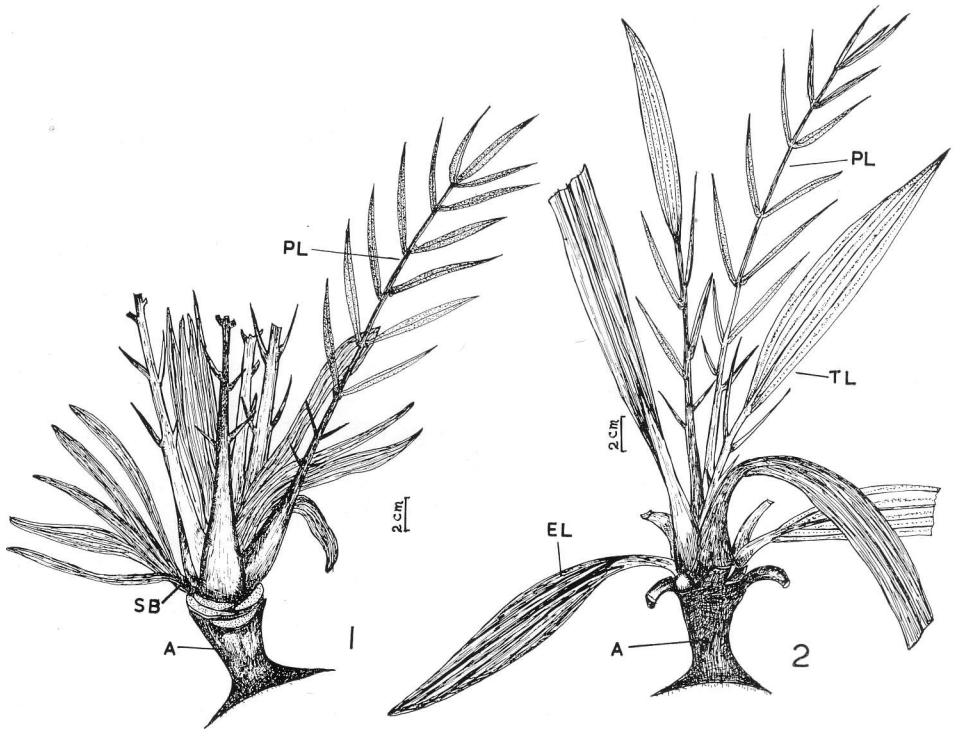
tures appear in specimens which are fairly mature and flowering. However, since the stem itself is short, the suckers present the appearance of having originated very early. Examination of post-juvenile specimens indicated that the suckers originate in the axils of leaves. Dissection of leaf sheaths yielded inflorescence primordia and a few vegetative buds. It is the latter which develop into sucker shoots. The developing sucker shoots differ from the inflorescence primordia in several respects. The most striking difference is evident in the stem. The stem of the sucker shoot develops a primary thickening meristem very early and grows in girth. The inflorescence axis remains flattened and does not grow much in girth by the process of primary thickening. While the spatheous bracts appear in regular order on the inflorescence apex, foliage leaves originate on the sucker shoot.

The vegetative bud which later forms the sucker shoot initially develops a small number of scales followed by adult leaf forms with the total absence of juvenile forms.

Further divergences in the structure of the sucker become evident at later stages. In contrast to an inflorescence axis, the sucker shoot normally develops numerous adventitious roots. Secondary suckers often arise on primary ones leading to a clumping of shoots.

Axillary shoots in *P. sylvestris*

The sucker-forming habit is not evident in normally growing specimens of *P. sylvestris*. However, young trees with a stem height of about three meters or



1, 2, *Phoenix farinifera*. 1, a bulbil bearing secondary bulbils; note the simple (juvenile?) leaves of the secondary bulbils. 2, a bulbil shoot showing transition from simple to pinnate leaves. (A, flattened axis; EL, entire leaf; PL, pinnate leaf; SB, secondary bulbil; TL, transitional leaf.)

less occasionally showed the development of axillary buds from the persisting leaf bases close to the ground level.

Some of the shoots emerging from the axils of persistent leaf bases resemble seedlings in their overall appearance. Sometimes these shoots may be mistaken for seedlings accidentally developing in that location. However, dissection of leaf bases indicated that such shoots had vascular connections with the main axis and that they developed from axillary meristems. The leaves of such shoots had a small number of leaflets and curved rachises. The lower leaflets were short and curiously boat-shaped, and the older ones were compressed within the parent leaf sheath. Some of the leaflets showed prominent folds in the lamina

resembling secondary plications (Fig. 15, 17, 18). On emerging from the main sheath, such leaves had expanded in an irregular manner and had an unusual look. The leaf spines were rudimentary and blunt. The rachis-petiole axis had a much reduced number of vascular bundles (Fig. 16).

The lower part of the axillary shoots was composed of the leaf sheaths and scales (Fig. 17). Some of the scales had an incipient rachis and a few reduced leaflets. The stem was short and stumpy, the major part being composed of the axis already produced by the axillary meristem before the development of any lateral organ (see Padmanabhan and Veerasamy, 1974, for details).

The further fate of these axillary

shoots was investigated. It was found that some of them survived beyond the stage of a few adult leaves but ultimately dried up. Lack of rooting from these axillary shoots appears to be one of the reasons why they do not survive even if covered by soil.

Bulbils in P. loureirii

The term bulbil is applied here to denote well-developed, green axillary shoots which have not yet formed a perceptible stem proper. Such bulbils were observed in specimens of *P. loureirii*. A bulbil is usually composed of a short scaleless axis (produced by the primary axillary apex), a few scales, and a cluster of short green leaves. The number of leaves in a bulbil varied from 6-12. A notable feature of these leaves (Fig. 4-8) was their condensed size and increase in number of leaflets according to their position, the first formed ones having a lesser number of leaflets.

In one case, numerous bulbils were found developing in the axils of several adjacent leaves in the crown of a mature specimen. These bulbils were exceptional in that they were bearing undivided leaves. When isolated and examined these resembled seedlings with juvenile leaves.

Secondary bulbils in P. farinifera

The occurrence of second order bulbils was noticed in *P. farinifera* where bulbil shoots themselves were developing secondary bulbils in the leaf axils (Fig. 1). In both the primary and secondary bulbils a few undivided leaves (resembling juvenile ones, Fig. 10) preceded the pinnate ones. Furthermore, a transition from juvenile to the adult form through partly divided leaves was noticed (Fig. 2). This situation closely simulates the transition taking place in normally growing seedlings. These observations indi-

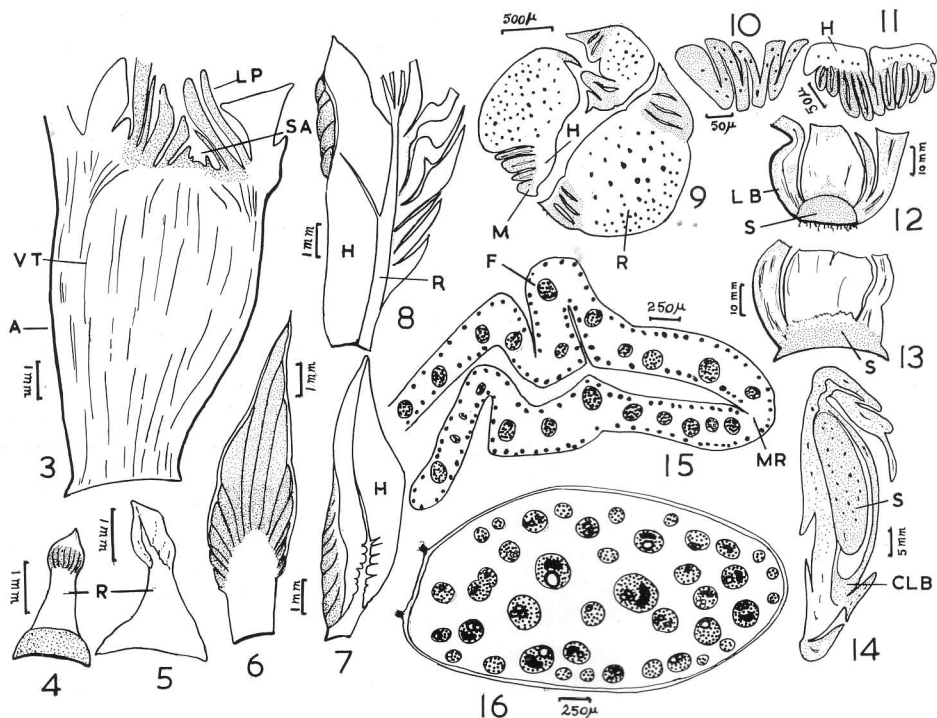
cate that the axillary shoot meristem is functionally similar to the seedling apex.

The axillary meristem

In the adult palm each leaf is associated with an axillary meristem. Normally these meristems become inflorescence primordia. They rarely produce bulbils as in *Cocos* (Davis, 1967). The juvenile leaves and the prophylls do not show axillary meristems. The normal axillary meristem starts as a minute dome-shaped structure enclosed by the leaf sheath and subsequently increases in size. In *Phoenix* it often attains a height of 800 microns. Further development in the apex proper takes place with the induction of inflorescence primordia. When the meristem is committed to develop as a vegetative apex, as in the case of production of bulbils or branches, a prophyll and several empty bracts are formed initially rather than the bracts subtending flowering branches of the inflorescence. Most bracts of this nature have a sheathing base and a short reduced rachis.

It is of interest to note that with the growth of the axillary primordium to a height of about 800 microns the apical dome is carried away from the axil by a short broad axis. The vascularization of this axis even before the initiation of bracts or prophylls is an unique feature. Furthermore, it is only through this axis that the bulbils receive their nutrition from the parent plant.

The sequence of appearance of spadices from the axils of leaves in the adult specimens of *Phoenix* does not follow that of leaves. This indicates that the axillary primordia remain uncommitted for a long time and are capable of either functioning as inflorescence meristems or as vegetative meristems leading to the origin of branches. The origin of normal vegetative branches in rare cases indi-



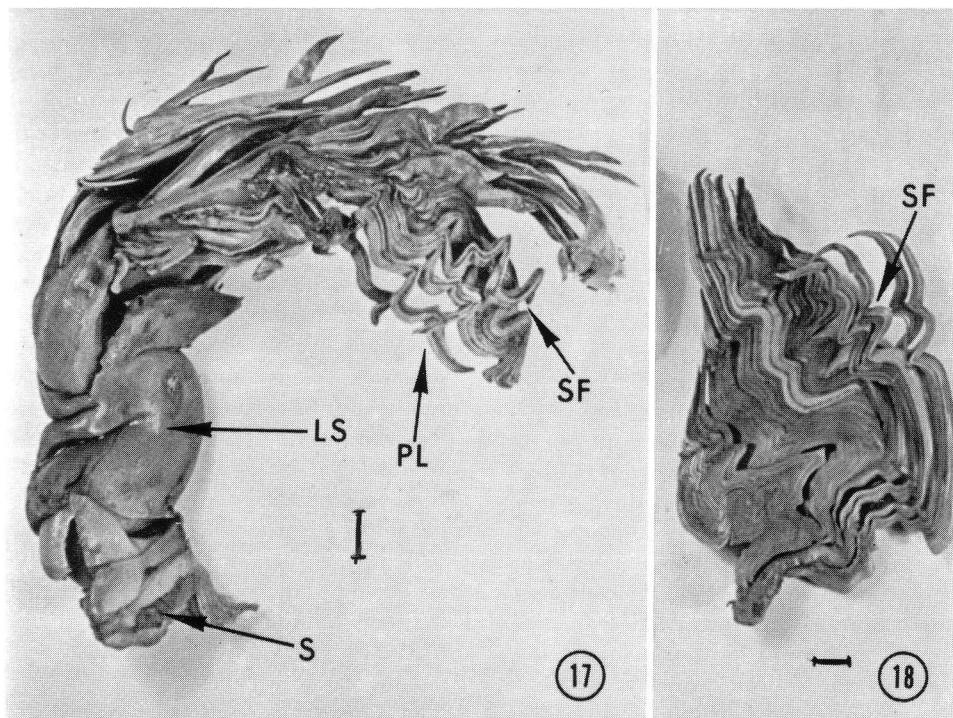
3-16, *Phoenix farinifera* and *P. loureirii*. 3-8, *Phoenix farinifera*. 3, longitudinal section through a young bulbil shoot. 4-8, views of entire leaf primordia dissected out from the bulbil shoot bud. 4, adaxial view of a young primordium. 5, adaxial view of the primordium shown in Fig. 4. 6, 7, abaxial and adaxial views of an older primordium. 8, adaxial view of an older primordium showing the tearing of haut tissue. 9-14, *Phoenix loureirii*. 9, transverse section through young leaf primordia. 10, transverse section through an entire leaf (juvenile) of the bulbil; note the plications. 11, transverse section through the haut region of an older leaf. 12, 13, base of flattened axillary shoot (bulbil) shown in adaxial (Fig. 12) and abaxial (Fig. 13) views. 14, transverse section through base of the axillary shoot shown in Fig. 12 and 13; note the concrescence of leaf bases. 15, 16, *Phoenix sylvestris*. Transverse sections through the lamina and the rachis-petiole axis respectively of a leaf primordium isolated from the axillary shoot. (ADX, adaxial side; CLB, concrescent leaf bases; F, secondary folding in leaflet lamina due to compression; H, haut; LB, leaf base; LP, leaf primordium; M, leaf margin (rein); MR, midrib region; R, rachis; S, stem; SA, shoot apex; VB, vascular bundle; VT, vascular trace).

cates that the axillary meristems may function as vegetative meristems from the time of activation. However, this type of activity is clearly different from the conversion of inflorescence primordia into vegetative shoots as a result of the onset of the phenomenon of phyllody (see Davis, 1973). In such instances the axillary meristems start functioning as inflorescence apices and produce spadices in the normal manner but become

transformed with the advent of the phyllodic condition.

Leaf development in the bulbils

As already mentioned, the first lateral organs to appear in the bulbil are the prophyll and bracts, while the first lateral organ is the prophyll (spathe) in the inflorescence apex. Following the differentiation of prophyll and bracts, eophylls



17, 18. *Phoenix sylvestris*. 17. An axillary shoot isolated from an old leaf axil. The effects of growing in a compressed space enclosed by the leaf sheath are evident. 18. A developing leaf showing the effect of compression on leaflets. (LS, leaf sheath; PL, pinnate leaf; SF, secondary folding due to compression; S, stem region; bars in 17, 18 indicate 10 mm.).

and adult leaves were found to develop in the bulbils (Fig. 2). Sometimes the bulbil stem is very short and rudimentary and is nothing more than a disc bearing the leaves all around and the apical meristem in the center (Fig. 12, 13). Longisections of the shoot bud at this stage show no abnormalities and closely resemble those of normal vegetative apices (Fig. 3).

The young leaf primordia were dissected out of the bulbils and studied individually. The primordia were essentially similar to those developing from normal apical meristems. However, there were differences in their appearance. The haud was well developed (Figs. 8, 9, 11) in the primordia of the bulbils but showed irregular rupturing. The leaflet

primordia were seen to be unusually crumpled and compressed. Furthermore, the developing leaflets exhibited irregular expansion and elongation. As a result, the abaxial side of the primordium was uneven with several leaflet primordia projecting upwards (Fig. 8). Comparison of the right and left halves of the leaf primordium showed that asymmetry was more pronounced than in the normal leaf (Fig. 7).

Certain other abnormalities were also observed. The lack of elongation in the rachis primordium in some of the young leaves (Fig. 6) resulted in a palmate alignment of the leaflets. Such primordia often resembled those of costapalmate leaves. The bases of the first formed prophylls of bulbils exhibited

lateral concrescence (Fig. 14). Transverse sections through these organs indicated that the concrescence may become irregular and infolding of parts of the sheaths is common.

Discussion

The axillary meristems in *Phoenix* develop regularly in association with almost every leaf in the adult palm. After initiation, the axillary apices appear to remain quiescent until the time the flowering stimulus reaches them. However, since some of these meristems may be triggered to develop vegetative branches and sometimes bulbils, it appears that they remain uncommitted during the quiescent period. It is also interesting that the activation of different axillary meristems in the same crown of a tree does not follow the acropetal sequence. Thus there may be dormant buds in the axils of leaves situated just below the level of an inflorescence.

The commitment of the axillary primordia to follow the vegetative course of development in rare cases appears to be controlled by unknown stimuli. Several causes such as injury to the primary apical meristem, insect attack, infection by virus, etc. have already been suggested as probable stimuli (Davis, 1973). The present investigation was not directed towards identifying the merits of these possible causes. However, it is important to differentiate the axillary growths on the basis of their mode of development. Firstly, there are cases wherein the normally unbranched palm develops vegetative branches identical with the main stem. Secondly, there are recorded cases of conversion of inflorescence buds into vegetative shoots, the phenomenon being designated as phyllody. Thirdly, the formation of so-called bulbils in the axils of leaves involves the activation of the axillary meristems. Except in the case of phyllody

wherein a pathogen may be involved or suspected, all others appear to be perfectly normal to the species in so far as the mode of development is concerned. Considering the low frequency of occurrence of axillary shoots in *Phoenix*, one may be tempted to call them abnormal shoots. The present study indicates that occasionally axillary primordia are activated though normally their growth is inhibited or suppressed altogether. Activation of vegetative buds was common in specimens that were not fully mature and had not started flowering. Probably this is the period in the life of the palm when the axillary meristems are not committed to produce inflorescences. The recorded cases of branching in *Borassus* (Davis, 1969) often show that the branches appeared when the main stem was about five feet tall. In cases wherein branching had occurred at several heights it is possible that the main stem was lost above this height due to destruction of its apex. Consequently, the axillary meristems could have been induced to form branches.

The bulbils produced in some species of *Phoenix* present morphological forms that deserve special consideration. These structures do not appear to be capable of establishment as independent plantlets since they have not been observed to produce roots. Furthermore, the bulbils were seen to die after some amount of growth. It is possible that the bulbils in these cases are not capable of vegetative propagation. However, the possibility of artificial root induction in these shoots cannot be ruled out. Scanty development of the stem is characteristic of bulbils and this character serves to identify the real vegetative branches which develop a prominent stem even in the initial stages. However, the bulbils exhibited another interesting phenomenon which was not common in branches. This was the production of entire leaves in the young

bulbil followed by appearance of transitional and completely pinnate leaves. This situation can be compared to the production of eophylls in the seedling and subsequent transition to compound adult leaves. It is likely that the bulbils develop autonomously and have their own control mechanisms. This is evident from the fact that bulbils appear in large numbers even as the apical bud of the main stem is very active. The production of secondary bulbils in shoots produced by bulbils is indicative of the absence of apical dominance, as it were, in the entire shoot.

The origin of shoot buds from inflorescences (phyllody) in some palms has been interpreted as due to viral infection and/or genetic factors. Davis (1973) believes that the former cause is unlikely. However, a parallel situation is known to occur in a number of dicotyledons from India that were affected by virus diseases (John, 1957). Hence the phenomenon may be a pathological expression which deserves further study.

Summary

Populations of three species of *Phoenix* (*P. sylvestris*, *P. loureirii* and *P. farinifera*) were screened for the occurrence of rare axillary shoots. Small axillary shoots, bulbils, and secondary bulbils were collected and studied. It was found that most of these rare axillary growths show the normal process of development of leaves. The axillary shoots in *P. sylvestris* showed a short axis, an apical meristem, and leaf primordia. Basal leaf

sheaths were often concrescent. Bulbil shoots were found in *P. loureirii*, and *P. farinifera*. They had a small compressed stem and leaves with a reduced number of leaflets. Presence of undivided leaves (eophylls?) followed by transition to the pinnate condition was an interesting feature in the bulbils. Secondary bulbils were developing in the axils of leaves of the first order in some specimens. The morphology and development of different types of axillary growths in species of *Phoenix* are discussed in relation to shoots produced as a result of phyllody.

Acknowledgement

I am thankful to Prof. S. Krishnaswamy, Head, Department of Biological Sciences, Madurai University, for facilities and encouragement.

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Ecological Studies of the Cabbage Palm, *Sabal palmetto*.

III. Seed Germination and Seedling Establishment.

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Seed Germination

The majority of germination studies in palms have been on commercial species, especially the African oil palm, *Elaeis guineensis* Jacq. (Hussey, 1958; Rees, 1961, 1962, 1963). Germination studies on wild palms are few in the literature. Bannister (1970) studied germination in the sierra palm, *Prestoea montana* (Graham) Nicholson (as *Euterpe globosa*), in growth chambers and in a Puerto Rican rain forest. Read (1968) presented data for the Caribbean genus *Pseudophoenix* H. Wendland ex Sargent. Germination data for other wild palms have been reported in several popular journals; however, none were scientific studies.

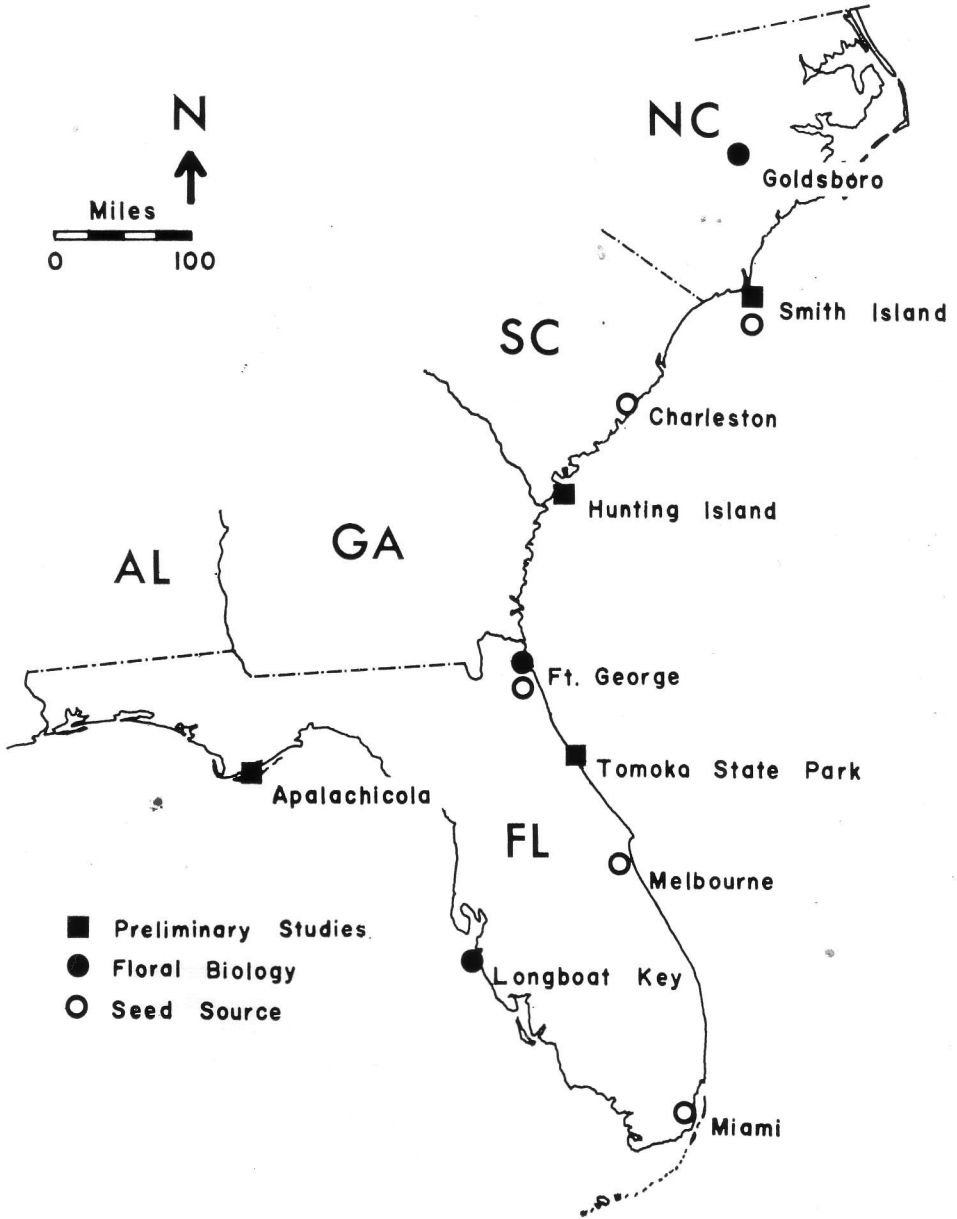
The inherent capabilities of seeds and their interaction with environmental factors determine the success or failure of the germination system. Both internal seed factors and external physical factors (Mayer and Poljakoff-Mayber, 1963) were investigated to determine the germination system in *Sabal palmetto*.

Materials and Methods

Seeds from five coastal populations (Brown, 1976a) were used to determine if germination response differed with latitude. Fresh, mature fruits were gathered in the fall and early winter of

1971–1972. Approximately 5,000 seeds from each site (Fig. 1) were collected and stored dry at room temperature (22° C). From these population samples, the required experimental samples were randomly selected. All experiments were carried out in the Southeastern Plant Environment Laboratory (N. C. State Phytotron) referred to below as the phytotron (Downs, Hellmers & Kramer, 1972).

Various experimental chambers in the phytotron were used for germination studies. Water-cooled Pfeiffer germinators were used for the temperature and salinity experiments. The illumination experiment was housed in an "Environmental Growth Chambers" walk-in controlled-environment room. Preliminary work suggested that 28 days was sufficient time to allow for germination under chamber conditions. Germination was considered successful upon emergence of the radicle from the seed. All germination tests were of a fixed model design with predetermined locations (populations), temperatures, salinity levels, and light conditions. Data were analyzed using the Statistical Analysis System (Barr and Goodnight, 1972). Details of the methodology and statistical analyses are recorded in Brown, 1973, and all statistical inferences are at the 95% confidence level.



1. Location of field study sites and seed sources.

Seed size and energy

Although there was a difference in seed weight in samples from Miami and Smith Island, the difference was not

significant. Average weight of seed over the geographic range was 14 grams.

Bomb calorimetry revealed an average caloric value of 3.6 Kcal/gram of seed.

Table 1. Germination under constant thermoperiods (values are percent germination based on average of 100 seeds after 28 days at indicated temperatures)

Temperature	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
15.0° C	0.0	0.0	0.0	0.0	0.0
17.5	0.0	0.0	0.0	0.0	0.0
20.0	7.1	0.0	0.0	0.0	0.0
22.5	55.4	46.0	45.0	30.4	50.8
25.0	86.0	89.0	82.0	75.0	75.0
27.5	92.9	98.0	92.9	92.8	95.9
30.0	99.0	99.0	96.0	87.0	97.0
32.5	95.0	97.0	80.0	42.0	87.9
35.0	47.0	66.0	48.0	11.0	59.6
40.0	0.0	0.0	0.0	0.0	0.0

This is a low value compared to many other seeds (Leith, 1968) and reflects the absence of high energy carbohydrates, such as starch, in the seeds of *S. palmetto*.

Hydration

Hydration studies using distilled water and seeds from all sites revealed rapid linear water uptake for the first 24 hours. After 24 hours, uptake was curvilinear until equilibrium was reached. Uptake was directly proportional to temperature over the range of 15° C to 40° C. Average increase in fresh weight due to water uptake was 45–55%, depending on seed source. Water potential of dry-stored seed was determined to be approximately –965 atm. Details of these findings are reported in Brown, 1973.

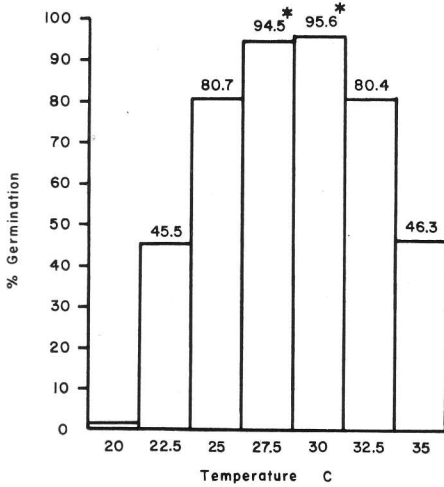
Constant Thermoperiods

Preliminary studies suggested that 30° C was optimal germination temperature for *Sabal palmetto*. Using this information and allowing 28 days incubation as a standard, further regimes were employed to determine germination response to constant temperatures.

Germination studies were conducted with 100 seeds from each population for each temperature. Thermoperiods used were: every 2.5 degrees between 15° and 35° C, and 40° C. Design was such that statistical tests for differences between population location (latitude) and temperature and interaction of temperature by location could be made. A daily record of germination was kept for 28 days.

No response was recorded at 15°, 17.5° and 40° C for the duration of the experiment (Table 1). Five of 10 dishes of Miami material responded at 20° C giving 7.1% total germination. As a result, only data from thermoperiods 20° through 35° C were analyzed statistically. Results from the Charleston population were so markedly different from all the others except for 25° and 27.5° C that the data were excluded from statistical analysis. This was a questionable population sample from the outset as only six trees were sampled, by proxy, at least one of which was a horticultural specimen of unknown origin.

Statistical analysis revealed significant temperature and location effects on percentage of germination; however, no



2. Effect of temperature on germination under constant thermoperiods (values are overall means, Charleston excluded; *indicates significant at 95% confidence).

latitudinal pattern emerged. In fact, there was no significant difference between means from Miami and Smith Island populations. Although 30° C was optimum temperature for all locations, it was not significantly different from 27.5° C but both of these temperatures resulted in significantly greater germination percentage than the other temperatures tested (Fig. 2). Read (1968) found a similar but narrower limit of response to temperature in several species of *Pseudophoenix*.

Alternating Thermoperiods

The alternating thermoperiods used were: 25°/15°, 30°/20°, 35°/25° and 40°/20° C with the higher temperature in effect for approximately 16 hours and the lower for eight hours. Daily germination was recorded for 28 days.

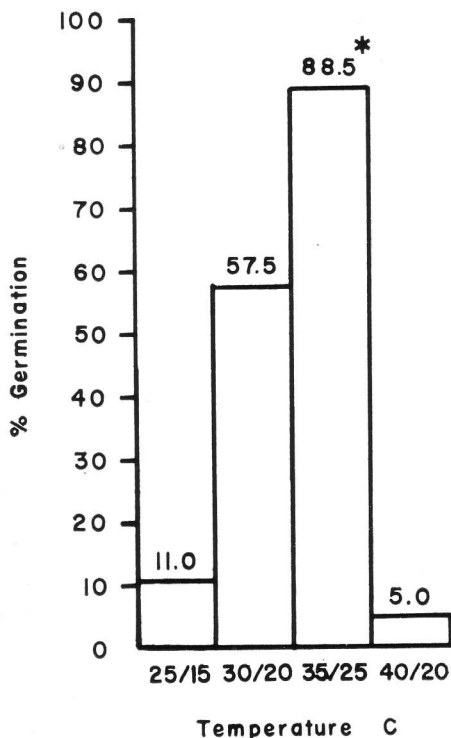
The response of the Charleston population was atypical as before and was excluded from analysis. Germination response was less uniform and lower than that under constant thermoperiods (Table 2). Analysis revealed significant temperature and location effects on percentage of germination. The 35°/25° C thermoperiod resulted in significantly greater percentage of germination than the other thermoperiods tested (Fig. 3). The location effect revealed a latitudinal difference: the two southern populations (Miami and Melbourne) had significantly greater germination than the mid-range (Ft. George) and northern (Smith Island) populations.

In an attempt to correlate the findings of the alternating thermoperiods experiment with natural conditions, field studies were conducted at Ft. George on July 14, 1972. Soil temperature conditions where seeds were actively germinating were determined. In an area under forest shade, seeds were germinating within the top 2.5 cm. of soil. Minimum temperature at this depth was 24° C and at

Table 2. Germination under alternating thermoperiods (values are percent germination based on average of 100 seeds after 28 days at indicated temperatures)

Temperature	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
25°/15° C	19.0	14.0	4.0	2.0	7.0
30/20	71.0	70.6	35.0	20.0	54.0
35/25*	100.0	96.0	80.0	34.0	78.7
40/20*	12.0	4.0	4.0	4.0	0.0

* Average of 50 seeds.



3. Effect of temperature on germination under alternating thermoperiods (values are overall means, Charleston excluded; *indicates significant at 95% confidence level).

the surface, 25° C. Maximum temperature at 2.5 cm. depth was 27° C and at the surface, 28° C.

On a sunny plot exposed to sun from approximately 1000 to 1600 EDT, seeds were not germinating within the top 2.5 cm. of soil. At this location temperature within the top 2.5 cm. of soil fluctuated widely and rapidly with passage of clouds over the area. Maximum reading at 2.5 cm. depth was 38° C, while maximum at the surface was 46° C. Some seeds were buried deeper than usual at this site due to a winter storm which covered the area with beach sand. Seeds at 7.5 cm. depth, where maximum temperature was 31° C, were germinating. These temperatures

and germination observations are in reasonable correspondence with those in the experimental germination studies. Even though maximum response occurred at a constant 30° C, germination in *S. palmetto* may occur slowly over long periods under normal diurnal temperature cycles in nature similar to that found in *Elaeis guineensis* by Hussey (1958).

Illumination

This experiment was conducted to determine if germination response is influenced by light or by darkness. For each population a set of 50 seeds was placed in a black cloth bag on a tray and another set of 50 left exposed, lying adjacent. The chamber used had a standard alternating thermoperiod of 30°/26° C and long-day photoperiod (9 hour day, 3 hour light break mid-way through the dark period). Daily germination was recorded for 28 days.

Charleston response was again atypical and excluded from analysis. Light was inhibitory at all locations but remained so for less time at the two southernmost locations where number of days to first germination in light was noticeably lower than at Ft. George or Smith Island (Table 3). Average germination for all populations was five times greater in dark than in light and began in 9.5 days compared to 24.5 days in the light. The inhibitory mechanism appears to break down in the presence of favorable moisture and temperature conditions with the passage of time.

Field observations revealed that seeds exposed to the sun do not germinate, while those in darkness buried by sand or organic debris do, when temperature and moisture are favorable.

Further carefully controlled experiments to determine the interrelationship of light quality and quantity, tempera-

Table 3. Germination under light and dark conditions (values are percent germination based on average of 50 seeds after 28 days; numbers in parentheses are average number of days to first germination)

Condition	Location					
	Miami	Melbourne	Ft. George	Charleston	Smith Island	Average (excluding Charleston)
Light	30.0 (22.2)	20.0 (20.8)	2.0 (27.6)	0.0 [*] (-)	6.0 (27.4)	14.5% (24.5)
Dark	82.0 (7.8)	72.0 (7.8)	72.0 (10.0)	38.0 (15.4)	76.0 (12.4)	75.5%* (9.5)*

* Indicates significant difference.

ture and moisture are needed to discern the adaptive significance, if any, of this mechanism.

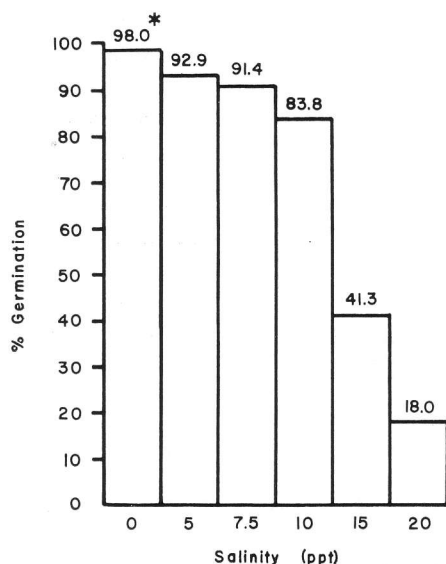
Salinity

A series of tests was conducted to determine the germination response of seeds exposed to salinity levels up to near sea strength (30 ppt). Dishes of 50 seeds were initially moistened with 0 (demineralized water), 5, 7.5, 10, 15, 20, and 30 parts per thousand NaCl solutions and placed in the 30° C chamber. No further solution was added. Daily germination was recorded for 28 days. Condition of seedlings, in regard to root and shoot development, was noted at termination.

Charleston response was again atypical and therefore excluded from analysis. Germination decreased with increasing salinity and there was no response at 30 ppt (Table 4). The responses at 5 ppt and 7.5 ppt were not significantly different from each other but both were significantly lower than the control (0 ppt). The greatest effect came between 10 and 15 ppt NaCl where average germination dropped from 83.8% to 41.3% and root development of some seedlings was noticeably abnormal (Fig. 4). At 20 ppt NaCl, abnormal root growth (stubby, non-branching primary roots) was recorded on all germinated seedlings in all populations. Higher maximum germination at 20 ppt NaCl was attained by both

Table 4. Germination under various substrate salinities (values are percent germination based on average of 50 seeds after 28 days at constant 30° C)

Salinity (ppt)	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
0.0	98.0	100.0	96.0	84.0	98.0
5.0	91.8	96.0	96.0	46.4	88.0
7.5	94.0	96.0	89.8	46.0	85.8
10.0	75.6	84.0	88.0	34.0	87.6
15.0	55.3	41.1	24.7	10.0	44.0
20.0	22.0	28.0	14.0	0.0	8.0
30.0	0.0	0.0	0.0	0.0	0.0



4. Effect of salinity on germination at constant 30° C (values are overall means, Charleston excluded; *indicates significant at 95% confidence level).

Miami and Melbourne populations, but abnormal subsequent seedling growth negated the importance of this.

The effect of salt on the viability of seeds becomes complex with increasing time and higher salinities. However, the results of this study and the study of viability after extended periods in sea-strength salt solutions reported in a previous article (Brown, 1976b) indicate that, initially, NaCl solutions up to 35

ppt are not toxic but inhibitory. Initial inhibition may be due to a water potential and imbibition problem but with the passage of time at substrate salinities of 15 ppt and above toxic effects begin to occur and carry over into seedling growth if germination occurs.

Mention has been made of the abundant local presence of this species around the edges of salt marshes. It is in these habitats that salt stress in regard to germination would occur. Analysis of top soil from such an area at Tomoka State Park, Florida revealed an average salinity of 5.13 ppt during the summer germinating season. The experimental results suggest that *S. palmetto* is well adapted to handle such salinity levels from the standpoint of seed imbibition and germination.

High Temperature Reaction

After exposure of seeds to the 40° C constant thermoperiod, in which germination did not occur, two groups of seeds were placed into 30° C chambers. One group of 50 seeds each from all five populations had received 28 days at 40° C, the other 56 days. Average germination after placement in 30° C for the five populations was 99.2% and 97.6%, respectively, and average time to first germination was 3.32 and 1.96 days, respectively (Table 5). Also, there was

Table 5. Germination at 30° C after 40° C treatment (values are percent germination based on average of 50 seeds after 28 days; numbers in parentheses are number of days to first germination)

Days at 40° C	Location				
	Miami	Melbourne	Ft. George	Charleston	Smith Island
28	100.0 (3.2)	100.0 (3.0)	98.0 (3.4)	97.8 (3.2)	100.0 (3.8)
56	98.0 (1.8)	98.0 (2.0)	100.0 (2.2)	98.0 (1.8)	94.0 (2.0)

little or no "tailing off" as maximum germination response in all cases was reached in 13 days or less. Some process is occurring at 40° C which, for at least 56 days, enables seed to emerge very quickly, at very high percentages, when placed at optimum temperature (30° C). The atypical and erratic germination results previously noted for the Charleston population were overridden by this high temperature treatment. Rees (1960) states that high temperatures (38–40° C) are required by *Elaeis guineensis* for early stages of the germination process. This is believed to be an adaptation to the hot dry season which follows fruit maturation. However, the occurrence of a high temperature reaction in *S. palmetto* has no apparent ecological significance in that it is not a prerequisite for germination.

Germination System Summary

The moisture and temperature requirements for germination of *S. palmetto* are satisfactorily met throughout the natural range by the coincidence of the rains and high soil temperatures of summer. Results of the various temperature experiments suggest that in the soil a minimum temperature at or above 20° C must be met before germination processes are initiated. Up to a point, reactions in the germination pathway can proceed at higher, sublethal temperatures, but for completion of steps resulting in radicle emergence, a maximum temperature somewhere between 35° and 40° C must not be exceeded.

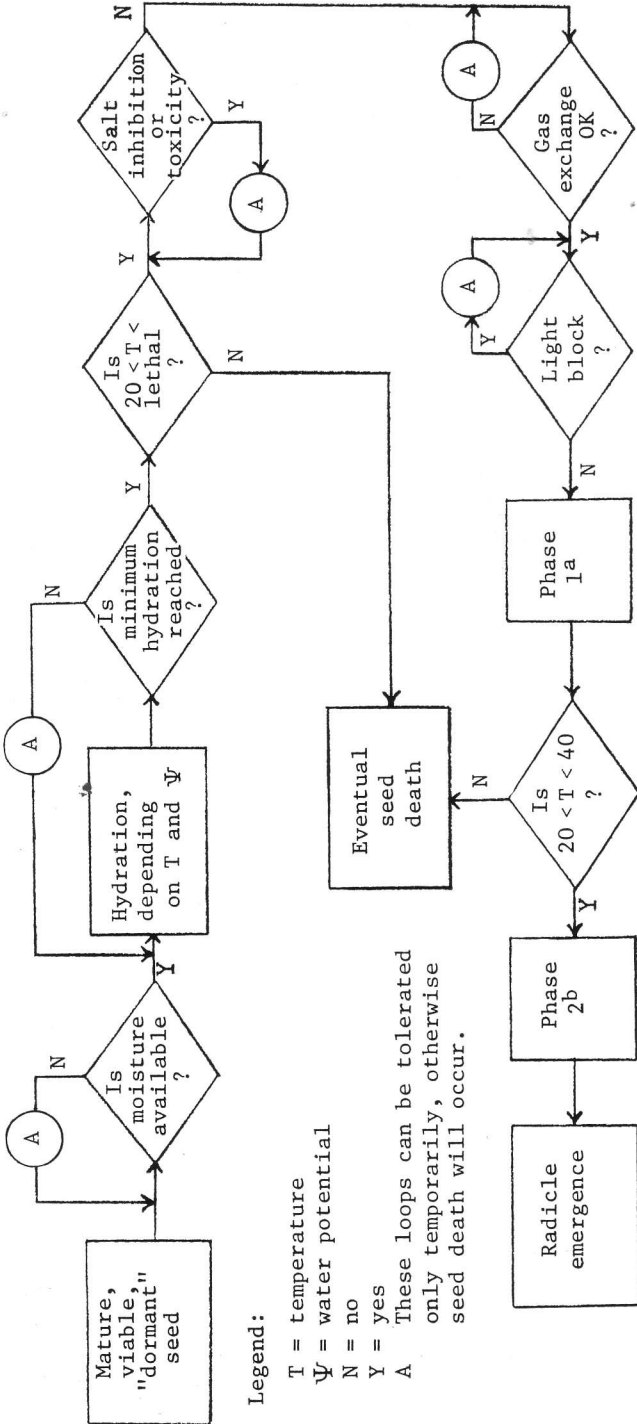
Substrate salinity levels normally encountered in the terrestrial estuarine environment have been adapted to and present no problem for germination.

The plant has evolved an incompletely understood mechanism whereby exposure to sunlight prevents or retards radicle emergence. This inhibition is readily

overcome when the seed is covered by sand or organic debris. This may be adaptively significant in preventing radicle emergence into an unfavorably dry microenvironment or it may be that the undeveloped embryo has a light-sensitive period necessary for certain early developmental steps before emergence.

Data analysis indicated no strong latitudinal differences in germination in this species except in response to alternating thermoperiods, where southern populations had significantly higher germination percentage. The response to salinity, illumination, and constant temperature by all populations indicate that these factors, individually, are rather constant in effect and occurrence over the latitudinal range of the species. The lower response to alternating thermoperiods observed with increasing latitude suggests a selection pressure against germination at temperatures departing from the maximum response range of 27.5° to 30° C. This is a logical occurrence as it would restrict germination to the warmer spring and summer months and tend to prevent germination in fall or winter when low temperatures unfavorable to seedling establishment are most likely to occur.

When conditions are satisfactory, the germination pathway culminates in radicle emergence. The radicle and shoot apex are pushed down into the soil by the downward extension of the cotyledonary stalk. The cotyledon remains in the seed and acts as a haustorium, expanding with absorption of the endosperm. The embryonic seedling is thus planted in the soil remotely from the seed in a manner common to several palm genera (Tomlinson, 1960a). This phenomenon has been evoked as an adaptation by palms to a normally dry habitat (Rees, 1960). The microhabitat of the germinating *S. palmetto* seed is certainly subject to periodic rapid drying



^aInitial biochemical activity (production of enzymes, breakdown and resynthesis of stored materials).
^bCell division and elongation.

5. Generalized flow diagram of possible sequence of germination events.

in summer months. The cotyledonary stalk may provide an adaptive mechanism to place the embryonic plant quickly below dry surface sands into layers where moisture is adequate for further development.

Figure 5 depicts possible events leading to germination and allows a concise consideration of the coordination of functions in the seed in response to environment (Amein, 1966).

Seedling Establishment

Seedling establishment is the stage of a plant life cycle which begins with the emerging seedling and continues until the seedling reaches the autotrophic state. Stebbins (1971) suggests that this stage is the weakest link in the life cycle of plant species in their colonization of new territory. *Sabal palmetto*, which outside of peninsular Florida is found in warmer habitats along the Gulf and Atlantic coasts, has been thought to be limited in its range by cold winter temperatures (Small, 1923). Observations of reproducing introductions at some distances north and west of the natural range have led me to question the validity of this explanation.

Investigations were thus made to determine the general environmental requirements of successful establishment of seedlings with particular regard to temperature. Field observations were made throughout both the natural and horticultural range. Controlled laboratory experiments were conducted on Miami and Smith Island seedlings in the phytotron walk-in environment rooms.

Morphology and Development

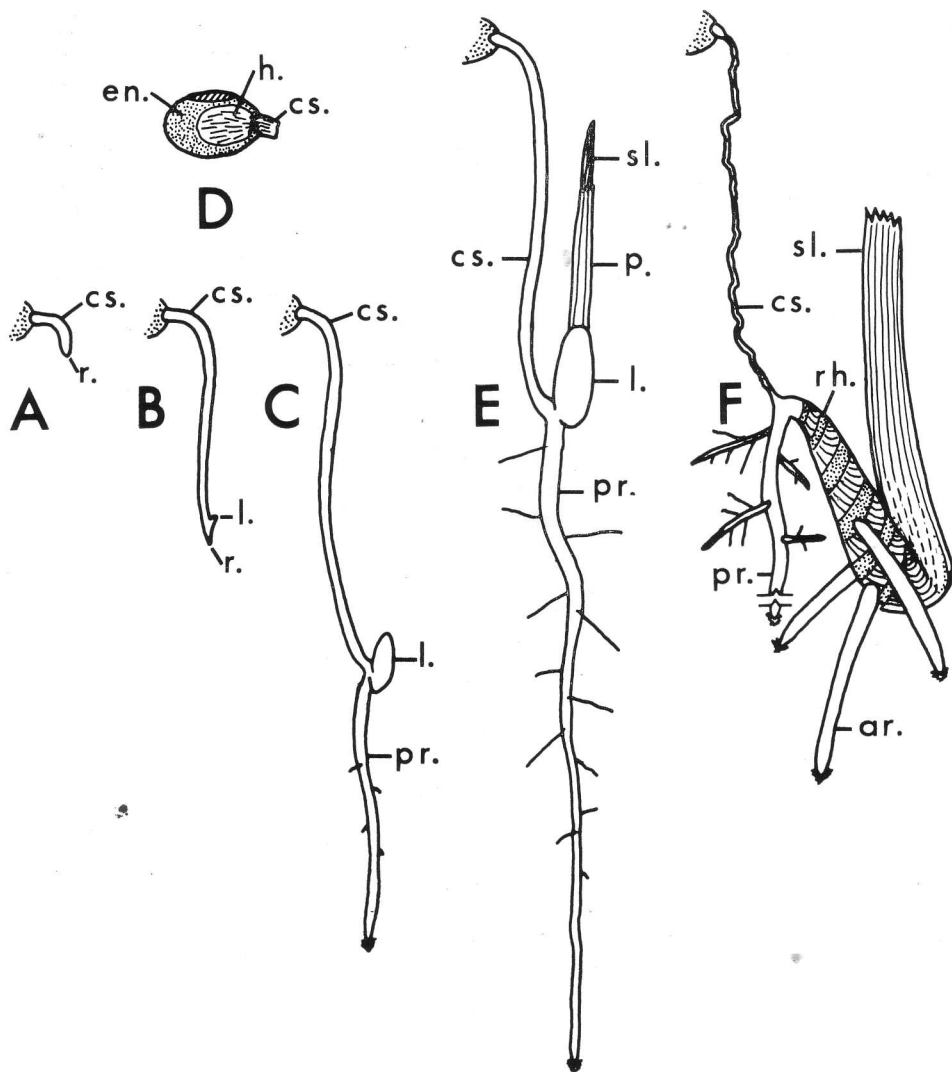
General considerations of early seedling development in palms are discussed by Tomlinson (1960b). In *S. palmetto*, after radicle emergence, further development occurs primarily as elongation of

the cotyledonary stalk, with its distally attached radicle and epicotyl, and growth of the haustorium (cotyledon) within the seed (Fig. 6).

Morphology of the emerging seedling is an important factor in establishment (Harper, Lovell, & Moore, 1970), especially as it relates to the ability to penetrate the soil. In *S. palmetto*, the elongating radicle-cotyledonary stalk structure, 1-2 mm. diameter and tubular, is well designed for this. The cotyledonary stalk, which exhibits negative geotropism, penetrates the soil and normally expands to about 4 cm. in length. Depth of placement of the radicle-epicotyl axis will depend upon the initial depth of seed deposition.

From this approximate depth of 4 cm., the primary root penetrates farther into the soil and becomes branched. Visible shoot growth begins with the development of the ligule which is ruptured by the expanding sheath and seedling leaves. The first seedling leaf emerges through the sheath and remains plicately folded while penetrating the soil to the surface. Once above the surface the seedling leaf expands and unfolds reaching a final length usually less than 15 cm. and width less than 1.5 cm. From this point on the seedling is autotrophic and essentially established. While the linear seedling leaves are expanding, stem growth is established obliquely downward resulting in formation of a rhizome (Tomlinson, 1960b).

Downward growth of the rhizome continues for an undetermined time, probably many years, until an upright position is assumed and the rhizome gradually emerges to form the trunk. A variable number of simple seedling leaves are produced for at least two years in the laboratory and probably much longer in nature. No fewer than 10 of these leaves are produced before



6. Morphology of early seedling development. A-C, successive stages in development to about $3\frac{1}{2}$ weeks, all $\times 2$; D, longitudinal section through seed at stage C showing haustorium, $\times 2\frac{1}{2}$; E, six-week-old seedling, $\times 2$; F, one-year-old seedling showing downward rhizome development, $\times 2$. (ar, adventitious root; cs, cotyledonary stalk; en, endosperm; h, haustorium; l, ligule; p, plumule; pr, primary root; r, radicle; rh, rhizome; sl, seedling.)

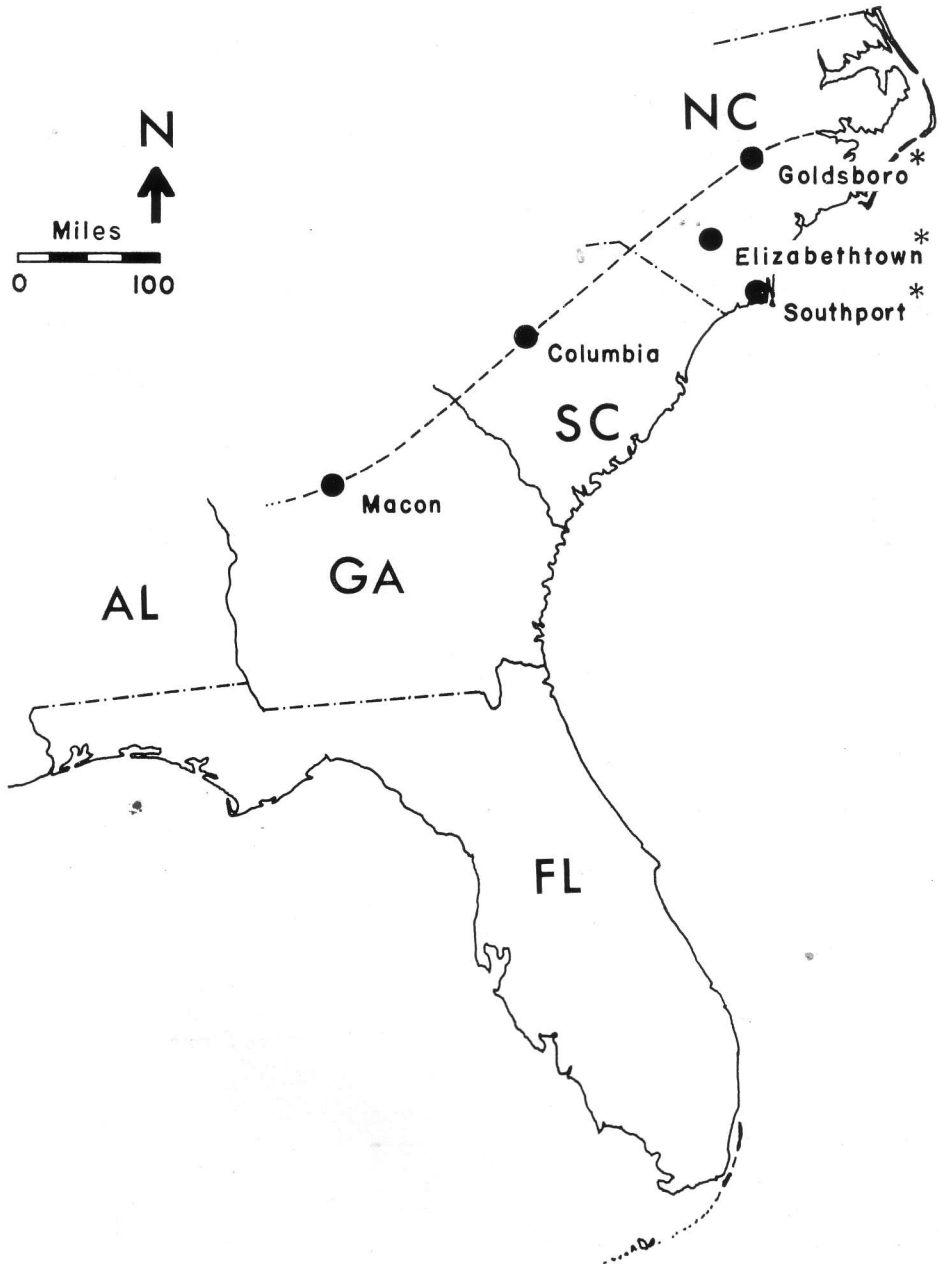
the first dissection into a few segments occurs.

Field Studies

Seedlings grow very little in nature during their first year due to a middle to late summer germination sequence over

most of the range. Above-ground growth by late fall normally consists of one fully expanded seedling leaf. The rate of production of seedling leaves in subsequent years is unknown.

The number of plants in the mature (reproducing) stage was noticeably small



7. Horticultural range of *S. palmetto* (location of observed reproduction outside the natural range indicated by*).

in the interior of maritime forests. Survival among seedlings to the three- to four-leaf stage was relatively high but greatly decreased beyond this stage. In contrast is the obviously high rate of survival of plants in all age categories along some water courses and edges of salt marshes.

The initial number of germinating seedlings in these two areas can be expected to be quite different due to seed predation (Brown, 1976b). This would explain the low initial number of seedlings in the maritime forest but it does not explain the loss of young established seedlings in the same habitat. Some factors, as yet unknown, are at work to cause this decrease in survival. Whatever the cause, it is not the lack of ability to establish seedlings which results in low density of *S. palmetto* in the maritime forest habitat.

Attempts were made to correlate the natural range of successful establishment with climatic factors, especially temperature. There was some correspondence with the mean annual number of days with minimum temperature of 0° C and below. Correspondence with the 30-day isogram existed along the South and North Carolina coast lines but did not hold south of South Carolina. A closer correspondence occurred with the mean length of freeze-free period. The 270-day isogram was close to the distribution line in all of Florida, Georgia, and South Carolina. Discrepancy occurred along the northern South Carolina coast and the North Carolina coast where the plant was found farther north. No correlation with annual or monthly rainfall or semiannual evaporation rate was detected.

Investigations into the horticultural range of the plant revealed that climatic factors do not appear to be limiting the species to its natural range (Fig. 7).

Observations in North Carolina revealed reproduction far to the north and inland of the species' northernmost natural extension. In Elizabethtown, Southport on the mainland opposite Smith Island, and Goldsboro, large old trees have given rise to numerous seedlings and juvenile plants in urban sites. It is noteworthy that many several-year-old plants are thriving in a hedge row without benefit of protection from structures at the Goldsboro site (Fig. 8). A single plant had been brought from Smith Island in 1910. All of these locations have climates colder than adjacent coastal areas as documented in U. S. Weather Bureau records.

The successful reproductive activities of plants at these locations suggests strongly that minimum winter temperatures are not limiting *S. palmetto* to its current natural range. This fact, along with the occurrence of established seedlings in widely divergent moisture, soil, and light conditions in the natural range, suggests that physical factors are minimally involved in seedling attrition. Thus, further biotic attrition, beyond seed predation, appears probable. Only long-term studies on survival of seedlings in the field will provide information on the causes and timing of seedling attrition.

Low Temperature Stress

A series of experiments was designed to determine the duration of certain cold temperature regimes required to terminate life processes in *S. palmetto* seedlings. Three thermoperiods were selected: 9°/-6°, 9°/0°, and 9°/6° (day/night temperatures, degrees C) with 9-hr. light periods. A control and initial growth chamber was established with 30°/22° C thermoperiod and long days (9 hr. plus 3-hr. light break during dark period). This chamber was set up to



8. *Sabal palmetto* reproduction outside the natural range at Goldsboro, N. C. A, plant brought in from Smith Island in 1910. B, progeny of plant shown in A.

approximate average temperature and light conditions throughout the natural range during the summer growth period. In addition, an intermediate chamber was maintained with 22°/14° C thermoperiod and short days (9 hrs. light). This chamber was used to acclimate plants moving in and out of the cold treatments. Seedlings were subjected to the treatment thermoperiods for various times: 9°/-6° up to 6 weeks, 9°/0° up to 10 weeks, and 9°/6° up to 12 weeks. The maximum, 12 weeks for 9°/6° thermoperiod, was selected to exceed the number of weeks of vulnerability to that average temperature range in North Carolina coastal plain winters.

The complete experiment was conducted with both Smith Island and Miami seedlings in an attempt to detect any difference in cold tolerance with latitude. Seedlings from earlier germination experiments were planted in even particle-sized quartz sand and grown off in the 30°/22° control chamber until they were approximately equal in development to seedlings in nature going into their first winter; *i.e.*, at least one fully expanded seedling leaf. All plants received standard Phytotron nutrient solution once a day and were flushed with demineralized water once a week. Details of methodology, scheduling, and statistical analysis are described in Brown (1973).

The results revealed no significant difference (95% confidence level) in response between Miami and Smith Island seedlings at the temperatures employed. After one week of exposure all plants from both populations in the 9°/-6° thermoperiod were dead. Although

a few individual Smith Island plants died after various exposure times at both 9°/0° and 9°/6° thermoperiods, all plants from both populations receiving maximum exposures to both thermoperiods survived. Visible signs of stress, manifested as leaf tip burn, occurred in both populations and for all durations of the treatment thermoperiods; however, Miami plants at 9°/6° thermoperiod showed the least damage of any group. The expected death at longer exposure times at the 9°/0° thermoperiod failed to materialize. The 9°/0° thermoperiod represents a temperature range rare in Miami for one day, much less one to 10 weeks. This would seem to indicate that, since no apparent selection for cold resistance has developed in the Smith Island population, low temperatures experienced in nature are not a limiting factor in establishment of seedlings of the species in its current range.

Growth Under Favorable Conditions

The 10 control plants used in the low temperature stress experiment were further utilized in studies grown under favorable temperature conditions. The goal of these investigations was to ascertain whether or not ecotypic differences occur between Miami and Smith Island populations.

Biomass and photosynthetic rate were determined. Shoot and root weights were taken and shoot/root ratios were calculated. Photosynthetic rate was determined for the seven best plants from each location in an open system using a cylindrical leaf chamber and differential gas analyzer. Details of methodol-

9. Growth of Miami and Smith Island seedlings under favorable conditions. A, eight-month-old groups. B, eight-month-old individuals. C, two-year-old individuals. Miami material on right in all instances. →

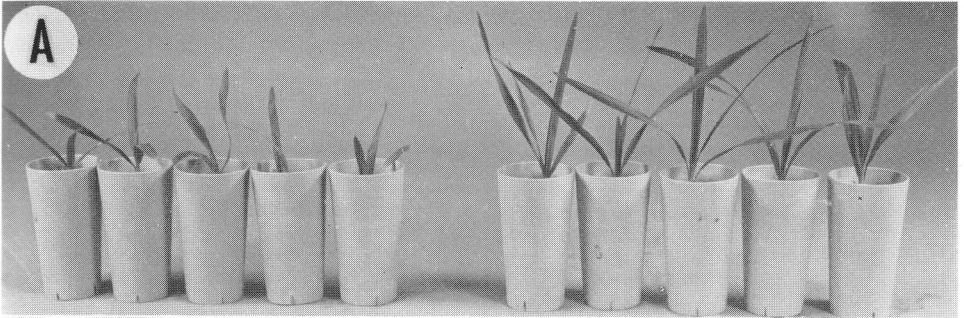
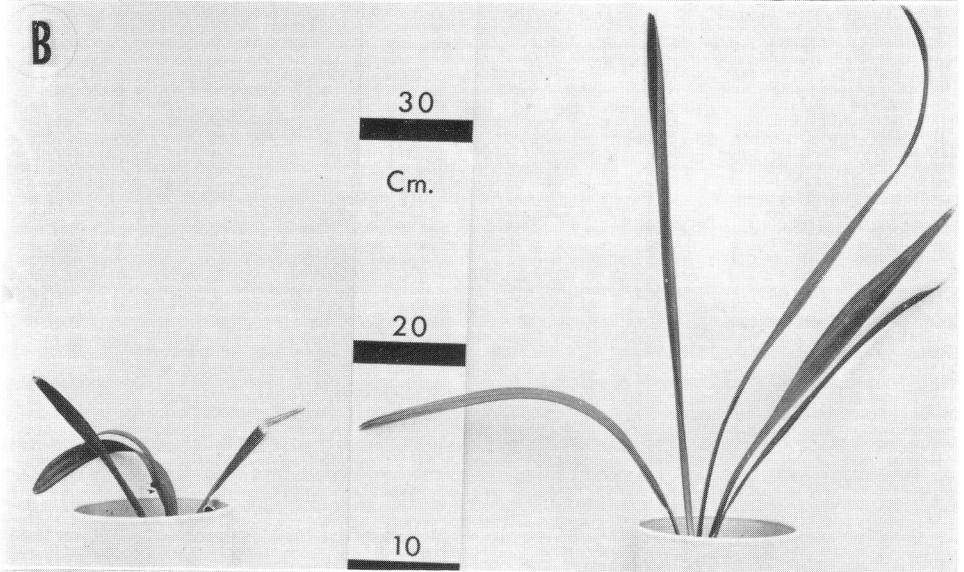


Table 6. Average biomass and photosynthetic rate determinations (biomass calculations based on 10 plants, each location; photosynthetic rate based on best seven plants, each location)

Statistic	Location	
	Miami	Smith Island
Shoot weight (g)	1.11	0.43
Root weight (g)	0.42	0.22
Total biomass (g)	1.53*	0.65
Shoot/root ratio	2.66	2.03
Photosynthetic rate (g carbon/cm ² /sec)	8.14×10^{-9} *	3.20×10^{-9}

* Indicates significant difference.

ogy are documented in Brown (1973). Biomass and photosynthetic rate means were statistically analyzed and inferences made at the 95% confidence level.

Approximately the same average number of leaves were produced by both populations over the 18-week study period (Miami, 4.1; Smith Island, 3.7), but growth rates and size of plants were noticeably different. The Miami plants were larger and had an expansion rate of 0.4 mm per day for the emerging leaf, twice that of Smith Island seedlings. In addition, foliar morphology was different. Miami seedlings had long, narrow leaves, while Smith Island seedlings had much shorter, broader leaves (Fig. 9).

Analysis revealed a close correlation between biomass and photosynthetic rate at each location. A significant difference in both biomass and photosynthetic rate occurred between locations (Table 6). Miami seedlings had a photosynthetic rate 2.54 times that of Smith Island seedlings. The efficiency of this unit-area photosynthetic advantage was evident in Miami total biomass which was 2.35 times greater. The greater shoot/root ratio of Miami seedlings indicates that a greater percentage of the total energy available is directed toward shoot growth than in Smith Island seedlings.

These differences occurred under identical growth chamber conditions indicating genetically fixed differences characteristic of ecotypes. Within the coastal zone, at least, *S. palmetto* exhibits physiological (photosynthetic) ecotypes responding to some unknown factor or factors varying between the extremes of the range. However, since edaphic and climatic factors are divergent between the two populations and rates were calculated under one set of conditions, no conclusions on the importance of the apparent ecotypic differences were made.

Seedling Establishment Summary

Based on its particular geographic range, *S. palmetto* appears well adapted for establishment in a wide range of habitats. Low survival rates in the interior of maritime forest habitats are not due to seedling establishment problems but to undetermined environmental factors at a later stage.

No evidence of low temperature restrictions on range extension were found. On the contrary, reproduction from horticultural plantings reveals that the species is quite capable of establishing seedlings farther north and west of its current natural range. This suggests

that some other stage of the life cycle is limiting the spread of the species.

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A Note on the Abscission of Spiny Leaves of Palms

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Spines on palms function presumably to preclude or to decrease the damage done by herbivores (Tomlinson, 1962b, and Uhl and Moore, 1973). Whereas old leaves are dropped from most plants, some plants with leaf spines appear to droop, not drop, their dead foliage, thereby providing their stems with a protective mesh of spines. Such a mesh would serve to protect the stem tissues as well as to hinder climbing herbivores such as squirrels and coatis bent on reaching the apical bud. Thus, there is some ecological importance to the persistence or abscission of old leaves (Tomlinson, 1962a) in that there may be a close association between the presence of spines and the process of abscission (Tomlinson, 1962b). A particularly striking example is the genus *Washingtonia* whose trunks are unarmed, yet well protected by skirts of dead leaves whose petioles have spines (McCurrah, 1960).

In this study, in order to test the association between abscission and spines, a number of common palm species were observed to determine if the percentage of leaves which are dead (but still attached to the trunk) is higher for species with spiny leaves.

Methods

In several locations in Costa Rica the more common palm species were studied to determine if the lack of abscission of old leaves was associated with the presence of spines on the leaves. The

numbers of green leaves and dead leaves still attached to the trunk were recorded for six to nine individuals of each of nine palm species. Old leaves were often in various states of decay, so only those with the petiole and rachis still prominent were counted. Only those individuals whose trunks were longer than their leaves were studied, so the force of gravity would have been operating uniformly to assist abscission; thus, young and small individuals whose dying leaves drooped onto the ground were not studied.

Nine Costa Rican palm species were studied, five near Puerto Viejo on Río Sarapiquí, one in Santa Rosa National Park, and three on the Osa Peninsula near the Agua Buena. The palms from the Osa and the Sarapiquí areas are wet lowland forest species, but the one from Santa Rosa occurs in old pastureland.

Results

The results of the counts of green and dead leaves are presented in Table 1 for the nine species. The only two species with spines on the leaves are *Acrocomia vinifera* and *Astrocaryum alatum*. These two species exhibited the highest percentages of leaves that are dead, 74% and 33%, respectively. (Statistically, the data totals of green leaves and dead leaves were analyzed with chi-square tests of independence for pairwise comparisons for each of the spiny-leaf species against each of the unarmed-leaf species. With a one-tailed hypothesis

Table 1. The numbers of green leaves and dead leaves on individual palms and summary data

Individual Number	<i>Acrocomia vinifera</i>	<i>Astrocaryum alatum</i>	<i>Socratea durissima</i>	<i>Geonoma congesta</i>	<i>Cryosophila albida</i>	<i>Prestoea decurrens</i>	<i>Asterogyne martiana</i>	<i>Cryosophila guagara</i>	<i>Synechanthus warscewiczianus</i>
1.	15-31	19-20	5-0	9-0	13-5	6-2	21-0	11-0	4-2
2.	15-44	23-9	6-0	11-0	17-5	16-1	23-0	25-5	5-2
3.	22-52	12-9	7-0	7-0	17-3	7-1	17-3	11-3	6-2
4.	15-35	14-9	8-1	10-0	16-3	7-1	19-3	9-2	7-2
5.	19-50	16-7	7-0	9-2	11-2	7-0	21-5	21-0	6-0
6.	17-57	19-3	5-0	7-0	17-5	10-0	17-1	19-2	7-1
7.	17-75	23-8		13-2			20-0	18-2	
8.	20-60	10-1						13-1	
9.								18-4	
Total	140-404	136-66	38-1	66-4	91-23	53-5	138-12	165-24	35-9
% Dead Leaves	74%	33%	3%	6%	20%	9%	8%	13%	20%
Mean # of Dead Leaves	51	8	0	1	4	1	2	2	2

that the greater proportion of dead leaves is associated with the spiny-leaf species, the tests revealed statistical significance with $p < 0.01$ in all cases except the comparison of *Astrocaryum alatum* and *Synechanthus warscewiczianus* where $0.05 < p < 0.10$.)

Perhaps more important than percentages are the actual numbers of dead leaves drooped about the palm trunks potentially to provide protection. Again, *Acrocomia vinifera* and *Astrocaryum alatum* exhibited the highest mean numbers, 51 and 8 dead leaves, respectively. Thus, the two species with spiny leaves apparently retain their old leaves more than the other seven species.

Discussion

The drooping of spiny fronds suggests that protection may be essential against herbivores which climb palm trunks. While spines on the living leaves may give protection against herbivory on the fronds, the function of drooping of the dead, spiny fronds must be related to trunk-climbing animals if the drooping has some adaptive value. Climbing herbivores such as coatis, squirrels, and monkeys could easily be deterred by spines, either on the trunk or on drooping, dead fronds. Of course, monkeys can drop from adjacent trees into the palm crown and thereby avoid the trunk armature; however, the drop involves

some risk in falling, and many palms grow in the open or in forest openings where monkeys cannot drop into them. Furthermore, it has been suggested by Uhl and Moore (1973) that one purpose of spines is to protect pollen and ovules. Many of the shade-tolerant palms may produce large flower and fruit crops only when they are exposed to full sunlight—a situation which arises through release after the fall of a tree which previously shaded a palm. Thus, maximum reproduction would occur at a time when monkeys would be unable to drop into the palm crowns.

If there is a relation between frond abscission and the occurrence of spines, it is likely to be more complex than that suggested by the data presented here. Palms without trunk spines and without frond spines should drop their dead fronds if a smooth trunk is any deterrent at all against climbing herbivores; this pattern is evident in the majority of species in this study (*Socratea durissima*, *Geonoma congesta*, *Presottoea decurrens*, *Asterogyne martiana*, and *Synechanthus warscewiczianus*). Palms without trunk spines and with spines on the fronds should retain their dead fronds, drooped about the trunk as in *Acrocomia vinifera* and *Astrocaryum alatum*. Palms with spines on the trunk but with unarmed fronds should drop their dead fronds because the

presence of a skirt of dead fronds would facilitate climbing herbivores trying to avoid the trunk armature; this case may be represented by *Cryosophila albida*, which has spines along the trunk. Finally, palms with trunk spines and frond spines both should drop their dead leaves because again the skirt of dead fronds would tend to negate the effect of trunk armature; unfortunately, there are no examples of this case in the present study although an example is *Astrocaryum standleyanum*.

It is noteworthy that the phenomenon of drooping spiny leaves in lieu of abscission—illustrated here for some palm species—occurs in other taxonomic groups such as thistles (Compositae: *Carduus* and *Cirsium*).

Acknowledgment

Gene Miller commented critically on this note.

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CLASSIFIED

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PALM BRIEFS

A Nomenclatural Note on *Hyophorbe*

A monographic study of the genus *Hyophorbe* is in preparation, but one of the conclusions requires advance publication in order to provide a name that can be used in *Hortus Third* and in another publication. It has become clear that the genus *Mascarena* is not adequately separated from *Hyophorbe* and that the palm commonly cultivated as *Mascarena lagenicaulis* must be transferred to the older genus. Study has shown that *Mascarena revaughanii* L. H. Bailey is not different from *M. lagenicaulis*, and in combining the two I am taking up the epithet that is descriptive and not likely to be confused with *Hyophorbe vaughanii*.

The five species are:

Hyophorbe amaricaulis Martius

Hyophorbe indica J. Gaertner

Hyophorbe lagenicaulis (L. H. Bailey) H. E. Moore, *comb. nov.*

Mascarena lagenicaulis L. H. Bailey,
Gentes Herbarum 6: 74. 1942

Mascarena revaughanii L. H. Bailey,
Gentes Herbarum 6: 72. 1942

Hyophorbe vaughanii L. H. Bailey

Hyophorbe verschaffeltii H. Wendland

HAROLD E. MOORE, JR.

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A Note on *Asraoa triandra* (Palmae)

Joseph (1975) has described a new genus and species of palm, *Asraoa triandra*, from Lohit District of Arunachal Pradesh, India. The collections were made in September and November, 1969

and again in January, 1970, at the same or different localities within the same district. The collector also observed female and male inflorescences on the same group of plants at different times. From the detailed description, the palm appears to be monocarpic, a characteristic of most of the caryotoid group of palms (Moore, 1973). In monocarpic habit, inflorescences develop basipetally from a terminal inflorescence which is generally a female, followed by axillary male inflorescences. This monocarpic habit is seen in all three genera (*Arenga*, *Caryota*, *Wallichia*) of the caryotoid group. *Arenga* Labill. has imparipinnate or undivided leaves, often aggregate inflorescences, distinct sepals and petals in staminate flowers, numerous stamens, trilocular ovary with 2-3 fertile locules, and homogeneous endosperm. *Caryota* L. has bipinnate leaves, solitary inflorescences, reduction of fertile locules to 1-2, and development of ruminate endosperm; the pistillate flowers have less united petals. *Wallichia* Roxb. has separate staminate and pistillate inflorescences, the female usually terminal, axillary inflorescences male, staminate flowers with sepals united in a low, cylindric, 3-lobed or undulate calyx, petals united in a short to long, more or less solid cylindric base with valvate lobes, stamens reduced in numbers, generally six, fruit 1-3-seeded, and endosperm homogeneous.

The detailed description of the genus *Asraoa* Joseph and examination of the holotype and isotypes shows its striking similarity with *Wallichia* Roxb. in vegetative and reproductive structures and also in its monocarpic habit. The description as dioecious may be due to the result of observations for a short duration. Moore (1960) reported variation in the number of stamens even in a single plant of the caryotoid group.

Moreover no satisfactory generic delimitation on number of stamens alone is possible from our existing knowledge of this group. Hence I feel it is ambiguous to accord a separate generic status to *Asraoa* Joseph solely on the basis of reduction in number of stamens when other characters as a whole do not permit it to remain distinct from *Wallichia* Roxb. The reduction in the number of stamens to three, which I have also examined from dissected flowers, is fairly constant. Therefore, I consider it only a separate species under the genus *Wallichia* Roxb.

Wallichia triandra (Joseph) S. K. Basu, *comb. nov.*

Asraoa triandra Joseph, Bull. Bot. Surv. India. 14 (1-4): 145. 1975 (1972)

I am grateful to Dr. S. N. Mitra, Joint Director, Botanical Survey of India, Indian Botanic Garden, Howrah for providing facilities and interest shown in palms. Thanks are due to Dr. J. K. Maheshwari, Director-in-Charge, Botanical Survey of India, Indian Botanic Garden, Howrah for encouragement.

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NEWS OF THE SOCIETY

Word from the Southern California Chapter is that their first Annual Banquet on March 20, 1976 was a huge

success with 110 members and guests. An interesting sight on the tour of the Palms Restaurant and patio was a four-headed *Livistona chinensis*. The after-dinner speaker was the noted naturalist Arnold Newman who spoke about the Rain Forest, Palms and Other Tropical Plants. Afterwards plants were auctioned off and four door prizes given to the lucky ticket-holders. The highlight of the evening was the competitive bidding on the extremely rare *Jubaeopsis caffra* from South Africa. It was the first time it had been available at an auction and was a seedling with only one leaf 3" or 4" high. It was bid up to \$32! This must be a record of some kind. Total of the auction was \$347.50 so bidding was lively and plants interesting, among them *Trithrinax acanthocomma*. The evening having been such a success, the banquet probably will become an annual affair.

The Miami members met at the garden and home of Mr. and Mrs. Don Thomas on April 17, 1976 to see slides taken at many faraway places by our host over the past twenty years. Members enjoyed the interesting garden with well-established palms, most of which had been planted by previous owner and former member Malcolm Kneale, who had been an avid palm fancier. The well-planted property makes an ideal setting for the charming house the Thomases built, utilizing the palms to create a delightful aspect.

Palm and Fern Fair

The Palm Beach County Chapter of The Palm Society, together with the International Fern Society, will hold a Palm and Fern Fair at the Mounts Agricultural Center, 531 No. Military Trail, West Palm Beach, Florida, on Saturday, October 17, 1976, at 10 a.m. There will be hundreds of varieties of rare and

beautiful palms and ferns for sale to both members and the public. Come early to get first choice.

T. B. BUHLER

Julien Marnier-Lapostolle

Our fellow Society member, Julien Marnier-Lapostolle, died at his Villa "Les Cèdres," Saint-Jean-Cap-Ferrat, France, on February 18, 1976.

Marnier-Lapostolle was an important patron of horticulture and a skilled and knowledgeable horticulturist. His botanical library was one of the finest in existence and included the significant source material. His collection of palms was the most complete ever assembled of the kinds that would withstand the winters on the Saint-Jean-Cap-Ferrat peninsula. The plants that he determined to be hardy there were consequently tested for growing in comparable climates, such as the coastal belt of Southern California, to which many of them found their way.

Marnier-Lapostolle's interest in plants was all inclusive and his Jardin Botanique of about eight acres and many greenhouses held 15,000 kinds. They required the services of thirty gardeners. Many comprehensive collections of families of plants were maintained, such as bromeliads, ferns, cacti, and succulents. He described his gardens in *Principes*, Vol. 5, No. 3, 1961.

He participated in many ways in the publication of botanical and horticultural writings. He was a generous and ready collaborator with botanical gardens and collectors. On one occasion he said that he tried to keep on hand at least five specimens of each kind of plant so that he could give away two and the three remaining would insure maintaining the species.

His honors are international. Among the French are the Chevalier de la Légion d'Honneur and Membre Correspondent

du Muséum National d'Histoire Naturelle de Paris.

Marnier-Lapostolle is survived by his widow, Suzanne, a son, three daughters, and four grandchildren. Madame Julien Marnier-Lapostolle has stated that she will continue to maintain the plants in memory of her husband.

DAVID BARRY, JR.

PALM LITERATURE

PEDROSA MACEDO, J. H., F. O. RITTER-SHOFFER, AND A. DESSEWFFY. A Silvicultura e a Indústria do Palmito. 61 pp., 30 figs., 1 map, 2 graphs. Instituto de Pesquisas de Recursos Naturais Renováveis, Porto Alegre, Rio Grande do Sul, Brasil. 1975. CALZAVARA, B. B. G. As Possibilidades do Açaízeiro no Estuário Amazônico. 103 pp., 17 figs., 1 map, 4 graphs, 16 tables. Faculdade de Ciências Agrárias do Pará, Belém, Pará, Brasil. 1972.

These two complementary studies, the first with a forestry and the second with an agronomy orientation, reflect the increasing importance of hearts of palm as a commercial product in Brazil. Pedrosa Macedo *et al.* are concerned with the palmito palm (*Euterpe edulis*) which occurs between 15 and 30° S Latitude in southern Brazil; Calzavara with the açaí palm (*Euterpe oleracea*) which grows in the lower Amazon region and along the northeastern coast of the continent. Current Brazilian production of palm hearts comes from wild palms in the two areas.

Both studies focus on the potential management of natural palm groves and recommended cultivation procedures in the respective areas. Environmental requirements, seed collection and germination, planting, tillage, plant parasites, and harvesting are discussed in each study. The points are also made that *E. edulis* cultivation in southern Brazil is

feasible on marginal lands of excessively steep slopes, and that in the lower Amazon cultivation of *E. oleracea* could be encouraged on the seasonally-flooded marginal lands immediately along the river.

In comparative terms, the studies bring out the advantages of each palm. *Euterpe edulis* yields the highest quality palm heart, but it is a solitary palm which must be propagated from seed. The product from *E. oleracea* is of lower quality, but that disadvantage is outweighed by the fact that the palm suckers exuberantly and that once established in an area it would regenerate naturally. Further, the açai palm bears an edible fruit of commercial value in the Amazon region for making fruit drinks and to flavor ice cream.

Distinguishing the Calzavara study is the considerable detail provided on the climatic requirements of *E. oleracea*, specific cultivation practices, and information on local processing industries. Pedrosa Macedo *et al.* have richly illustrated their study with color photographs and have included a comprehensive list of current and planned research projects in southern Brazil involving *E. edulis*.

In addition to these two studies, another recent indication of the greater attention being paid in Brazil to hearts of palm is the inclusion, for the first time, of production figures by state in the *Anuário Estatístico do Brasil* 1974. For 1973, some 35,500 metric tons of canned palm hearts were produced in the country. Over seventy percent of the total came from, together, the States of Pará, which covers the lower Amazon, and Maranhão, adjoining it to the southeast. Clearly, *E. oleracea* is currently being exploited to a much greater degree than *E. edulis*.

DENNIS JOHNSON
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LETTERS

"Valhalla," Osborne Lane
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The Editor, Principles

DEAR SIR:

I have been trying now for 11 years to grow palms. I have in that time and am now growing successfully orchid species, bromeliads, cactus and succulents, as well as carnivorous plants with usually a great measure of success. Palms, however, have defeated me!

Of all things growing on this earth the palm must be about the very slowest of all! For instance I sowed *Trachycarpus excelsus* [= *T. fortunei*] at the birth of my daughter who is now 11 years old. My daughter has grown to just over 4 feet, the palm a measly 3 feet! The largest palms I have now, *Washingtonia*, *Phoenix canariensis*, and *P. reclinata*, are all 11 years old and are all 4 feet high!

The trouble was for the first number of years and still to this date that there is virtually no information on the cultivation of palms WHICH INCLUDES YOUR OTHERWISE EXCELLENT JOURNAL.

Accustomed to plants which go through regular dry seasons I did not water any palm at all for at least the first 6 years of trying to grow them, nor did I give them any special soil or fertilize in any way.

It was only through bitter and frustrating experience that slowly I learned that these plants in fact must be watered almost daily in our summer and that 1 bag of manure per plant per season is just about sufficient.

The book *Palms of the World* has been of some help in this respect as also the very odd article in your journal, but the information in any source I have seen is at best scanty and not nearly sufficient.

I ask you, how the devil is one supposed to know how to grow these plants if one cannot read up on it!!!

All this has naturally resulted in a marked lessening of enthusiasm for these plants. I am simply not prepared to wait another 20 years until my "fast growing" species reach the miserable size of 10 feet or so. I have had it!

Perhaps you will publish this, probably not, but in any case best regards.

Yours sincerely,
ROLF RAWE

Editor's response.

Mr. Rawe's letter, itself a contribution to understanding palm-growing in South Africa, does call attention to a problem of long standing, how to obtain more articles and notes on culture. Much attention is paid to the culture of commercial crops at experiment stations in various parts of the United States and elsewhere, but there is apparently no corresponding emphasis on the culture of palms except for those few, such as the African oil palm, *Elaeis guineensis*, the coconut, *Cocos nucifera*, and the betel palm, *Areca catechu*, that are plantation crops. Let it be noted again that the editor welcomes contributions to our understanding of palm culture and wishes there were more of them. Meanwhile, Mr. Rawe has been referred to *Cultivated Palms* published by the American Horticultural Society in January, 1961, as one source of information and the following may help those who try to grow *Normanbya*.

P. O. Box 33, Gordonvale
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Australia

DEAR PROFESSOR MOORE,

I decided to send a letter containing a few notes on my experiences with the

raising of seed of *Normanbya normanbyi*. I hope the seed I sent the Seed Bank reached good homes and have germinated and grown well for it is a beautiful palm and seems to be very fast growing.

The large seeds germinate after about four weeks usually; sometimes I have had them germinate in two weeks, but usually they are not slow. The question regarding container size and germination method required seems simple, and I answer those people interested by saying that this palm germinates before you know it.

The seed can appear to be quite inactive when it has enormous roots. No emerging shoot is apparent until the embryo has usually two large roots about 5 inches long. When the shoot is about 2 inches tall the two initial roots will be over 10 inches long and about $\frac{1}{4}$ inch in diameter. For this reason I place the seeds in a shallow tray on a layer of soil only $\frac{1}{4}$ inch deep and lightly cover them. Each day from the second week onwards I take out several seeds and inspect them for root growth.

When the roots appear the seeds are planted individually in deep pots, a depth of 6 inches seems to give best results. For some reason the seedling is greatly disadvantaged if these first roots are hampered but later it can take root crowding as well as most palms.

I have tried planting ungerminated seeds in 3-inch pots and have found that the growth is retarded when the seedling makes its first leaf. Trying to dig up tiny seedlings in the forest is most annoying; the roots penetrate several feet even though the plant might only have three leaves and stand about 6 inches tall.

The seedlings seem to grow in any soil that is rich and moist. I have some in black sand, others in dark loam and more in heavy clay. They all show similar growth. Half shade seems to be best if a sturdy and vigorous palm is desired.

When the seedlings are about 2 years old and have reached the 12-inch pot size they can be planted out (climate permitting) but unless the grower lives in a district which receives over 70 inches of rain annually they should not be planted on shallow soil that is likely to dry out. I dig deep holes in low places where water collects and fill them with rotted foul manure and plant the palm over this so that the base of its trunk is slightly below the level of the surrounding ground.

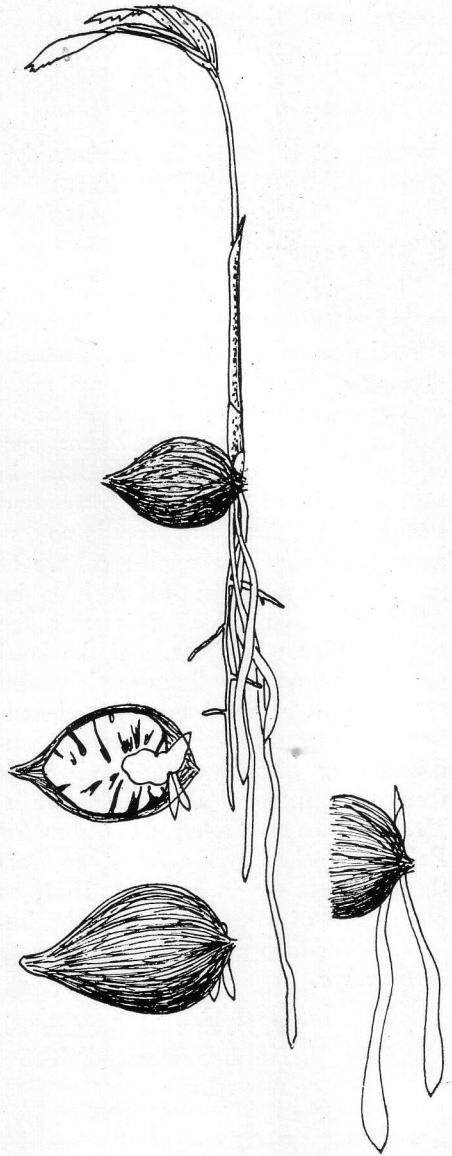
They love water; the moundlike mass of roots formed in wet soil is an indication of this. In a hot and wet climate *Normanbya* grows very quickly and adopts the typical multiplane leaflets after three years. In ten years it will grow to 15 feet if well watered and fed and allowed good light. When young it resembles *Drymophloeus* in foliage and is an attractive container palm.

As the seedling forms a trunk it suddenly adds height, the internodes being rather long. The trunk is at first very slender; I first thought that my palms were not going to grow fully when they formed trunks only a few inches in diameter and several feet tall. However a gradual change takes place, the leaves take on their recurved and plumelike adult form and the trunk thickens greatly, somewhat like a *Carpentaria*.

I hope this palm does become widely established in other countries for it has a rather small range here. Admittedly there must be many thousands of individuals in the wild but its population is only a fraction of what it originally was. It is most common between Cooktown and the Daintree River but occurs farther north. Hopefully southern Florida growers will be able to raise it. When young it seems to be very delicate; friends of mine in south Queensland (a climate not unlike southern Florida) have had trouble keeping seedlings through the dry season, the earlier part

of which can be rather cool. But it does seem to be much hardier when older so should be successful after two years protection from cold.

Sincerely,
ROBERT TUCKER



1. Seeds and seedling of *Normanbya normanbyi* in different stages of germination, one seed in section.