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

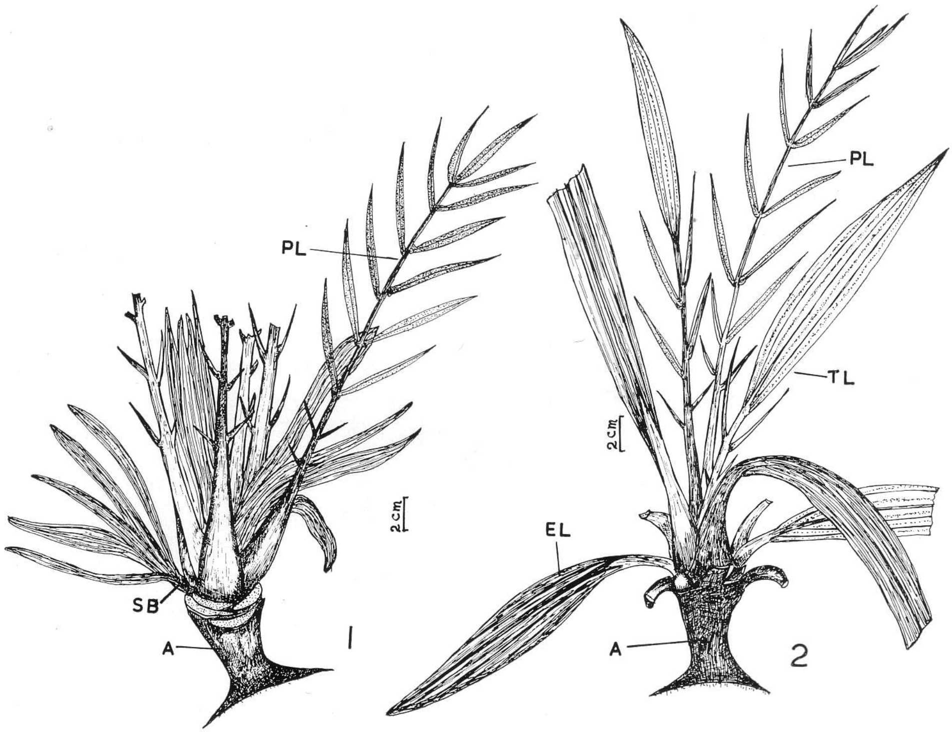
Phoenix loureirii and *P. farinifera* normally produce suckers or lateral branches at ground level. These structures appear in specimens which are fairly mature and flowering. However, since the stem itself is short, the suckers present the appearance of having originated very early. Examination of post-juvenile 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 spathaceous 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

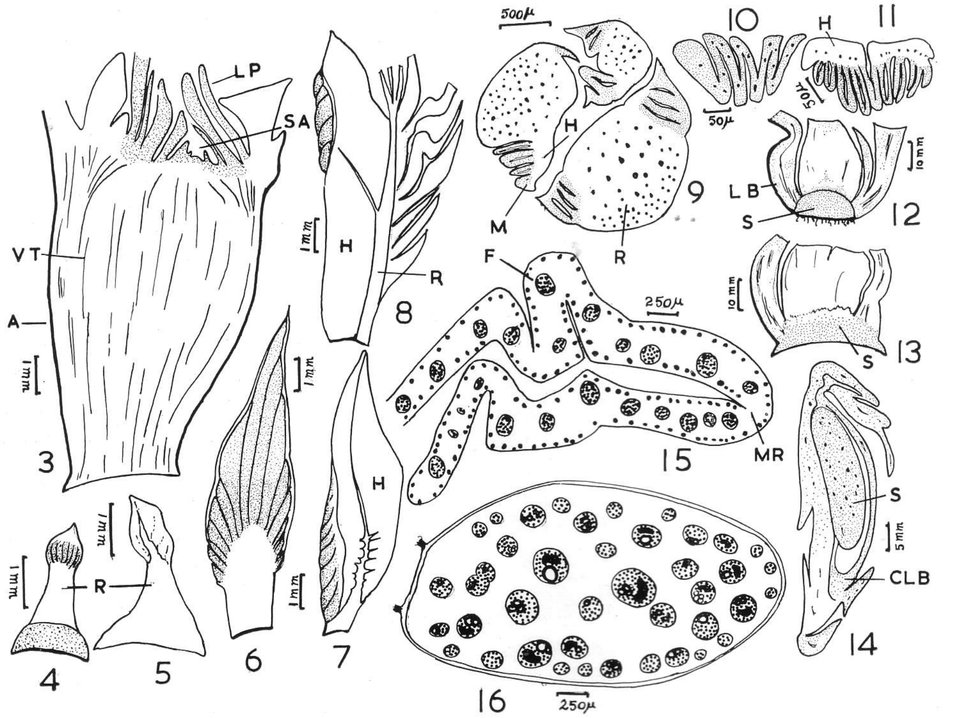
The occurrence of second order bulbils was noticed in *P. farinifera* where bulbil shoots themselves were developing secondary bulbils in the leaf axils (Fig. 1). In both the primary and secondary bulbils a few undivided leaves (resembling juvenile ones, Fig. 10) preceded the pinnate ones. Furthermore, 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 indicate 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-

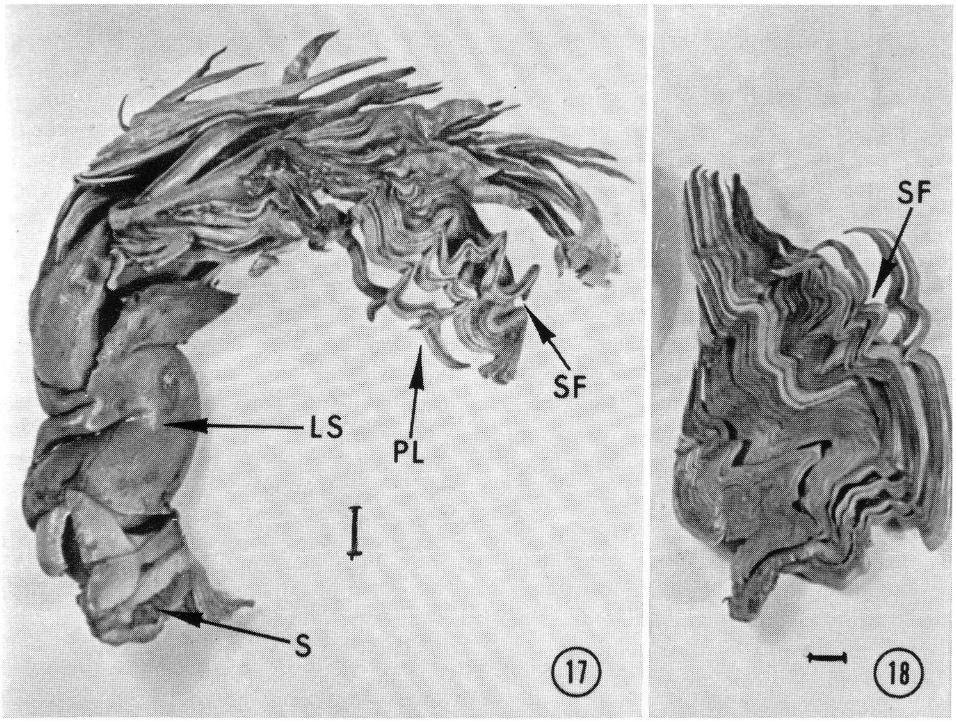


3–16, *Phoenix farinifera* and *P. loureirii*. 3–8, *Phoenix farinifera*. 3, longitudinal section through a young bulbil shoot. 4–8, views of entire leaf primordia dissected out from the bulbil shoot bud. 4, adaxial view of young primordium. 5, adaxial view of the primordium shown in Fig. 4. 6, 7, abaxial 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 haut 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.

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