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Author(s): Martin H. Zimmermann and P. B. Tomlinson

Source: *Botanical Gazette*, Vol. 133, No. 2 (Jun., 1972), pp. 141-155

Published by: [The University of Chicago Press](#)

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BOT. GAZ. **133**(2):141–155. 1972.

THE VASCULAR SYSTEM OF MONOCOTYLEDONOUS STEMS¹

MARTIN H. ZIMMERMANN AND P. B. TOMLINSON

Harvard University, Cabot Foundation, Petersham, Massachusetts 01366

ABSTRACT

The course of vascular bundles and its developmental pattern in monocotyledons has been reinvestigated. This shows the existence of an "inner" and an "outer" vascular system. The inner system is more extensive, three-dimensionally very complex, and "open-ended" in a distal direction, i.e., centripetally toward the apical meristem. The outer system is open-ended in basal and peripheral directions and usually poorly developed. In many monocotyledons, it is represented by the fibrous bundles in the cortex of the stem. Occasionally, the outer system is more fully developed as in *Strelitzia*, where it is represented by fully developed vascular cortical bundles or as a secondary vascular tissue in those monocotyledons which show secondary growth (e.g., *Dracaena*, *Cordyline*, *Pleomele*). We suggest that dicotyledons differ from monocotyledons in having only an outer system. This might lead to a clarification of the phylogenetic relationship between the two groups.

Introduction

Among the many structural features in which monocotyledons differ from dicotyledons, probably the most constant and distinctive is stem anatomy. Monocotyledons usually have individual primary vascular bundles containing both phloem and xylem "scattered" throughout a single transverse section of the stem. In addition, most of them lack secondary growth. In dicotyledons, on the other hand, primary bundles, where they are discrete, are usually in a single ring; but secondary growth eventually produces the typical dicotyledonous stem with a xylem core, enclosed in a thin cylinder of phloem. There are minor exceptions to this generalization. Some dicotyledons (e.g., species in the Amaranthaceae, Nyctaginaceae, Piperaceae) have more or less scattered primary bundles. There are a few monocotyledons (e.g., *Cordyline*, *Dracaena*, and *Yucca*) with a vascular cambium which produces secondary vascular bundles within secondary ground tissue. Furthermore, there are dicotyledons (e.g., certain Amaranthaceae and Chenopodiaceae) in which the mode of cambial

activity is superficially similar to that of these monocotyledons, because discrete conducting strands are produced within secondary tissue. Finally, there are a few monocotyledons with the bundles in a single ring as in aerial stems of *Dioscorea*, which is very specialized, or small plants as in the Mayacaceae, Petrosaviaceae, and certain Eriocaulaceae (*Tonina*), which are probably simplified by reduction.

The vascular architecture of a large number of dicotyledons is known in detail, and a considerable understanding of their pattern of development has been achieved (cf. ESAU 1965). On the contrary, monocotyledonous vascular systems have, until recently, largely eluded our understanding because of their great complexity, which is largely beyond the reach of orthodox methods of investigation. The crux of the problem lies in a study in precise detail of how the monocotyledonous vascular system originates in the apical region. New methods had to be developed in order to make this possible.

During the past few years we have studied the stems of many large monocotyledons, starting with the palms and later extending our observations to other families (ZIMMERMANN and TOMLINSON 1965, 1967, 1968, 1969; TOMLINSON and ZIMMERMANN 1966*a*, 1966*b*, 1968*a*, 1968*b*). Our investiga-

¹The work leading toward this publication has been supported by a grant from the National Science Foundation (GB-5762-X) to one of us (P. B. TOMLINSON).

tions have revealed a previously unrecognized pattern which we believe to be fundamental for monocotyledonous stems as a whole. We believe that we have also recognized the developmental principle which underlies this structural pattern and can therefore suggest the way in which this principle in monocotyledons differs from that in dicotyledons. In addition, we believe that some of the more constant features of monocotyledonous morphology can be explained by this principle. This may have important consequences in taxonomic interpretation and ultimately in understanding the phylogeny of monocotyledons.

A particular problem is that of communicating our results. The monocotyledonous vascular pattern is so complex that it is difficult for anyone to comprehend it who is not dealing with it directly and studying it thoroughly. Yet, if the principle of growth and resulting structure is as fundamental as we think, we feel that we should make an effort to present it to nonspecialists in a generalized and easily understood form. The present paper attempts to do this. Our presentation, therefore, becomes that of a working hypothesis. Our observations have shown that the vascular patterns of monocotyledonous stems represent a series of variations on a basic theme. At this stage, we should like to emphasize and simplify the theme without saying too much about the variation. We appreciate that an enormous amount of additional work still has to be done, but it will be easier to proceed with broad comparative investigations once the fundamentals, or what we believe to be the fundamentals, are more widely comprehended.

Methods

A description of methods becomes necessary in the present paper, because the numerical complexity of monocotyledonous vascular systems called for drastically new procedures. Classical methods of plant anatomy are inadequate to deal with the large number of vascular strands encountered in the stems of large monocotyledons. For example, a transverse section of a coconut palm stem contains about 20,000 central vascular bundles and tens of thousands of fibrous cortical strands. It is simply impossible with any methods previously available to trace the course of these over long distances or to be certain if there is any regularity in the way in which they interconnect. Reconstruction from camera-lucida drawings of serial sections is too time-consuming and too unreliable a procedure. Clearing pieces of tissue is useless. Dissection of bundles from partly rotted stems is of very limited value. Our analysis of the vascular structure of palms began with the realization that

progress could be made only if we developed methods which enabled us to "find our way" through the maze of vascular tissue which the coconut stem represents. Our methods now permit this kind of analysis.

Early we conceived the idea of putting individual images of transverse sections onto individual frames of motion-picture film. This has become our main method of structural analysis. We found later that this basic idea was not new (POSTLETHWAIT 1962). However, for reasons to be explained below, the method had not previously become a significant research tool. Structural analysis with frame-by-frame cinematography to provide new information can now be accomplished in two different ways.

MOTION-PICTURE ANALYSIS BY THE SURFACE METHOD.—The first method is to photograph directly the surface of a specimen planed on a microtome. If this is done frame by frame with a motion-picture camera, serial or sequential images can be stored for subsequent analysis. This had been done by other workers in the past, but the method was of limited value because it was restricted to very short sequences and dealt only with small objects which could be mounted on a rotary microtome (POSTLETHWAIT 1962). In all existing microtomes, the clamp holding the specimen is advanced because it gives the most precise advance. However, for the large objects we have to analyze, we do not require very precise advance, and it is not necessary to cut thin sections (which are usually discarded anyway). For our analyses, it is necessary to cut a long specimen continuously without having to reclamp it. For this reason, the specimen itself has to be advanced. This has been accomplished with a specially designed "continuous-advance" clamp which we use on a Reichert "OME" sliding microtome. The specimen is advanced through rollers in two possible ways. The rollers themselves, driven through a gearbox by hand, may advance the specimen. This arrangement is best suited to firm specimens with straight sides. Alternatively, a jack pushes the specimen, from below, through the rollers which then move passively. This latter arrangement is particularly useful for soft or irregular specimens. In both arrangements, the camera is focused vertically down onto the cut surface. It is fitted with extension tubes for close focusing and a short Telephoto lens to provide sufficient working distance. The cut surface of the specimen is brightly and evenly illuminated with microscope lamps, and exposure requirements are measured with a 1- or 2-deg spot-exposure meter. With this device, we can take motion pictures by single-frame exposures at the rate of 50

cm of specimen length in a half-day. This may involve, e.g., taking 2,500 single frames of transverse-sectional views, i.e., one every 200 μ .

MOTION-PICTURE ANALYSIS THROUGH THE MICROSCOPE.—Whenever the resolution of macrophotography is insufficient, we have to produce serial or sequential sections on the microtome and photograph them one by one with the motion-picture camera through the microscope. This can be done at any desired magnification provided each section is precisely lined up with the previous one. This can be accomplished either by using a drawing tube incorporated into the microscope-camera system or, more conveniently, with the shuttle microscope. These methods have been described in a previous publication (ZIMMERMANN and TOMLINSON 1966). More recently, we have devised a similar shuttle microscope for very low magnifications. By combining all these methods, we can now analyze specimens of virtually any size and at any magnification.

ANALYSIS OF FILMS.—Production of films by the surface method is quite “blind,” i.e., one generally has no conception of the nature of the resulting information until one sees the film. When one works through the microscope, however, one may quite easily see essential structures, although subsequent film analysis yields a great deal of additional detail. Films are projected with a Data Analyzer, which is a Kodak projector modified so that films can be run without flicker at any speed forward or backward. The image can be projected via a mirror onto graph paper on a table in front of the investigator, and measurements of lateral displacement of bundles can be plotted. It is important to realize, of course, that “movement” is only simulated and results from the translation of one dimension into time.

These methods are not merely more elegant than classical methods of investigations, they are more revealing. With them, one can analyze a three-dimensional structure very quickly, so that it takes a few days instead of perhaps a year to analyze the course of vessels in a small piece of dicotyledonous wood. Three-dimensional features of structure can easily be seen which, with standard techniques, escape the observer entirely. In addition, structures which are conceptually difficult to grasp can be demonstrated in a manner which makes them instantly comprehensible. Our experience of working with these methods on a real problem is comparable to switching on light in a large dark room in which one has been groping around with a flashlight.

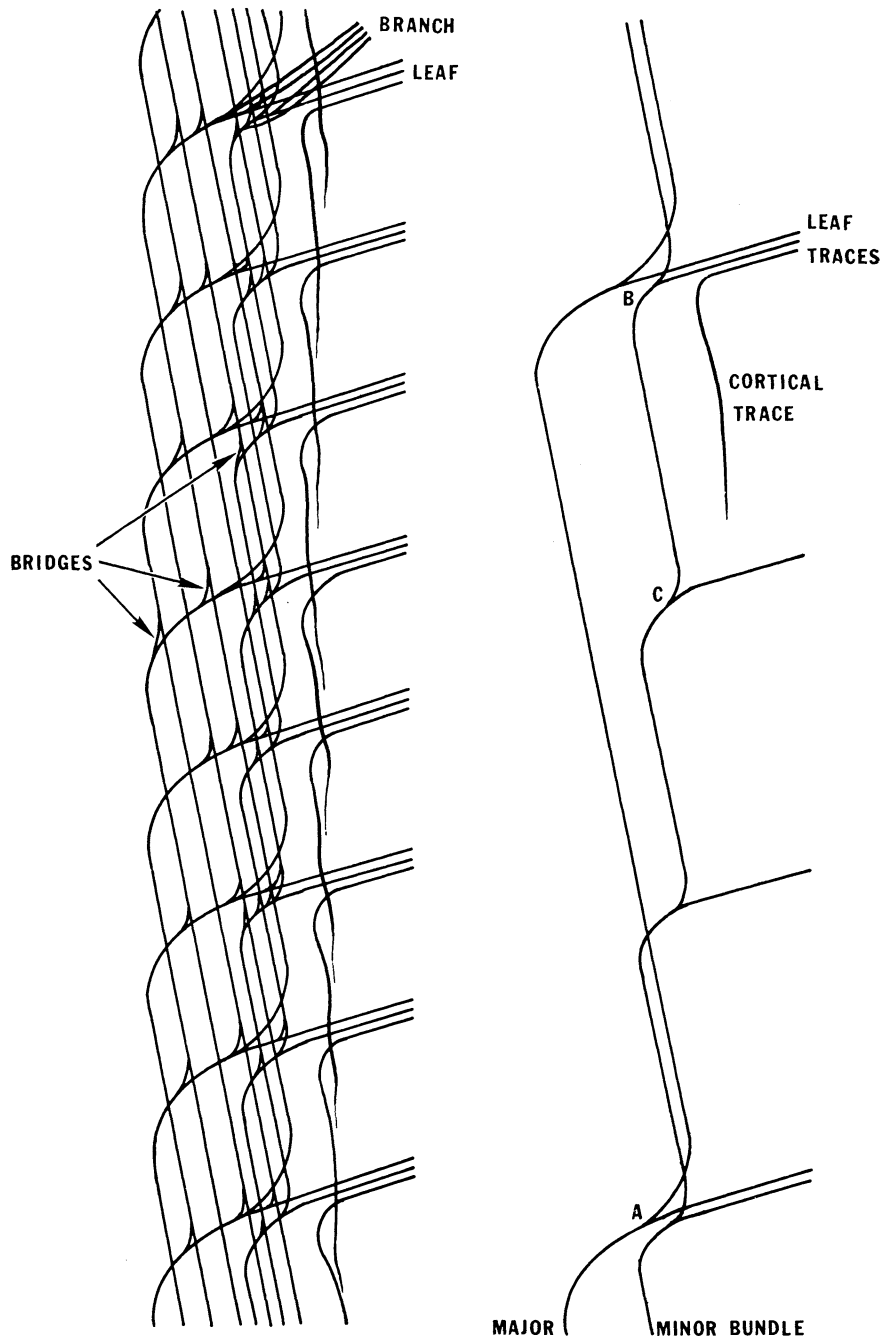
As one works with cinematographic methods, one automatically begins to use terms like “comes,” “goes,” “departs,” etc., i.e., terms which are de-

scriptive of motion. It should be understood that such terms are used merely for convenience. Their real meaning is a strictly topographic one and has nothing to do with motion itself or with direction of development.

Vascular system of mature stems

Figure 1 shows in an idealized and simplified way the monocotyledonous vascular system of a mature vegetative stem in a radial plane. The diagram represents the principles which were first found in *Rhapis* (Palmae) and *Prionium* (Juncaeeae) (ZIMMERMANN and TOMLINSON 1965, 1968) but subsequently also in other species in several families. Eight leaf insertions are shown, the vascular supply to each leaf represented by only three bundles—two vascular leaf traces (one major, one minor) and a fibrous cortical trace. These three elements, which essentially make up the vascular structure of the stem, are shown separately in figure 2. In an actual stem, the total number of bundles continuous into a leaf is of the order of hundreds, and there is a gradation from those which originate centrally to those which originate peripherally. This large number of traces is accommodated in a broad leaf insertion which, in most monocotyledons, completely encircles the stem.

The fundamental feature of the monocotyledonous vascular system is the *upward-branching leaf trace*. Whenever a leaf trace is followed on its way from the central cylinder to the leaf—i.e., from below upward—it “produces” half a dozen or so branches. Most of these are bridges, i.e., short vascular branches which connect to neighboring axial bundles. However, one particular branch (occasionally more than one or none) retains its identity and can be followed further upward so that it “replaces” the leaf trace which has been “lost” from the stem at the leaf insertion. For descriptive purposes, one could, of course, regard the leaf trace as branching off the continuing axial bundle, but there are good developmental reasons for not doing this. In addition to bridges and the continuing axial bundle, there can be further branches which we have called “satellites” because of their distinct topographical relation to the leaf trace. These satellite bundles are part of the vascular supply to an axillary bud or vegetative branch (cf. ZIMMERMANN and TOMLINSON 1965). Four satellites are shown at the uppermost node in figure 1, two from the minor and two from the major leaf trace. It should be emphasized that these derivative bundles, which make up what we have called the “leaf-trace complex” cannot be distinguished by any pronounced anatomical features but only by their three-dimen-



FIGS. 1-2.—Fig. 1 (*left*), Simplified diagrammatic representation of the monocotyledonous vascular system shown in a radial plane. Eight nodes are shown; each leaf is supplied by one major, one minor, and one cortical bundle. Upward-pointing branches of leaf traces are bridges and a continuing axial bundle. The uppermost node shows, in addition, satellite bundles to an axillary branch. Fig. 2 (*right*), The three constructional elements from which the diagram on the left is made up. They are a major bundle with a leaf-contact distance of six internodes (*B-A*), a minor bundle with a leaf-contact distance of two internodes (*B-C*), and a basipetally blindly ending cortical bundle. When counting internodes, note that only every other node is shown in the right-hand diagram (fig. 2).

sional distribution. This is why they remained unobserved by earlier authors.

THE AXIAL BUNDLE.—In our earlier papers, the axial bundles had been called “vertical bundles” which is perhaps unfortunate when one considers the structure of horizontally oriented rhizomes which have the same vascular principles found in upright aerial stems. The term axial bundle is now preferred. Axial bundles have arbitrarily been distinguished as “major,” “intermediate,” and “minor,” although there is a gradual and continuous range of bundles from the “most major” to the “most minor” ones. Major bundles reach the stem center and have the longest distance between two successive leaf traces (*A-B* in fig. 2). This distance can be measured in numbers of internodes and has been called the leaf-contact distance. In minor bundles, leaf-contact distance is much shorter and the bundles remain peripheral, as illustrated in figure 2. The leaf-contact distance of the minor bundle is two internodes (*B-C*); that of the major bundle, six internodes (*B-A*).

THE EXTENT OF SIMPLIFICATION OF FIGURE 1.—It may be useful to describe very briefly to what extent figure 1 has been simplified in order to make it representable by a reasonably comprehensible drawing. The diagram has been foreshortened, and the number of nodes has been reduced. In reality, axial bundles run much more nearly parallel to the stem axis than shown in the figure. In *Rhapis*, for example, leaf-contact distances in major bundles are at least 15 internodes rather than the six shown. Furthermore, in *Rhapis* each leaf is connected to the stem by about 100 vascular and 1,000 fibrous cortical traces. It would be obviously hopeless to try and draw all of these at one time. Leaves at their insertion enclose the stem entirely; they are arranged in a 2/5 phyllotactic spiral, which is represented in a single plane in figure 1. There are not merely two classes of vascular bundles, there is a continuous spectrum from major to minor traces. The vascular bundles of the central, uncrowded part of the stem describe a helical path. In other palms, this internal helix may or may not be present, or there may even be two contrarotating helices, as in *Geonoma*. The actual path of a bundle, therefore, obviously cannot be shown in a two-dimensional drawing. Finally, the lower extremities of the cortical bundles are often anastomosing (as in *Rhapis*), although there are examples (as in *Prionium*) in which they retain their individuality.

Pattern of differentiation

So far we have analyzed in quantitative detail the course of the visible provascular strands in the

apical region of monocotyledonous stems only in five individual plants—two aerial shoots and one rhizome of *Rhapis* (ZIMMERMANN and TOMLINSON 1967), a shoot of *Prionium* (ZIMMERMANN and TOMLINSON 1968) and one of *Dracaena fragrans* (ZIMMERMANN and TOMLINSON 1969). This may seem a small number on which to base a generalized hypothesis until it is realized that the interpretations are substantiated by the structural analysis of a diversity of plants and furthermore that this complex analysis has not been attempted before. Analyses have indeed been made by other workers but always of small or specialized plants, e.g., by PRIESTLEY, SCOTT, and GILLET (1935) on *Alstroemeria*, by SHARMAN (1942) on *Zea*, by SIMPSON and PHILIPSON (1969) on *Ripogonum*, and by HITCH and SHARMAN (1971) on festucoid grasses. These investigations are important and informative, but there are certain aspects of development which do not become clear in the study of relatively reduced vascular systems of essentially herbaceous species. Anyone who has analyzed a considerable number of the larger woody monocotyledons will necessarily have to come to this conclusion.

The sequence of events during the development of the vascular pattern has been described in detail in three earlier papers (ZIMMERMANN and TOMLINSON 1967, 1968, 1969) and summarized by TOMLINSON (1970a). The principles are herewith very briefly repeated, including only essential details. Figure 4 shows in a much simplified manner the situation in the meristematic crown of a large monocotyledon, such as *Rhapis*, and a careful comparison of figure 4 with figure 1 will be used to show the reader how the vascular pattern develops. Initially we describe the situation in an unbranched stem; the complexity introduced by branching is explained later.

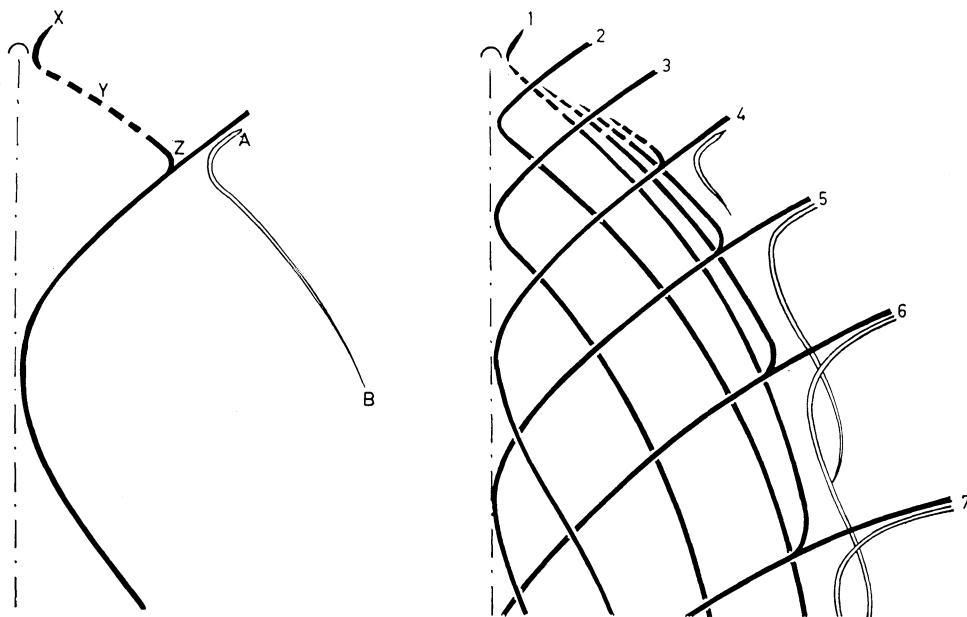
PHYSIOLOGICAL POLES.—In our interpretation of monocotyledonous growth, we regard the vascular system as originating in the form of procambial strands connecting certain physiological “poles” or growth centers. These growth centers may include leaf (and branch) primordia and certain meristematic regions of the stem, such as the existing vascular system, the young cortex, etc. Differentiation of vascular strands between two physiological poles may be considered analogous to an electric current which flows between two poles of different electric potential. In this context, we are not concerned with the question of any “direction of differentiation” between the poles, although the question of this “direction” of procambial differentiation has been accorded a great deal of attention by plant

anatomists for other reasons (cf. ESAU 1965). This is not to say that this question is of no significance. It surely is, but, for our present purposes, direction of vascular differentiation is not the most fundamental problem.

The elements of the vascular system, in a large monocotyledon, such as a palm, are shown by the bold lines in figure 3, and the hypothetical physiological poles by the letters *X*, *Y*, and *Z*: *X* is in the base of a young leaf primordium; *Y* (the dashed line in fig. 3) is an umbrella-shaped meristematic region which we have called the cap, situated below the apical meristem; *Z* is a trace to a leaf at a somewhat later stage of development. Provascular strands can differentiate between *Y* and *Z* as well as between *X* and *Y*, thus ultimately leading to a vascular connection between *X* and *Z*. We must reemphasize that any "direction" in which this linkage takes place does not concern us. This type of vascular linkage continues for an extended period during the early stages of leaf development so that extensive vascular connections between a leaf and the center of the stem are made. Then, during further development of the leaf primordium, a polarity change takes place. The pole which was of polarity *X* assumes polarity *Z*, corresponding to a change of the leaf primordium from a relatively

young stage (*X*) to a relatively old stage (*Z*). But, at the same time in the older leaf primordium, tissues in the leaf base between existing leaf traces still retain the potential of a pole (which was indicated by *X* in the younger stage but now is marked *A* in the older stage in fig. 3). However, the position of a leaf at this stage of development is now such that this late differentiation falls outside the lower limits of the meristematic cap, and connection is made with the pole *B* in the meristematic cortex (open line between *A* and *B* in fig. 3). Any connection further down is not possible because there is now no pole corresponding to *Y*. It is this late production of vascular bundles which gives rise to the fibrous cortical system which is described further below. Let us return to the vascular system of the central cylinder and describe the situation in a little more detail, for the drawing shown in figure 3 is drastically oversimplified.

CENTRAL CYLINDER.—A more realistic though still very much simplified representation of the developmental pattern of the monocotyledonous vascular system is given in figure 4. This pattern is not hypothetical; it is what one sees if one analyzes a palm bud by the methods we have used. Precise examples have been provided in our published papers. The difference between this and figure 3 is



FIGS. 3-4.—Fig. 3, The elements of vascular development in monocotyledonous stems. Bold lines indicate the inner system. A leaf trace at *X* contacts the meristematic cap (*Y*). The cap is regenerated from older leaf traces (*Z*). This takes place in two distinct stages. Strands originating at *Z* often remain "uncommitted" for a long time at their upper end within the cap (*Y*). The outer system (*A-B*) is shown with an open line. Fig. 4, The pattern of vascular development very drastically simplified. The seven youngest leaf primordia are numbered 1-7. Only one vascular (inner) and one cortical (outer) bundle are shown for each leaf. The vascular (inner) bundles are only major ones with a leaf-contact distance of six internodes as in fig. 1. Minor bundles are not shown in order to avoid crowding of the illustration.

that pole *Z* (an existing leaf trace) connects with pole *Y* (the cap) long before the upper end of the connecting strand is determined as a new and visible leaf trace (i.e., linking with pole *X*) at its upper end. Thus, the continuity shown in figure 4 takes place in two distinct steps. In structural terms, this is exactly what one sees at a certain developmental stage; continuing axial bundles do end blindly in the meristematic cap. It is only later that continuity is completed. In figure 4, seven developmental stages of a leaf (numbered 1–7) are shown. These stages can be seen in a single crown where each is represented by a different leaf. In figure 4, the complete connection between *X* and *Z* does not arise until developmental stage 7 has been reached. First, the leaf trace (at *Z*) connects with the cap (*Y*) at position 4 via an axial bundle. As the leaf enlarges (stages 5 and 6), it maintains vascular contact with the cap. The axial bundle at this phase of development continues to be generated by the lower periphery of the cap until finally its upper end is “captured” by a newly arising leaf trace (*X*). In our diagram, this is shown happening when the leaf is at position 7 and distal connection is being made with a new leaf primordium in position 1. As soon as this happens, the vascular bundle is “left behind” and becomes a visible procambial strand (e.g., the bundle shown from leaf no. 2 in fig. 4 which would connect in this theoretical diagram with a leaf at position 8). The “undetermined” upper ends of vascular bundles have already been described by PRIESTLEY et al. (1935) for the small monocotyledon *Alstroemeria*, although the authors did not realize at the time that they had touched upon one of the fundamental features of monocotyledonous vascular development.

Figure 4 is still very much simplified for the sake of clarity. It shows only one type of contact between leaves, namely, between numbers 1 and 7. This leaf contact will move to positions 2–8, 3–9, 4–10, etc., as new leaf primordia arise. Leaf traces (poles *X*) arising nearest to the apical meristem produce major bundles. From figure 4, it is obvious that, if a leaf primordium continues to produce new leaf traces and serves as pole *X* until it has reached developmental stage 3, *X*–*Y* contacts can still be made. At stage 2, e.g., this would lead to a connection with a leaf at stage 5 or 6. In stage 3, it could lead to a connection with stage 4. The “leaf-contact distance” of such connections is obviously shorter, and the resulting bundles are called intermediate and minor bundles. They differ from major bundles, not only in their shorter leaf-contact distance, but also in that they do not reach as far into the stem center. This is a simple topographical consequence of their late development.

To avoid crowding of the illustration, the development of intermediate and minor bundles is not shown in figure 4. This simple developmental process is sufficient to account for the seemingly complex vascular system in the central cylinder of monocotyledons.

CORTEX.—To understand further the vascular system, we have to refer to the well-known observation that the leaves of larger monocotyledons have an encircling attachment and each of them connects with the stem via many leaf traces (in a large palm, several hundred). Initially, a leaf primordium is very narrow; as it grows, the diameter of its encircling base increases until it has reached that of the mature stem. This increase is from a few microns to several centimeters. Obviously, there is initially room for very few leaf traces, but more becomes available as leaves and stem grow. During this time, as we have seen, new leaf traces are initiated continuously. The first ones connect with the inner portions of the cap, thus producing major bundles. Later ones connect with progressively more peripheral portions of the cap, thus producing intermediate and, finally, minor bundles. This has been illustrated in an earlier paper (ZIMMERMANN and TOMLINSON 1968, p. 1108, fig. 17).

As its diameter increases, the developing leaf will eventually reach a position where the whole of its base is outside the cap (stage 4 in fig. 4). Nevertheless, it continues to produce leaf traces, although these can no longer make vascular contact within the cap. Instead, they make contact with the meristematic area of the future cortex. This type of connection is shown in both figures 3 and 4 as open lines and represents the fibrous cortical system. The physiological continuity is represented in figure 3 as a contact between poles *A* and *B*.

Let us once more look at the postulated physiological polarities (fig. 3). Pole *X* connects with *Y*, and *Y* with *Z*, with the overall result of a connection between *X* and *Z*. New *X* centers arise continuously in the leaf base over an extended period. The location of new *X* centers in the leaf base is between existing ones, which are now represented by continuous provascular strands. At this stage, for purposes of comparison, we have called the new leaf-trace initiating poles *A*. In reality, we have good reason to assume that *X* and *A* are physiologically similar. In the same sense, *Y* and *B* are similar. This means that no *direct* contact can be made between *X* and *Z*. A contact can be made only indirectly via *Y*; otherwise, new leaf traces would make a shortcut to old leaf traces of the same leaf in position 4 (fig. 4). They do not do this.

DEVELOPMENT OF LATERAL ORGANS.—In the

previous description, we have dealt with the monocotyledonous shoot in its simplest possible state—an axis in which the only appendages are leaves. The situation in nature is complicated by additional lateral appendages such as vegetative branches, inflorescences, and roots. During our work, we have often been in a position to investigate the vascular attachment of these organs, so that we can indicate how their presence modifies the system so far described. The initiation of primordia of lateral organs other than leaves adds new growth centers which are governed in their vascular development by the principles outlined above. *The type of vascular attachment is determined by the time of initiation of the lateral organ in relation to the development of the axial system itself.* These relationships are summarized in the diagram shown in figure 5.

In branch primordia which are initiated very early (corresponding to stage *A* in fig. 5) and therefore near the center of the meristematic cap, the presence of a growth center simply redirects a portion of the “uncommitted” major, intermediate, and minor axial bundles into the base of the lateral organ. This is possible because the lateral axis itself establishes leaf primordia and a meristematic cap. The net result of this developmental process is that, in the mature shoot, a portion of the axial system is directed from the main axis into the lateral axis. Examples of this can be found in the development of lateral branches in palm inflorescences, as we have described for *Rhapis* (e.g., TOMLINSON and ZIMMERMANN 1968*a*, p. 298, fig. 13). The size of the lateral branch determines the number of redirected bundles. The maximum possible number is found in the specialized example where the shoot apex itself dichotomizes, resulting in two equal meristematic caps and a consequent distribution of the vascular system equally between two new daughter axes. Examples of this have been described recently in *Flagellaria* (TOMLINSON 1970*b*) and *Nyssa* (TOMLINSON 1971). Sympodial branching below the inflorescence in many woody monocotyledons, which involves the precocious development of a renewal shoot, is made possible, in part, by this type of development.

If the lateral branch meristem makes vascular contact with the main axis in the area where minor bundles of the cap are still uncommitted, some of the minor bundles are redirected into the lateral branch. This is shown in figure 5, *B*. It is very common in vegetative axillary buds of *Dracaena fragrans* and has been illustrated in one of our earlier papers (ZIMMERMANN and TOMLINSON 1969, p. 381, fig. 13).

The third type of branch attachment, which leads to satellite-bundle development, has already been mentioned. Here, the lateral organ is initiated sufficiently early to serve as an alternative pole of type *Y* (fig. 3) in such a way that vascular connection is made with any available pole *Z*, i.e., with existing leaf traces. This is shown in figure 5, *C*. This type of connection occurs only while the lateral organ is in a position corresponding to stages 3 and 4 in figure 5. This situation is also very common in aborted inflorescences and has been illustrated elsewhere (e.g., ZIMMERMANN and TOMLINSON 1965, p. 172, fig. 6).

In the fourth type of situation, branch initiation occurs below the cap and the level of development of central cylinder bundles. The vascular connection is essentially like that of the cortical system except that the lower physiological pole (*B* in fig. 3) is represented by existing bundles at the periphery of the vascular cylinder (fig. 5, *D*). Examples of this type are found in the vascular attachment of roots and late-developing vegetative branches and inflorescences (TOMLINSON and ZIMMERMANN 1968*b*). To use a simple terminology we have employed earlier, these are “demand” bundles (TOMLINSON 1970*a*, p. 261).

Vascular development of a branch often takes place over a longer period of time, so that more than one type of attachment is involved. In *Dracaena fragrans* we have often found axillary buds which are connected to the main axis via both axial bundles and satellites (fig. 5, *B, C*). Fully developed *Rhapis* inflorescences are attached to the main axis via both satellites and demand-type bundles (fig. 5, *C, D*) as we have illustrated elsewhere (TOMLINSON and ZIMMERMANN 1968*a*, p. 298, fig. 13). We have found this type of inflorescence attachment in many other palms as well. Finally, it may be stated that roots are connected to the central cylinder entirely via demand bundles, signifying their late development. The mature structure thus shows clear evidence of the time of initiation of the vascular connection between lateral and main axis.

Concept of an “inner” and an “outer” vascular system

As long as *Rhapis*, *Pronium*, and other plants of similar construction were dealt with, not much significance could be ascribed to the cortical trace system, because in these plants it is obviously rudimentary. Eventually, however, we encountered plants in which this cortical system consisted of functioning vascular bundles. In these plants, it became possible to speak of an “inner” and an

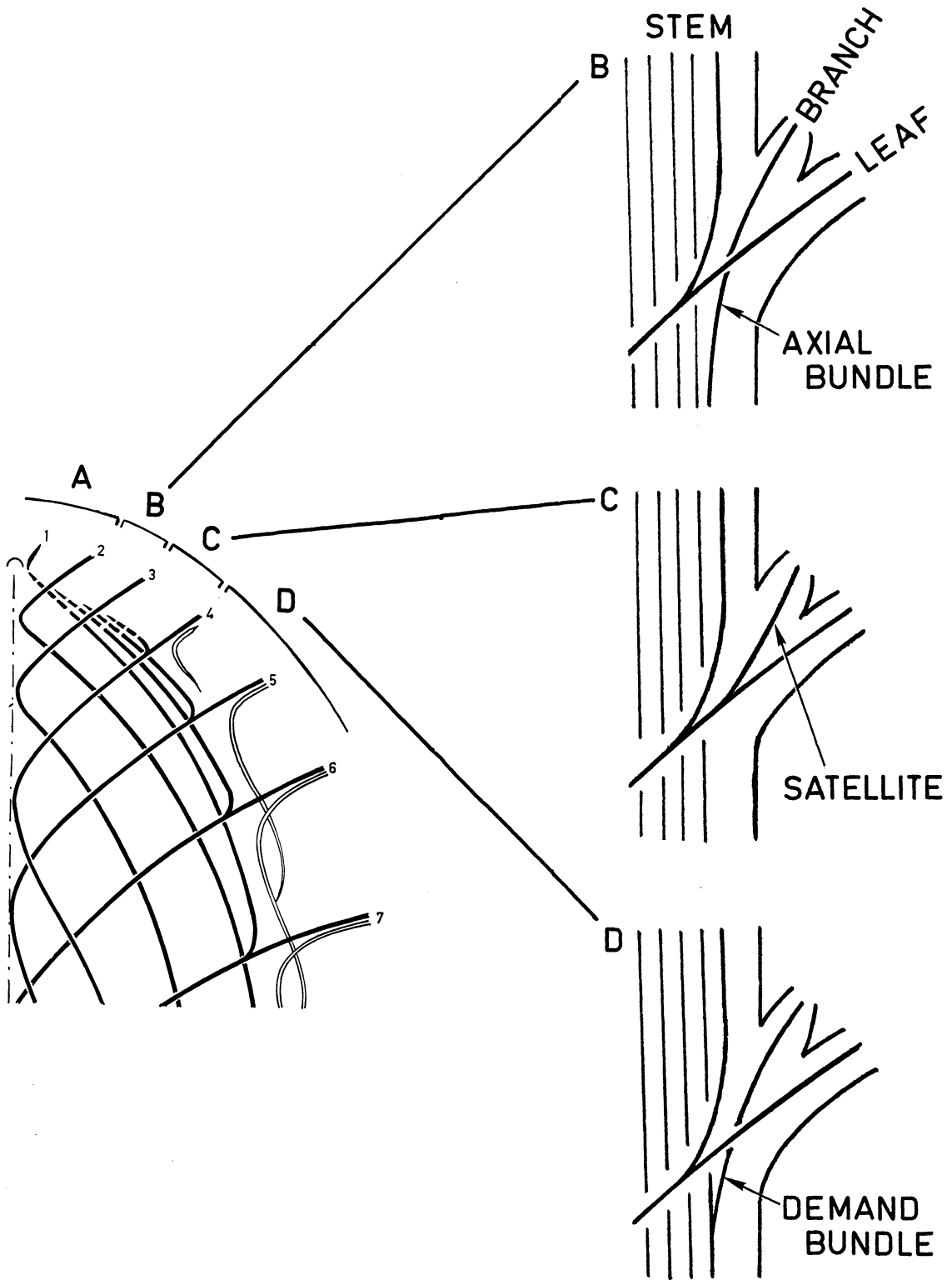


FIG. 5.—The time at which a lateral branch makes vascular contact with the main axis determines the type of vascular branching. In position *A*, major bundles, in position *B*, minor bundles connect directly with the branch; in position *C*, satellites develop; in position *D*, bundles of the lateral axis attach to existing axial bundles of the main stem.

“outer” vascular system. The inner system is that of the central cylinder (drawn with bold lines in figs. 3 and 4), the outer one that of the cortex (drawn with open lines in figs. 3 and 4). Since the cortex of monocotyledons has strict topographic limits which do not necessarily coincide with a distinction based on development, it is better to define the inner vascular bundles as those derived from the cap and the outer vascular bundles as those derived outside the cap. The two systems, as we have seen, can be distinguished in still another way: the developing inner vascular system is open-ended distally, with the “uncommitted” ends toward the inside of the axis; whereas the outer system, during its development, is open-ended basally, with the “uncommitted” ends toward the outside of the axis.

In some monocotyledons, like *Prionium*, the pole *B* (fig. 3) loses its physiological capacity to effect linkage early in leaf development, with the result that each individual outer leaf trace ends blindly below, tapering out in the cortex. In the mature stem, these traces can be recognized as fibrous bundles in the cortex (ZIMMERMANN and TOMLINSON 1968). The situation in *Rhapis* is very similar, except that the strands anastomose among themselves and occasionally include narrow conducting elements (ZIMMERMANN and TOMLINSON 1965, 1967). This is particularly clear in the rhizome of this plant. In *Strelitzia* the outer system develops more fully. The course of bundles is similar to that of *Rhapis*, but the strands differentiate into vascular bundles with well-developed vascular tissues (fig. 6).

The outer vascular system is most elaborate in monocotyledons like *Dracaena* which have secondary growth (ZIMMERMANN and TOMLINSON 1969, 1970). Here, there is a vascular cambium which produces secondary vascular bundles. To go back to our diagram in figure 4, we can say that the vascular cambium assumes the function of pole *B*. Hence, we can homologize the secondary vascular bundles of monocotyledons of the *Dracaena* type with the cortical bundles of plants like *Prionium* and *Rhapis*. If this is true, plants of the *Dracaena* type should lack cortical bundles completely. A survey of a large number of this kind of monocotyledon showed indeed that this prediction was correct, lending support to this suggested homology.

Comparison of monocotyledons with other plants

In a single transverse section of a monocotyledonous stem, it is not usually possible to distinguish between inner and outer vascular bundles. In *Rhapis*, *Prionium* (illustrated in earlier papers),

and *Strelitzia* (illustrated in fig. 6), all inner bundles are in the central cylinder, and all outer bundles are in the cortex. In some species, this is not the case. In many palms, some of the cortical bundles are part of the inner system. This complication will be described in a future paper and does not concern us any further here. The only firm statement we can make is that, in a transverse section of a monocotyledonous stem without secondary growth, all bundles of the central cylinder are inner bundles. Some of the cortical bundles may or may not be inner bundles; the outermost ones are almost certainly outer bundles. If there is secondary growth, all secondary bundles are outer bundles, the outermost primary bundles *may* be inner bundles.

The inner vascular system is characterized by obviously upward-branched leaf traces and is, as far as we can see, unique to monocotyledonous stems. Dicotyledons, conifers, and tree ferns have vascular systems which are more similar to the outer system. Leaf traces in these plants do not have upward-pointing branches. This becomes clear as one studies a complex dicotyledonous vascular system like that of the sugar beet (*Beta vulgaris* L.), in which vascular bundles are not restricted to a single ring and which, therefore, resemble monocotyledons superficially. The sequence of development is such that each younger leaf primordium makes vascular contact with stem tissue further down and further out, similar to the open lines shown in figure 4.

It could be argued, of course, that, in plants like *Sequoia* in which the vascular system is initially open-ended in a distal direction (ESAU 1965), the situation is not different from that in the monocotyledonous stem during the developmental stage of the connection of *X* and *Z* (fig. 3). In other words, one could say that the vascular system of conifers and dicotyledons is similar to the inner system of monocotyledons. But, although direction of differentiation is temporarily acropetal in *Sequoia*, the new strand is not really open-ended, because it is committed to a specific leaf. Open-endedness, in the long run, is still at the lower “end” of the strand as growth continues basipetally into the secondary area below, as in *Dracaena*.

Inner and outer system in relation to “demand” and “supply” type bundles

In an earlier publication we have made the distinction between “demand” and “supply” types of bundles in monocotyledons, and this has particular value in describing the connection of lateral organs to the main axis (TOMLINSON 1970a, p.

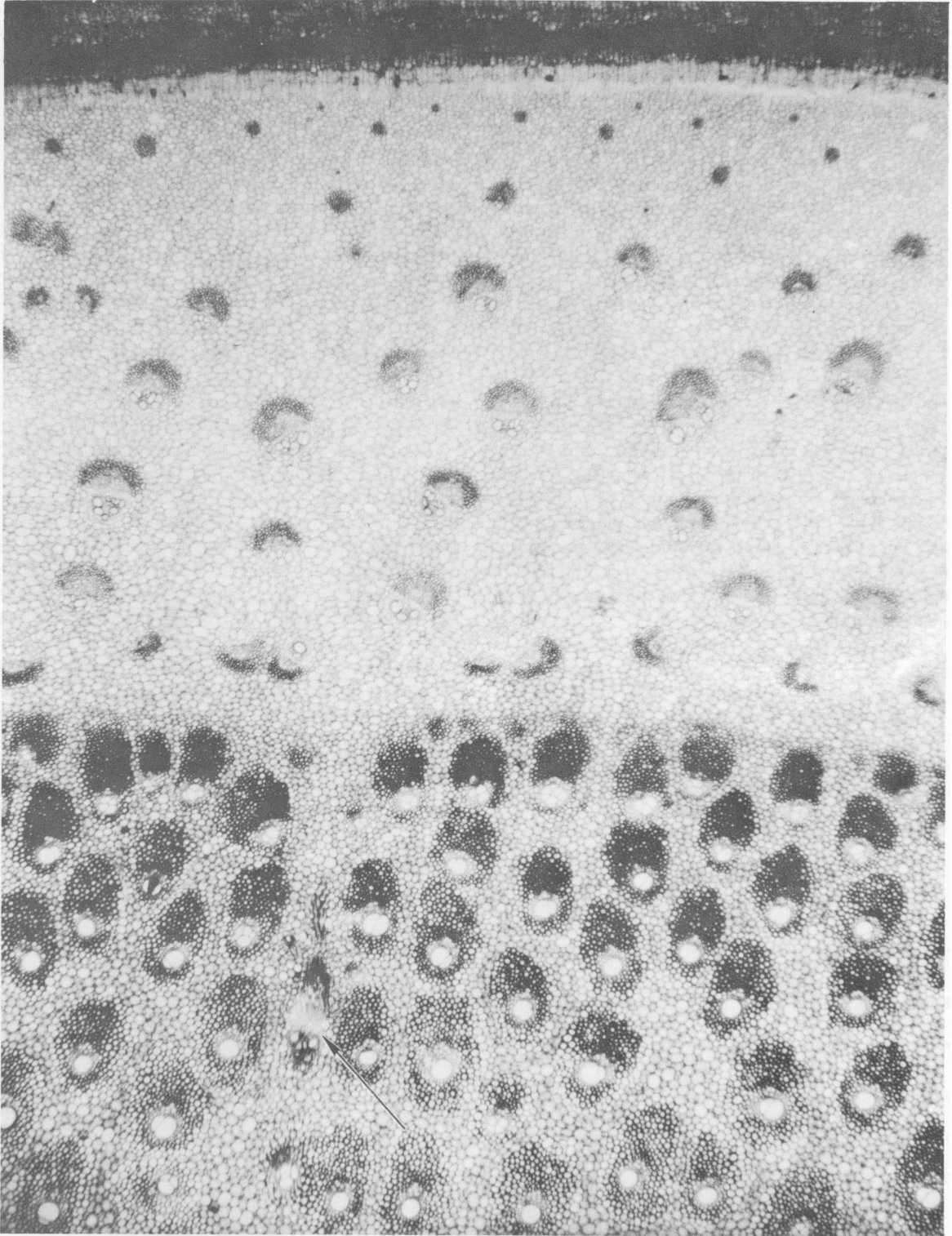


FIG. 6.—Transverse section through the peripheral area of a stem of *Strelitzia nicolai*. The inner vascular system is represented by the bundles in the central cylinder (lower half of photograph); and the outer system, by vascular bundles in the cortex (upper half of photograph). Note the leaf trace on its way to the leaf in the lower left (*arrow*).

261). This nomenclature in no way conflicts with the new one; its conception is merely somewhat more physiological. In figure 3, we could say that $X-Y$ and $A-B$ are "demand-type" traces, $Y-Z$ is a "supply-type" trace as are bridges and satellites. To be consistent, then, we would have to say that the supply-type bundles are unique to monocotyledons.

In conclusion, we should emphasize that we do by no means desire to set up too rigid a terminology. Indeed, if one clings too dogmatically to terms, one can create more confusion than understanding. We shall mention just a single example. If a vascular strand in *Coleus* is interrupted, it is bridged basipetally from the upper vascular end. Physiologically speaking, this is a "supply bundle"; yet, morphologically, we might want to call it an "outer bundle." It is really idle to quarrel about such cases; terms should not be created to be defended but rather to help us communicate. Even though we are fully aware of the fact that we have to go a long way yet, it is gratifying to realize that we are now finally beginning to understand the vascular system of large monocotyledons, a vascular system which has been utterly puzzling in its complexity. Table 1 summarizes our present state of understanding.

Historical concepts

In the early history of plant anatomy, there was a notable attempt to generalize about the distinction between dicotyledons and monocotyledons in terms of shoot development. This takes us as far back as the end of the eighteenth century and the

concept of exogenous and endogenous growth. DESFONTAINES (1798) introduced this distinction by visualizing that in the growth of monocotyledonous stems the youngest vascular bundles originate in the center of the stem in continuity with the youngest leaves, thus displacing older bundles toward the stem periphery (fig. 7, left). Since growth processes were regarded as being initiated in the stem center, the term endogenous growth seemed appropriate. Exogenous growth, on the other hand, was considered to be characteristic of dicotyledons because peripheral bundles were thought to be the youngest. No doubt the soft (cambial) layers of the inner bark gave this superficial impression. Although this concept may seem naive to modern plant anatomists, it must be remembered that it was based on the examination of large, and truly representative, monocotyledons (DESFONTAINES studied the date palm), and it tried to relate structure to development. The idea was initially widely accepted and was used by DE CANDOLLE (1813) in an influential textbook as a basis for distinguishing monocotyledons as "Endogènes," with an endogenous vascular system, from "Exogènes," with an exogenous vascular system. DESFONTAINES' theory was thus brought to the attention of a number of critical observers who were stimulated to examine monocotyledonous anatomy in an attempt to verify it. The distinguished anatomist HUGO VON MOHL (1824) eventually demolished the idea on the basis of his research on palms. He showed that the overall course of vascular bundles in the palm stem involved crossing over of bundles in a way which

TABLE 1
COMPARISON OF "INNER" AND "OUTER" VASCULAR SYSTEM IN DIFFERENT PLANTS

	Inner vascular system	Outer vascular system
<i>Prionium</i> (Juncaceae)	Fully developed; vascular bundles in central cylinder	Abortive; nonanastomosing fibrous bundles in cortex
<i>Rhapis</i> (Palmae)	Fully developed; vascular bundles in central cylinder	Abortive; anastomosing and small vascular bundles in cortex
Many large palms	Fully developed; vascular bundles in central cylinder and some fibrous cortical bundles	Abortive; outermost fibrous cortical bundles only
<i>Strelitzia</i> (Strelitziaceae)	Fully developed; vascular bundles in central cylinder	Presumably functional; anastomosing vascular bundles in cortex
<i>Puya</i> (Bromeliaceae)	Fully developed; vascular bundles in central cylinder	Absent (no cortical bundles present)
<i>Dracaena</i> (Agavaceae)	Fully developed in mature primary stem. Small in extent (only innermost primary bundles) in seedling and outgrowing axillary buds	Functional; outermost primary bundles in establishment growth phase, continuous with anastomosing secondary bundles below
Tree ferns, conifers, and dicotyledons	Absent	Primary bundles; in conifers and dicotyledons, continuous with secondary vascular tissue below

could not be explained by the simple progressive displacement implicit in DESFONTAINES' theory (fig. 7, right). VON MOHL's results were confirmed by his contemporaries, notably DE MIRBEL (1844), who also showed that some monocotyledons (e.g., *Dracaena*) have exogenous growth. Consequently, the concept of exogenous versus endogenous vascular systems rapidly disappeared, although "endogen" and "exogen" as alternative terms for monocotyledon and dicotyledon, were long persistent.

Subsequent history shows that the essentially correct observations of VON MOHL on the structure of palm stems were progressively obscured by gen-

erations of writers who had no firsthand familiarity with palms. We have shown elsewhere that the representations of monocotyledonous vascular systems in modern textbooks are largely mythical (TOMLINSON and ZIMMERMANN 1966c). One reason for this is undoubtedly that elementary botany courses presently take the corn stem as a "type" for the monocotyledonous stem. *Zea mays* is, in fact, a very specialized grass, and its study, independent of an intimate knowledge of less specialized plants, has not led to any understanding of monocotyledonous growth. The only alternative generalization, the stelar theory, is even less in-

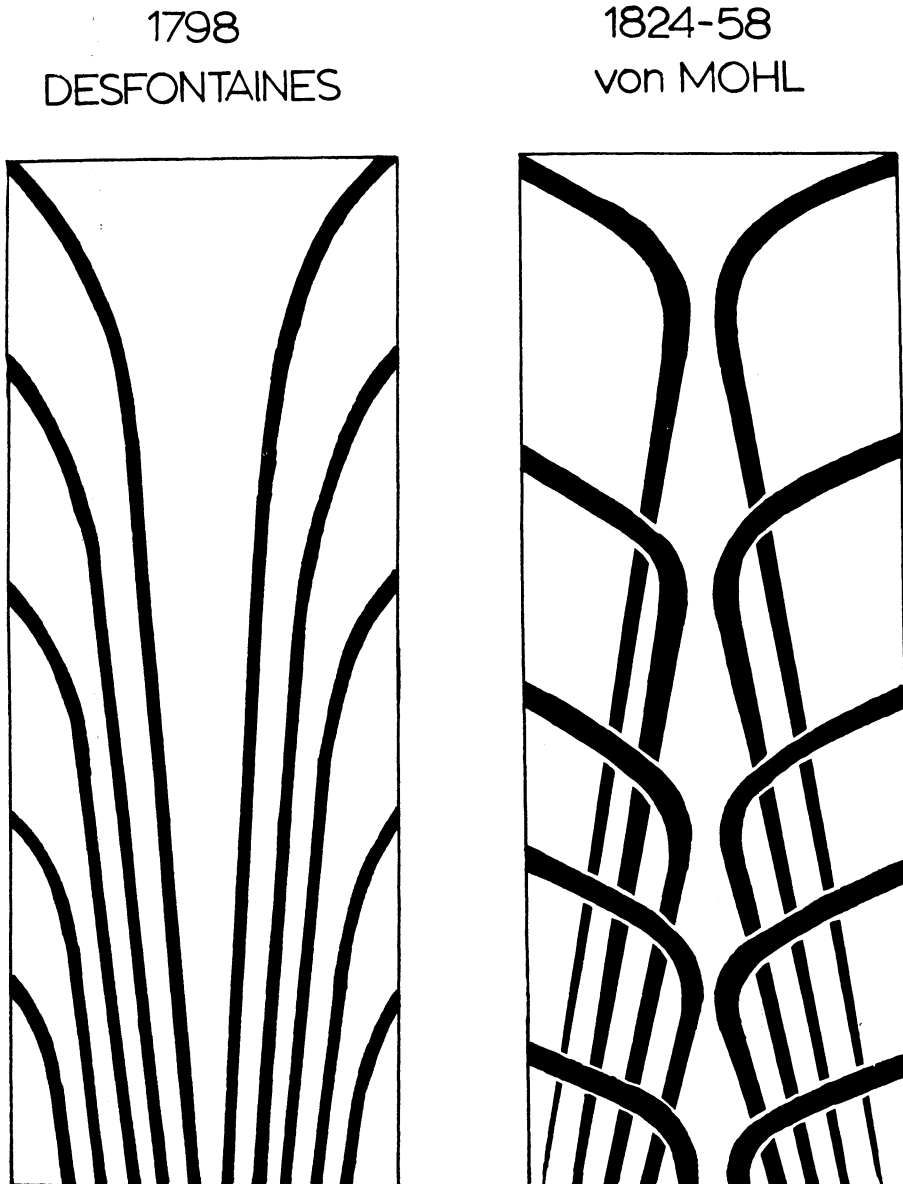


FIG. 7.—Two historical palm stem diagrams (from ZIMMERMANN and TOMLINSON 1965, originally after MONOYER 1925)

formative (VAN TIEGHEM and DOULIOT 1886; SCHOUTE 1903). Monocotyledons are incorporated into the framework of this scheme only by virtue of the cumbersome term "atactostele," which is no more than a cloak for ignorance. The distribution of vascular bundles in monocotyledonous stems, we now know, is the result of a beautifully ordered developmental process, and yet the term means "a stele without order"!

In our attempt to revitalize a neglected subject on the basis of new knowledge, we do not necessarily seek to reinstate the old terminology of "endogenous" and "exogenous" growth, although these words would perhaps be appropriate. During the course of the past century, the terms have assumed topographical meaning with reference to the origin of lateral organs. The terms "inner" and "outer" are easy to understand and to remember and do not need to be a source of confusion.

Taxonomic implications

It is possible that our concept of an inner and an outer vascular system may be of value in analyzing the interrelationships between monocotyledons and dicotyledons. A connection between the two major groups of angiosperms is, according to current taxonomic dogma, sought between the Alismatales among monocotyledons and certain of the herbaceous magnolialean orders, specifically the Nymphaeales, among dicotyledons. The consequence of this interpretation is that all authors of modern systems of classification (and many older authors as well) treat the Alismatales as a "primitive" group, so that, in a linear sequence, this order comes first in a description of monocot-

yledons (e.g., HUTCHINSON 1959; CRONQUIST 1968; TAKHTAJAN 1966). Whatever merit there may be for this on the basis of reproductive morphology, it does raise problems in understanding how large woody plants in the Monocotyledonae can be derived from herbaceous and specialized ancestors.

If, as we suggest, there are fundamental differences between dicotyledons and monocotyledons in their vascular systems which can be recognized in structural terms and for which the developmental explanation seems to be at hand, it should be possible to establish two things. First, if those dicotyledons which are putatively closest to the ancestors of the monocotyledons have any indication of a monocotyledonous type of vascular system, in our terminology, do they have any indication of an inner system? Second, if there are any indications among presumed primitive monocotyledons that their vascular system is dicotyledon-like, in our terminology, is only the outer system developed? There is already a partial answer to this second question, because, from the extensive literature and from the work of one of us (P.B.T.) on the systematic anatomy of aquatic monocotyledons (an assemblage which includes presumed primitive forms), there is every indication that a clear distinction between inner and outer systems does exist, although the inner system may be reduced to the extent that individual vascular bundles cannot be distinguished (e.g., CHRYSLER 1907). This would suggest that these groups of plants are unmistakably monocotyledons.

Application of our methods and concepts to plants with nymphaelean affinity may therefore throw light on the puzzling relationship between monocotyledons and dicotyledons.

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GENETICS OF LUPINUS. V. INTRASPECIFIC VARIABILITY FOR REPRODUCTIVE TRAITS IN LUPINUS NANUS

AUGUSTE HOROVITZ¹ AND JAMES HARDING

Department of Environmental Horticulture, University of California, Davis, California 95616

ABSTRACT

Genotypic differences among forms of *Lupinus nanus* were established for the reproductive traits of flowering time, flower size, pollen production, ovule production, length of anthers, length of stigmatic hairs, coherence between keel margins, blue reflectance from corollas, honey guide marking, and autofertility. These forms outcrossed at significantly different rates when exposed to the same pollination environment. Attempts are made to relate reproductive traits to reproductive mode.

Introduction

Different genetic forms of the Californian annual *Lupinus nanus* spp. *nanus* were found to outcross at different rates when subjected to the same pollination environments (HARDING and HOROVITZ 1969; HOROVITZ and THORP 1970). These differences presumably result from genetic variation for diverse reproductive traits. Some effects of one obvious variable trait, flower color, have already been investigated (HOROVITZ and HARDING, in press). The purposes of this study are (a) to examine the pollination system of *Lupinus nanus*, (b) to trace genetically controlled variation for floral traits grouped according to mode of action

during pollination, namely, timing devices, attracting devices, and mechanical devices, (c) to compare variation in a fertility characteristic which probably results from inbreeding and, therefore, reflects different propensities for selfing, and (d) to link the reproductive traits of genetic forms to outcrossing rates estimated from progeny test data. The study is based on 20 genetic stocks, each derived from wild populations near Lake Berryessa, California. Phenotypic differences in reproductive properties were established when plants were growing under uniform greenhouse conditions. Flowers of similar age and occupying similar positions on the plant were used for comparisons. In the case of quantitative differences, a standard analysis of variance was performed, and where the analysis revealed a significant *F*-value, DUNCAN'S

¹ Present address: Department of Botany, Tel-Aviv University, Israel.