

General and peculiar features of vascular organization and development in shoots of *Bougainvillea glabra* Choisy (*Nyctaginaceae*)

Z. PUŁAWSKA

Institute of Botany, University of Wrocław, Kanonia 6/8, Wrocław, Poland

(Received: April 5, 1971.)

Abstract

In the present study developmental relations between peripheral meristematic cylinder and vascular bundles of the young parts of the shoots and the relations between these bundles from the young elongating parts and those formed during secondary thickening has been elucidated. The suggestion is advanced that the limited lateral extension of bundles is an important developmental feature of the vascular system of *Bougainvillea glabra* Choisy. The organization of the vascular system in thick fast growing sprouts and in the thin slow growing lateral shoots are described. It is shown that the quantitative differences in vascular organization between both types of shoots are the manifestation of a close morphological harmonisation of the entire shoot, and particularly of its entire vascular system.

INTRODUCTION

The family *Nyctaginaceae* to which *Bougainvillea* belongs has a peculiar vascular system. There is a cylinder of meristematic tissue in the peripheral part of the shoot. In annual elongating stems, internally to this cylinder collateral bundles are scattered in the parenchyma on the entire cross section. The oldest bundles lie near to the centre of the shoot, and the younger ones near the meristematic cylinder or they are embedded in it. During secondary thickening the meristematic cylinder gives rise to new vascular bundles.

The opinions as to the mode of secondary thickening are controversial (Balfour, 1965; Esau and Cheadle, 1969), and the development and arrangement of vascular bundles in the apical parts of the shoot has only been described by Balfour and Philipson (1962). These authors examined a 400- μ segment of the subapical part of a shoot of *Bougainvillea spectabilis* Willd. The study of the development of vascular bundles in so short a segment is insufficient for elucidating the deve-

developmental relations between the meristematic zone and the vascular bundles of the young parts of the shoot, and the relations between the vascular bundles from the elongating parts of the shoot to those arising during secondary thickening.

The present studies on the vascularisation of *Bougainvillea glabra* Choisy shoots were undertaken to throw some light on these problems.

MATERIAL AND METHODS

The investigations were performed on a 20-year-old, profusely branched specimen of *Bougainvillea glabra* Choisy, a climbing shrubby plant native of Brazil, in the glasshouse of the Institute of Botany of

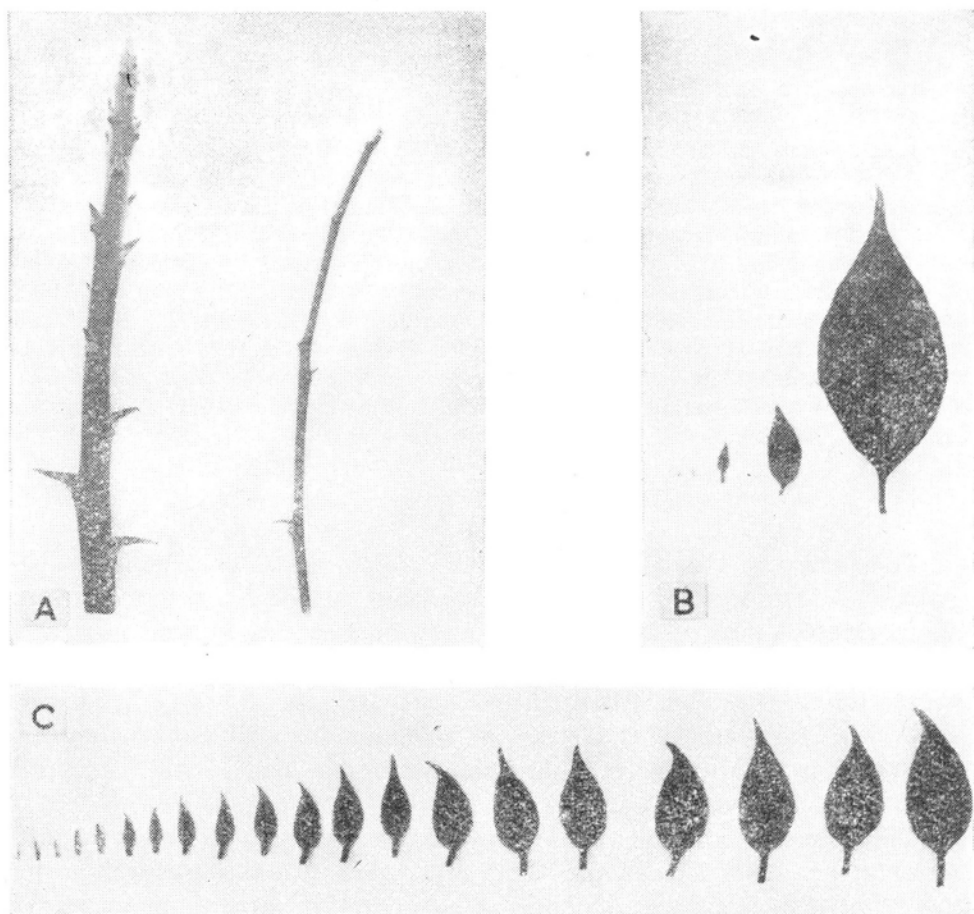


Fig. 1. Comparison of thick sprout with thin lateral shoot:

A — apical segments of thick and thin lateral shoots, B — successive leaves from thin lateral shoot (the oldest and youngest ones excepted), C — successive leaves from thick sprout (the oldest and youngest ones excepted). Natural size.

Photo by M. Niewitecki

the Wrocław University. The shoots of this plant show elongation growth almost the year round and may be divided into two kinds: thick sprouts which in one year may reach a length of 12 m or more; thereafter their growth is arrested and they no more increase in length. They start from the origin of the older thick sprouts, are capable of creeping and constitute the axes for the development of thin lateral branches. The latter elongate for many years, the activity of the terminal bud recommencing repeatedly after periods of rest. In the course of one season a segment of at most some tens of centimetres is added.

On all shoots, in the axils of the alternately arranged leaves two buds arise: one proximal to the leaf — vegetative, and the other lying higher — the flower bud. The bases of the flower axes remain on the mother shoot in the form of thorns (Fig. 1A).

The length of the elongation zone of the thick sprouts varies widely, generally between 10 and 28 cm. The slender lateral shoots seldom show a zone of elongation exceeding 5 cm. The longer this zone the thicker the stem, the more leaf primordia in the bud and the smaller the differences in the developmental stages between them (Fig. 1B, C). The thicker the stem the more vascular bundles are seen on the cross section.

A description in detail is given of the arrangement of bundles in one whole annual sprout 50 cm long and in one whole three-year-old lateral shoot 54 cm long as well as in the apical parts of some other selected shoots.

The young parts of shoots were fixed by the routine method in CrAF (0.5-0.5-20), embedded in paraffin and then sectioned transversely on a microtome and stained with safranin O and fast green. A continuous series of microtome sections from a sprout was taken on a length of 20 cm, and from a lateral shoot on a 5-cm length. Older parts of the shoot previously fixed in 70 per cent alcohol were free-hand sectioned and inspected in glycerin. Some of the free-hand sections were stained with safranin O and fast green and mounted in balsam. Leaf venation was examined on serial cross sections and whole leaves which were cleared in 2 or 4 per cent NaOH solution in dependence on their age.

The diagrams of the longitudinal course of the vascular bundles, prepared from drawings of the serial cross sections show the bundles arranged in one plane as if in an opened and flattened shoot oriented with its surface to the observer. The bases of the successive leaves beginning from the youngest one are numbered from 1 to \times (e.g. Fig. 5).

The leaves exhibit spiral phyllotaxy, on the thickest sprouts according to the limiting divergence 99.3° (Fig. 2B), and on the thinner ones and all the lateral shoots according to the limiting divergence 137.5° (Fig. 2A, C).

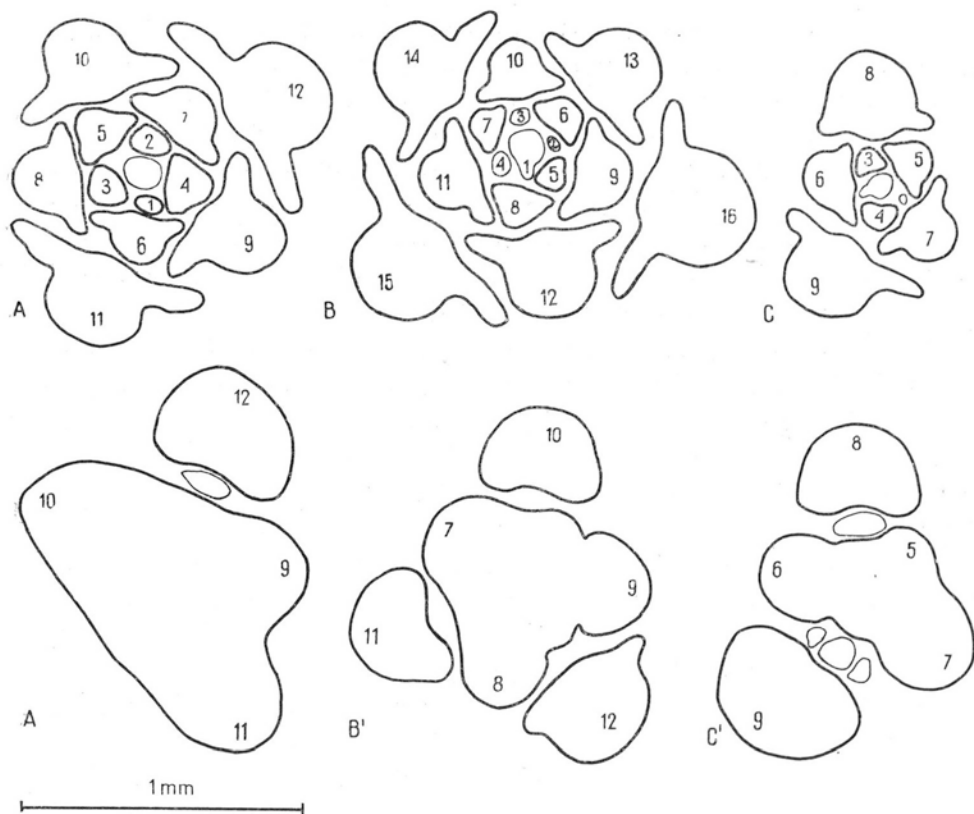


Fig. 2. Leaf arrangement on cross sections through tip and at a certain distance below the tip:

A — cross section through shoot apex with limiting divergence 137.5° , A' — cross section through the same shoot at a distance of 600μ from the tip; B — cross section through the shoot apex with limiting divergence 99.3° ; B' — cross section through the same shoot 600μ below the tip; C — cross section through tip of lateral shoot with limiting divergence 137.5° , C' — cross section through the same shoot 600μ below the tip.

OBSERVATIONS AND RESULTS

Organization of vascular system

I. Longitudinal course of bundles in thick sprouts

A. Thick sprout with limiting divergence 137.5°

On this 50 cm long shoot the leaves in the number of 51 are alternately arranged according to the limiting divergence 137.5° (Fig. 2A, A'). The zone of elongation growth is 26 cm long and comprises 42 undeveloped

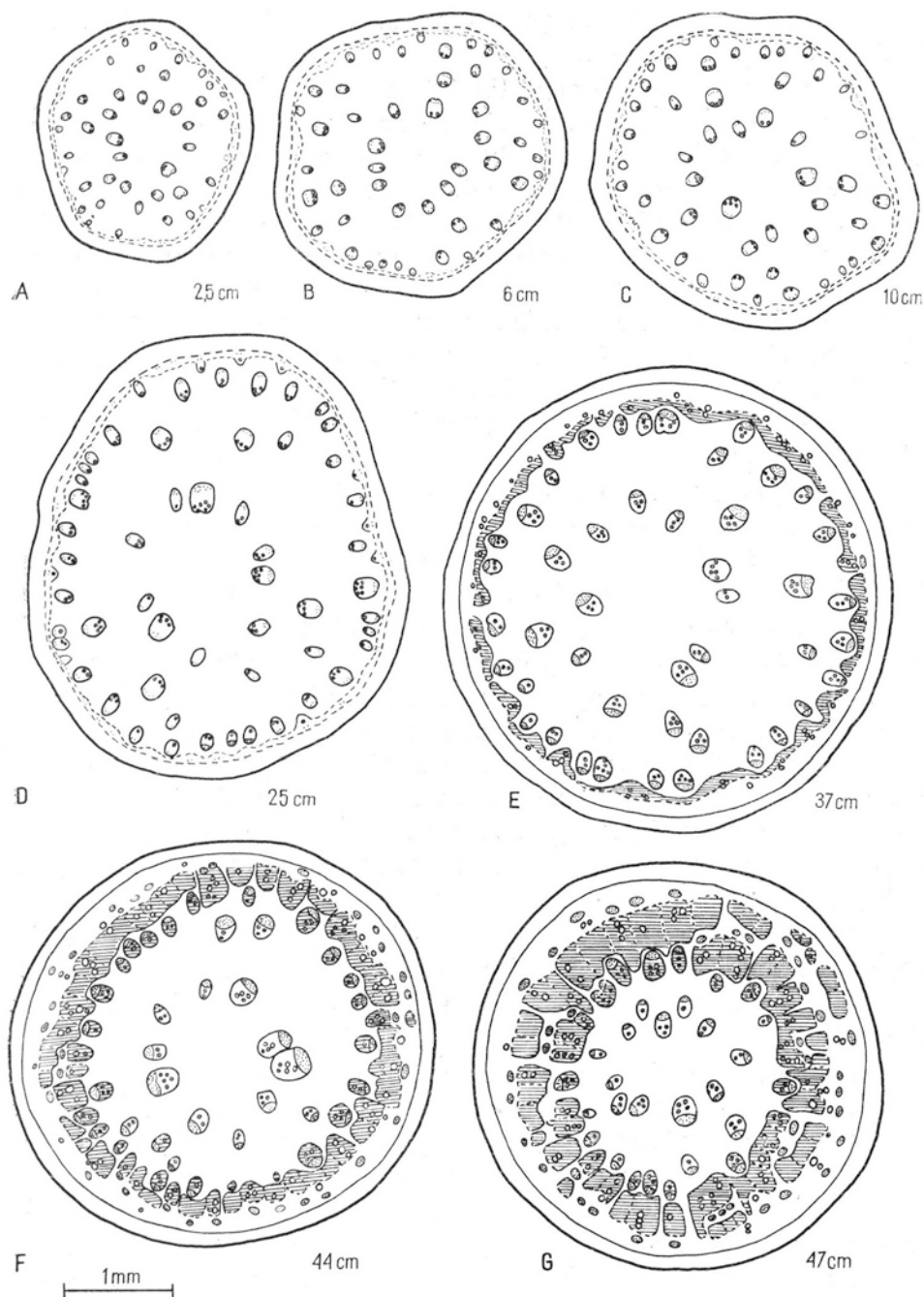


Fig. 3. Cross sections through internodes of thick sprout. On the right side of each diagram the distance from the tip of the shoot is given in centimetres:

A, B, C, D — cross sections from the zone of elongation growth; outer border of meristematic cylinder marked by interrupted line; E, F, G — cross section of part of stem not elongating; outer limit of meristematic cylinder marked by continuous line. Vascular elements of xylem in the bundles denoted by circles, phloem part of bundle dotted. Hatched areas denote fibres and the not numerous parenchyma cells between them. Other explanation in text.

leaves. The bases of the 27 youngest leaves are densely agglomerated in the apical 2 cm long part.

On the cross section through the internodes at all levels, the bundles lying closest to the centre of the shoot form a more or less regular inner ring (Fig. 3A-G). The outermost bundles are adjacent to the cylinder of meristematic tissue or partly embedded in it. In the elongating internodes (Fig. 3A-D) bundles are scattered in the parenchyma lying between the peripheral and inner ones — conventionally termed intermediate. In the nonelongating internodes, the outermost ring of bundles adjacent to the cylinder is embedded in the fibres; in the oldest internodes of the shoot described, the number of outer bundles embedded in the fibres is increased to two irregular rings. The bundles of the inner ring and the intermediate ones (Fig. 3G) are embedded in the parenchyma of the central part of the stem.

In each node three bundles depart from the inner ring and run to the leaf: a median and two lateral ones. The departure of the bundles from the stem into the leaf is gradual, starting from the inner ring generally at a distance of one internode below the base of the given node (Fig. 4A). Before departure to the leaf, an intermediate bundle joins each of the lateral ones, forming the extreme bundles of the leaf.

In place of the departing bundles, two intermediate ones are included into the inner ring — one on each side of the departing ones (Fig. 4A-F). In each node definite bundles undergo subdivision (Fig. 4B, C). Some of the bundles formed by division form connections with those included into the inner ring (Fig. 4D). In this way the gap in the inner ring is closed and the number of bundles between the nodes remains the same.

Four peripheral bundles by-pass the median one departing to the leaf; they run between the lateral bundles and depart higher to the vegetative bud (Fig. 4E, F, G). The remaining peripheral bundles close the leaf-branch gap, and from some of them bundles depart to the flower bud.

Instead of the two intermediate bundles which are included into the inner ring in the node, and in the place of two other intermediate bundles departing to the leaf as its extreme bundles, four other intermediate and peripheral bundles enter (Fig. 4I) after closure of the gap.

When studying the longitudinal course of the bundles, as lower end was assumed the level of their departure from the peripheral ring. The results are presented schematically. One diagram shows the longitudinal course of the bundles, disregarding the fact that in the particular nodes some of the bundles unite, and others previously connected separate (Fig. 5, diagram A, A'). Owing to this simplification the diagram is clear, and reveals the fundamental and simple principles of the entire system dissimulated by secondary changes. The second diagram (Fig. 5B, B')

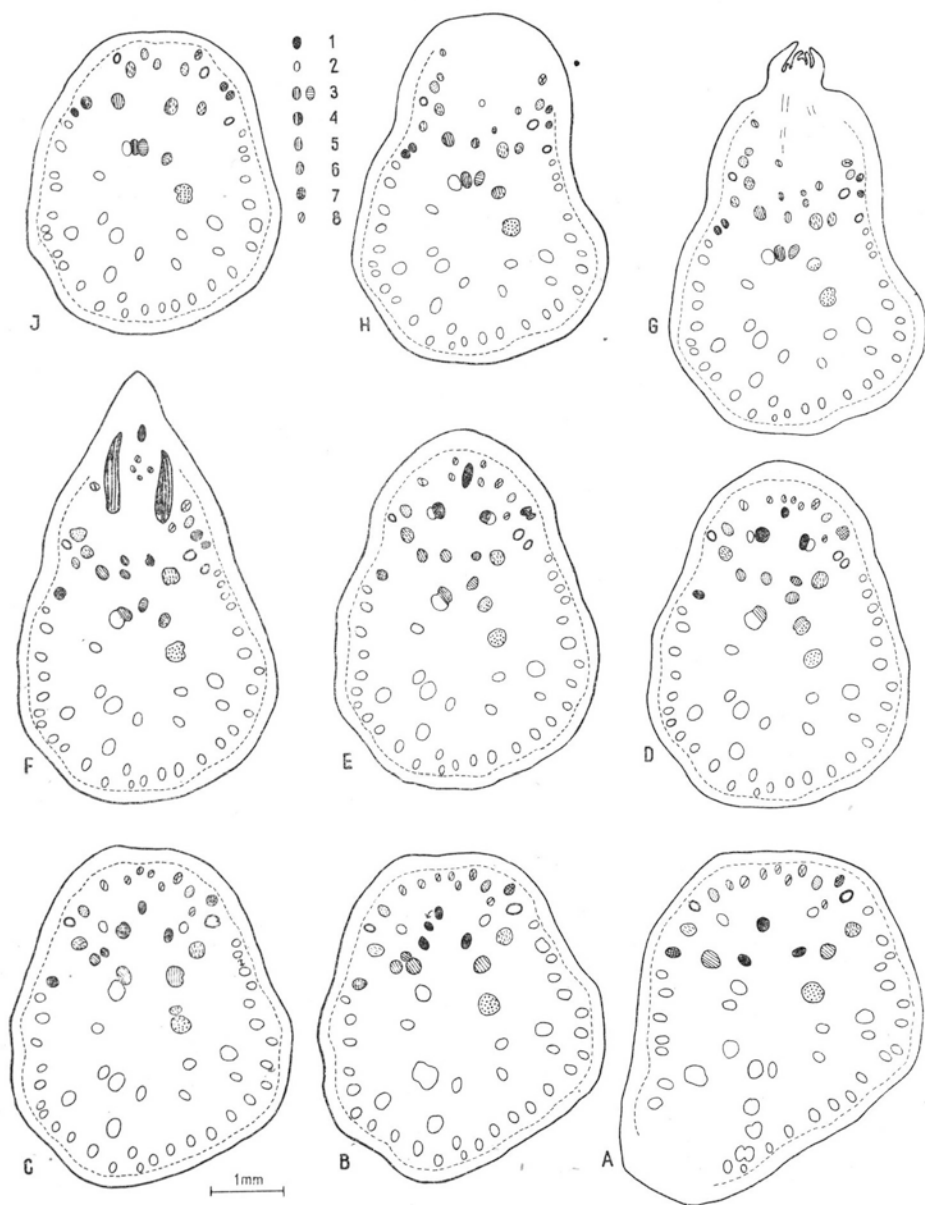


Fig. 4. Cross sections through the node of thick sprout:

1 — median and lateral bundles of leaf; 2 — extreme bundles of leaf; 3 — intermediate bundles which are incorporated into inner ring in node; 4 and 5 — intermediate bundles which after closure of the gap fill the space left by the bundles incorporated into the inner ring; 6 and 7 — extreme bundles of higher situated leaves; 8 — bundles departing to lateral buds. On all drawing the youngest bundles embedded in the meristematic zone are omitted. Other explanations in text.

shows the secondary characteristics of the longitudinal bundle system omitted in the preceding diagram.

The level of departure of the particular bundles from the peripheral ring is denoted on diagrams A and A' by a dot, and the site at which the given intermediate bundle is included into the inner ring is marked by a line perpendicular to the bundle.

The basic features of the longitudinal course of the bundles are as follows (Fig. 5A, A'):

- 1) All the bundles of one leaf: the median, two lateral and two extreme ones run generally next to one another (e.g. the bundles of leaf 42), less frequently in the lower segments they are separated by bundles running to another leaf (e.g. bundles of leaf 46 or 45).

- 2) The extreme youngest bundles are never included into the inner ring and reach the leaf as intermediate bundles. On the other hand, all the remaining bundles or those from which they derive run at first as peripheral bundles (in the diagram these segments are not shown), further as intermediate bundles, and finally they are included into the inner ring from which they depart to the leaf.

- 3) Each bundle at a definite point of its longitudinal course may divide into two new ones. The bundles formed by this division either belong to the same leaf (e.g. the median and left lateral bundle of leaf 42) or to two different leaves (e.g. left extreme bundle of leaf 38 and median of leaf 30). In this way primary interconnections between the bundles of the same leaf or between the bundles of different leaves arise.

- 4) The median bundle and one or, less frequently, both the lateral ones belonging to the same leaf arise usually from the subdivision of the same bundle. In the present description the lower segment of the bundle from which — after division — there arises, beside the median bundle proper, for instance the left lateral one of leaf 42 or both the lateral ones of the same leaf as in the case of leaf 41, is also called median bundle. In this aspect, the median bundle departs from the peripheral ring at the greatest distance in terms of the greatest number of internodes, from the base of the leaf corresponding to it, whereas both the extreme bundles depart closest to the leaf base.

The quantitative characteristics of the longitudinal course of bundles such as the number of internodes through which analogous bundles of the particular leaves run, and the number of plastochrones separating the interconnected bundles change either regularly from the base to the shoot apex or without a definite pattern as if accidentally from one node to another.

The regular changes in the longitudinal course of the bundles are as follows:

- 1) The median bundles of leaves 43–39 after separating from the peripheral ring run through 8 internodes: through three lower ones as

intermediate bundles, and then through the five upper ones as inner ring bundles. The median bundles of 38—27 leaves, after departing from the peripheral ring run through 10 or 11 internodes including two or three lower ones, where the bundles are intermediate and 8 upper ones where they belong to the inner ring. The median bundles of leaves 26—9 run through 13 internodes including five lower ones where they are intermediate and eight upper ones where they belong to the inner ring. The median bundles of the youngest leaves run, similarly as in the base of the shoot, mostly through eighth internodes.

2) The bundles of one leaf are interconnected with those of other leaves either within the peripheral ring or after departing from it. The diagram shows only those connections which occur beyond the peripheral ring.

The connections between the bundles of leaves n and $n-3$ and n and $n-8$ are the closest connections possible at a divergence of 137.5° from the left side of the sinistrorse spiral, and the connections between the n and $n-2$ and n and $n-5$ leaf bundles from the right side of the spiral.

Sometimes in the base part of the shoot are the connections between the bundles n and $n-3$: For instance the median bundle of leaf 45 joins the left lateral one of leaf 48. In the middle and apical part of the shoot, the interconnections between the bundles occur every eight instead of every three leaves. Thus, the left extreme bundle of leaf 38 is connected with the median of leaf 30. On the other hand, from the right side of the sinistrorse spiral, the bundles are connected every five leaves, but never every two. We see for instance the right lateral bundle of leaf 43 connected with the median of leaf 38, and the right lateral bundle of leaf 33 with the median of leaf 28.

The bundles of the same leaf are usually interconnected with those of two other leaves: one on the right and the other on the left. In this way a closed system of primary bundle interconnections arises. In the basal part of the shoot the bundles of leaf n join those of leaves $n-3$ and $n-5$. Thus, the left lateral bundle of leaf 43 is connected with the median and right lateral bundles of leaf 40, and the right lateral bundle of leaf 43 with the median of leaf 38. In the middle and apical part of the shoot the bundle of leaf n joins the bundles of the $n-8$ and $n-5$ leaves. The left extreme bundle of leaf 35 is connected with the median of leaf 27, and the extreme bundle of leaf 35 and the left lateral of leaf 30 are interconnected.

This means that, in general, in the course of ontogenesis the leaves n , $n-3$ and $n-5$ in the basal part of the stem were at similar development stages as leaves n , $n-5$ and $n-8$ in the middle part, since bundles of such leaves become connected which differ by an appropriate degree of development.

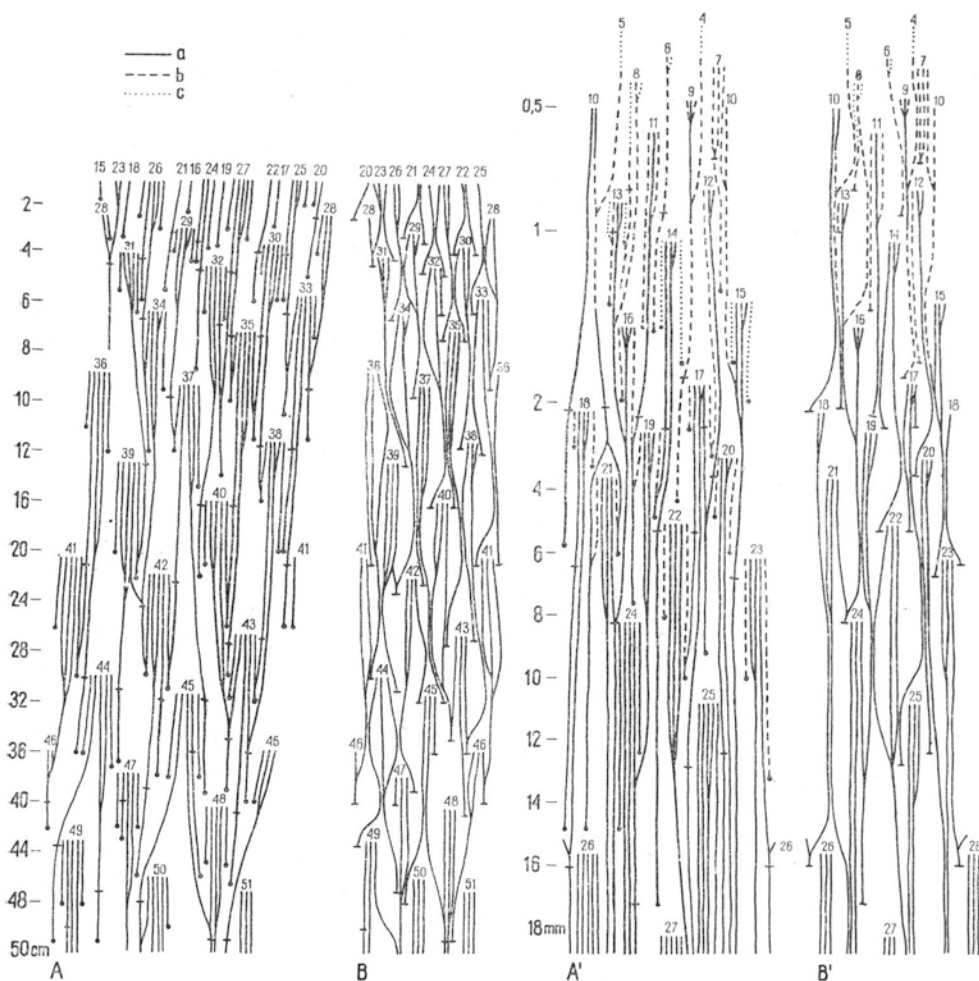


Fig. 5. Diagram of longitudinal course of bundles in sprout with limiting divergence 137.5°

Simplified diagram of course of bundles in lower (A) and apical (A') segment of stem, and diagrams of course of bundles forming inner ring in lower (B) and apical (B') segment of stem: a — bundles in which both vascular elements of primary xylem and those of primary phloem are differentiated, b — bundles in which only elements of primary phloem are differentiated, c — procambial bundle. The dot denotes the site at which the given bundle departs from the peripheral ring. The line perpendicular to the given bundle denotes the site at which this bundle is incorporated into the inner ring

Vascular supply to one leaf consists of five bundles, and each one of these may be connected with one of the five bundles of two other leaves. Thus various combinations are possible: the right extreme, youngest bundle of leaf 35 is connected with the left lateral, an older one of leaf 30, and the left extreme of leaf 35 joins the median — the oldest bundle of leaf 27. This example shows indirectly that a bundle separates into two

new ones when two different leaves to which these bundles belong are separated by an appropriate differentiation interval. The variability in the mode of connection of the bundles is the expression of a close harmonisation of the whole shoot, and particularly of its vascular system.

Irregular changes in the longitudinal course of the bundles concern the arising of lateral bundles. The right and left lateral bundle arise in a different way almost for each leaf. Usually from the median bundle of a given leaf one lateral bundle separates: right or left, and a second one arises independently from these two (e.g. lateral bundles of leaf 42). Less frequently two lateral bundles separate from the median of the given leaf (e.g. the lateral bundles of leaf 39), or both lateral bundles form independently of the median one (e.g. bundles of leaves 45 and 33).

The extreme bundles of all leaves depart from the peripheral ring — with but small variations — at the same distance from the base of the given leaf. The right extreme bundle separates, namely, at a distance of three, and the left at a distance of two internodes below the base of the given leaf.

Beside the above discussed primary, there are still secondary connections between the bundles they are shown in the diagram (Fig. 5B, B') representing the arrangement of the bundles forming the inner ring.

In each node one or two intermediate bundles are included into the inner ring, one on its right and the other on its left side. Mostly these two bundles unite, they also do with some bundle of the inner ring. (In the diagram the united bundles are maximally close to each other, but distinctly separate).

In the basal part of the stem one or two bundles which are incorporated into the inner ring in the given node n run upwards to leaf $n-5$, for instance both the bundles incorporated into the inner ring in node 50 or the bundle in node 48 on its right side (Fig. 5B).

In the middle and apical part of the shoot the bundle which is incorporated into the inner ring on the right side of node n runs to leaf $n-5$, mostly as its left lateral bundle. Thus, the left lateral bundle of leaf 38 is incorporated into the inner ring in node 43, whereas the bundle joining the inner ring on the left side of node n runs to leaf $n-8$ as its median bundle, e.g. the median bundle of leaf 35 is incorporated into the inner ring in node 43.

In the middle and apical part of the shoot the bundles which are incorporated into the inner ring in node n generally join the median bundle of leaf $n-5$. Since one of the bundles incorporating into the inner ring runs to leaf $n-5$, and the other to leaf $n-8$, a complex arises consisting of bundles of every third leaf.

Bundles of various leaves thus interconnect owing to the division of one bundle into two new ones (primary connections) or on the principle of connection and separation of bundles independent from one another.

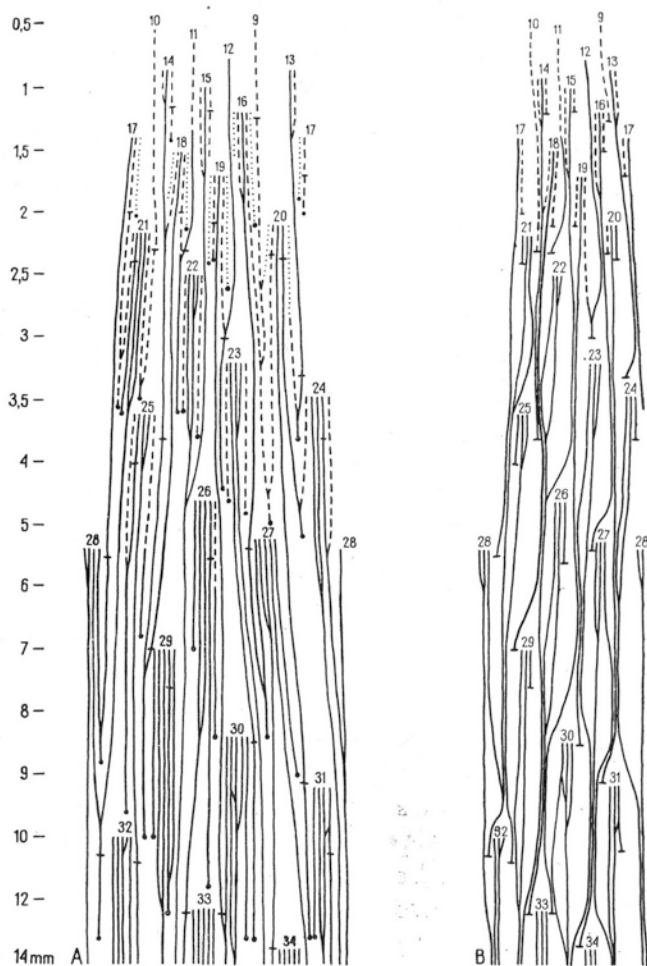


Fig. 6. Diagrams of longitudinal course of bundles in sprout with limiting divergence 99.3° . Notations as in fig. 5

If we would disregard the secondary connections and arrange the bundles of the particular leaves next to one another at the same distance from the centre of the stem, a cylinder would be formed. In this cylinder all the bundles of the same leaf would lie next to one another like the components of a single trace. The bundles of the particular leaves would then be situated in relation to each other according to the possibilities left by the limiting divergence according to which the leaves are disposed on the shoot.

The arrangement of the bundles in this imaginary cylinder would, therefore, be similar to that in the stems of many gymnosperms and dicotyledones with spiral phyllotaxy in which a single bundle departs from the stem to the leaf, and the vascular system has the form of a ring.

It would seem that in *Bougainvillea* the entire supply to one leaf corresponds to a single trace in other plants. In a single trace on the flanks of the central strand which determines the length of the whole bundle new strands differentiate higher and higher. Owing to this a single bundle arises widest at the base of the leaf corresponding to it, and tapering lower down in the stem. The mode of formation of lateral bundles in *Bougainvillea* is erratic and variable in as much as is the arising of the component parts of single trace.

A specific feature of the anatomical structure of *Bougainvillea* shoots would thus be the division of the vascular tissues of a single trace into individual minute bundles separated by parenchyma. The lower segments of these bundles run in the meristematic zone, and the middle and upper ones at a smaller or greater distance from this zone, embedded in the parenchyma of the middle part of the stem.

The general principles of the longitudinal course of bundles in the apical part of six other thick sprouts examined in detail are the same as in the one here described.

B. Thick sprout with 99.3° divergence

The essential features of the longitudinal course of the bundles are the same as those discussed above. The differences concern only quantitative characteristics, and these are above all dependent on the unequal limiting divergence in both the shoots. When leaves are arranged according to the limiting divergence 99.3° , the bundles of every 3, 4, 7, 11 leaves etc. can connect. The connection between the bundles of every 4th and 11th leaf are the nearest connections from the left side of the sinistorse ontogenetic spiral and the connections between every 3rd and 7th bundle are the nearest connections from the right side of the spiral.

In the examined 14 mm apical segment of this shoot from the left side of the ontogenetic spiral, the bundles of every 11th leaf unite most frequently. For instance the extreme left bundle of leaf 27 is connected with the median one of leaf 16. The bundles of every 4th leaf are rather exceptionally connected (Fig. 6A). The middle of the n leaf is distant by as little as an angle of 12.3° to the left (cf. fig. 2B), and sometimes the median bundle of the $n-11$ leaf lies on the right instead of the left side of the bundles of leaf n . For instance the median bundle of leaf 17 is situated on the right instead of the left side of the bundles of leaf 28, and the median bundle of leaf 10 lies on the right instead of the left side of the bundles of leaf 21. In this situation the bundles of leaf n and $n-4$ can unite. For instance the extreme left bundle of leaf 28 is connected with the right lateral and right extreme bundle of leaf 24, and the left extreme bundle of leaf 21 unites with the right lateral bundle of leaf 17. Some-

times the bundles of the same leaf are connected with the bundles of leaves younger by 4 and by 11 plastochrones. Thus, the left lateral bundle of leaf 20 is connected with the right lateral bundle of leaf 16, and the extreme bundle of leaf 20 unites with the median of leaf 9.

From the right side of the ontogenetic spiral the bundles unite every 7 leaves, and never every three. For instance the right lateral bundle of leaf 19 is connected with the median of leaf 12.

Since the bundles of the same leaf unite usually with those of two other leaves: one on the right and another on the left, a closed system of connections arises. Thus, the left extreme bundle of leaf 21 joins the right lateral bundle of leaf 17, and the extreme bundle of leaf 21 unites with the median of leaf 10.

The right and left lateral bundles of nearly every leaf form in a different way. The character of this variability is the same in this shoot as in the previously described one.

The extreme bundles depart from the peripheral ring more or less at the same level for all the leaves. The right extreme bundle departs from the peripheral ring at a distance of four, and the left one of three internodes below the base of the given leaf.

A characteristic trait of the longitudinal arrangement of the bundles forming the inner ring are the secondary connections between the bundles of leaf n and $n-4$ (Fig. 6B). They form in a similar way as the secondary connections between the bundles of every third leaf in the shoot with divergence 137.5° .

The thick sprouts on which the leaves are disposed according to the limiting divergence 99.3° are always thicker than those with divergence 137.5° . The number of bundles on the cross section is dependent on the number of internodes in which median, lateral and extreme bundles of particular leaves run. The more bundles are seen on the cross section the thicker the shoot. When the limiting divergence is equal to 99.3° , the bundles are more numerous. The leaves are then, namely, disposed at smaller distances than at the divergence of 137.5° : four leaves on one turn of the spiral instead of three.

II. Longitudinal course of bundles in lateral shoot

On the 54 cm shoots the leaves in the number of 45 are alternately arranged according to the limiting divergence 137.5° (Fig. 2C). The lower 3-year-old segment is about 12 cm long and bears eight leaves. The middle 2-year-old segment is 29 cm long and has 13 still preserved leaves. The upper annual segment is 13 cm long and has 23 leaves, and the zone of elongation is about 6 cm long.

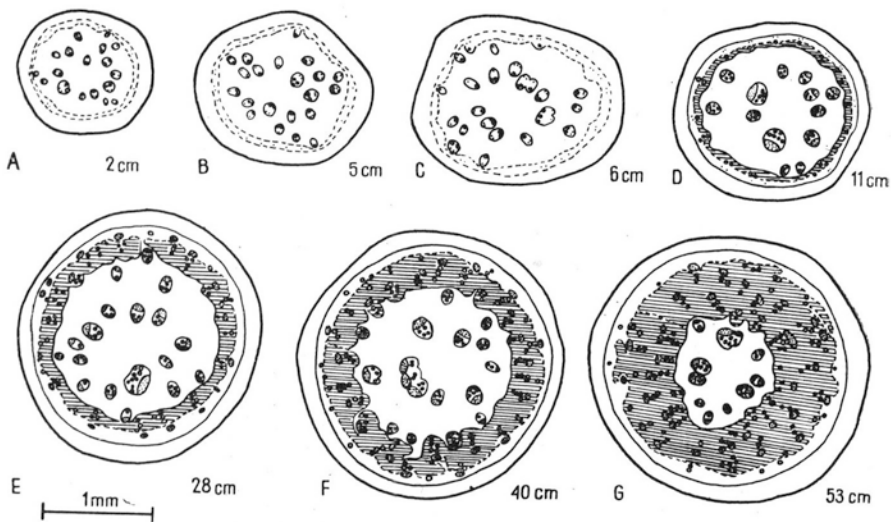


Fig. 7. Cross sections through internodes of lateral shoot. On the right side of each drawing the distance from the tip of the shoot is given in centimetres:

A, B, C, — cross sections in the zone of elongation growth, D, E, F, G — cross sections of parts of stem not growing in length. Notations as in fig. 3

On the cross section through the internodes at any level the bundles situated closest to the centre of the shoot form the inner ring (Fig. 7A–G); they are — similarly as on the thick sprouts — 10–12 in number. The intermediate bundles, particularly those adjacent to the meristematic cylinder are less numerous in the lateral shoot than in the thick shoots. This difference is best visualised in the cross sections below the elongation zone of both types of shoots (Fig. 3E, Fig. 7D).

In 2- and 3-year-old segments of the lateral shoot there are correspondingly two (Fig. 7E) and three (Fig. 7G) irregular circles of bundles embedded in the fibres.

The innermost circle in the 3-year-old part is formed by the lower segments of the bundles which depart to the leaves set in the first year. The next ring is composed of the lower segments of bundles departing to the leaves set in the second year. The outermost bundles which adhere to the cylinder of meristematic tissue are the lower segments of these bundles prolonged to the youngest leaves set in the third year.

The longitudinal course of the bundles in the entire lateral shoot is shown by the diagrams (Fig. 8) drawn in the same way as for the thick sprouts.

The general principles governing the longitudinal course of the bundles are here the same as in sprouts, and all the differences are only quantitative. In general, in the lateral shoots, bundles of nearer lying

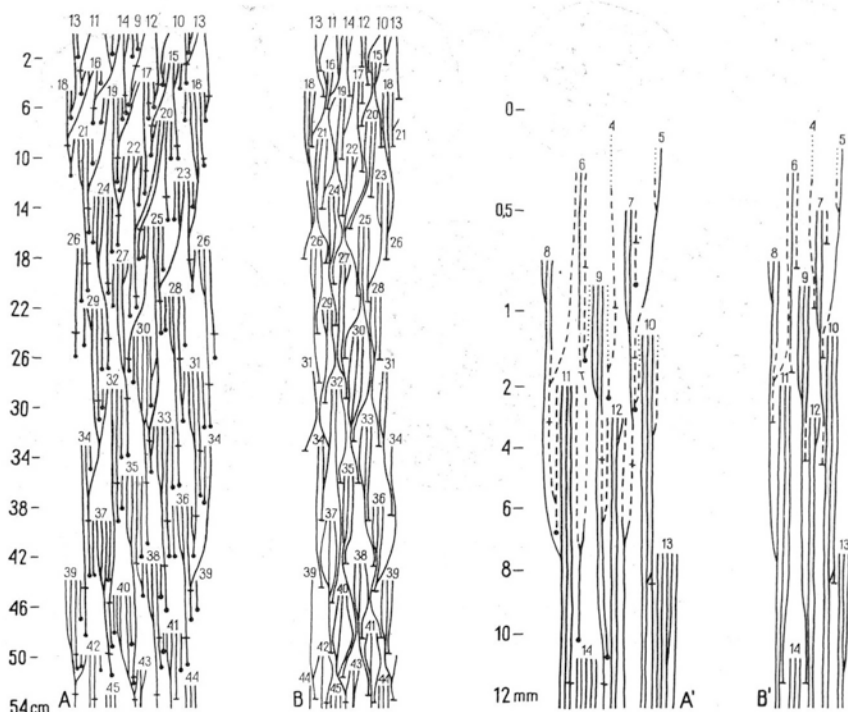


Fig. 8. Diagrams of longitudinal course of bundles in sprout shoot with limiting divergence 137.5° . Notations as in fig. 5

leaves unite than in the thick shoots with the same divergence of 137.5° . From the left side of the ontogenetic spiral the bundles of every third leaf unite; for instance the left extreme bundle of leaf 38 is connected with the right lateral bundle of leaf 35, and the left lateral bundle of leaf 32 joins the median of leaf 29 and so on (Fig. 8A). In this shoot, however, the bundles of every 8th leaf never unite. From the right side of the ontogenetic spiral the bundles are connected every two or five leaves. Thus, the right lateral bundle of leaf 21 is united with the left lateral one of leaf 19, and the right lateral bundle of leaf 23 joins the median of leaf 18. Sometimes the bundles of the same leaf are connected with those of leaves younger by 2 and 5 plastochrons. For instance the right lateral bundle of leaf 36 is united with the left lateral bundle of leaf 34, and the right extreme bundle of the same leaf joins the median of leaf 31.

A characteristic feature of the longitudinal course of bundles forming the inner ring are secondary connections between the bundles of every third and every second leaf (Fig. 8B).

In each node, usually two intermediate bundles are included into the inner ring: one on its right and the other on its left side. The bundle incorporated into the inner ring on the right side of node n runs to the

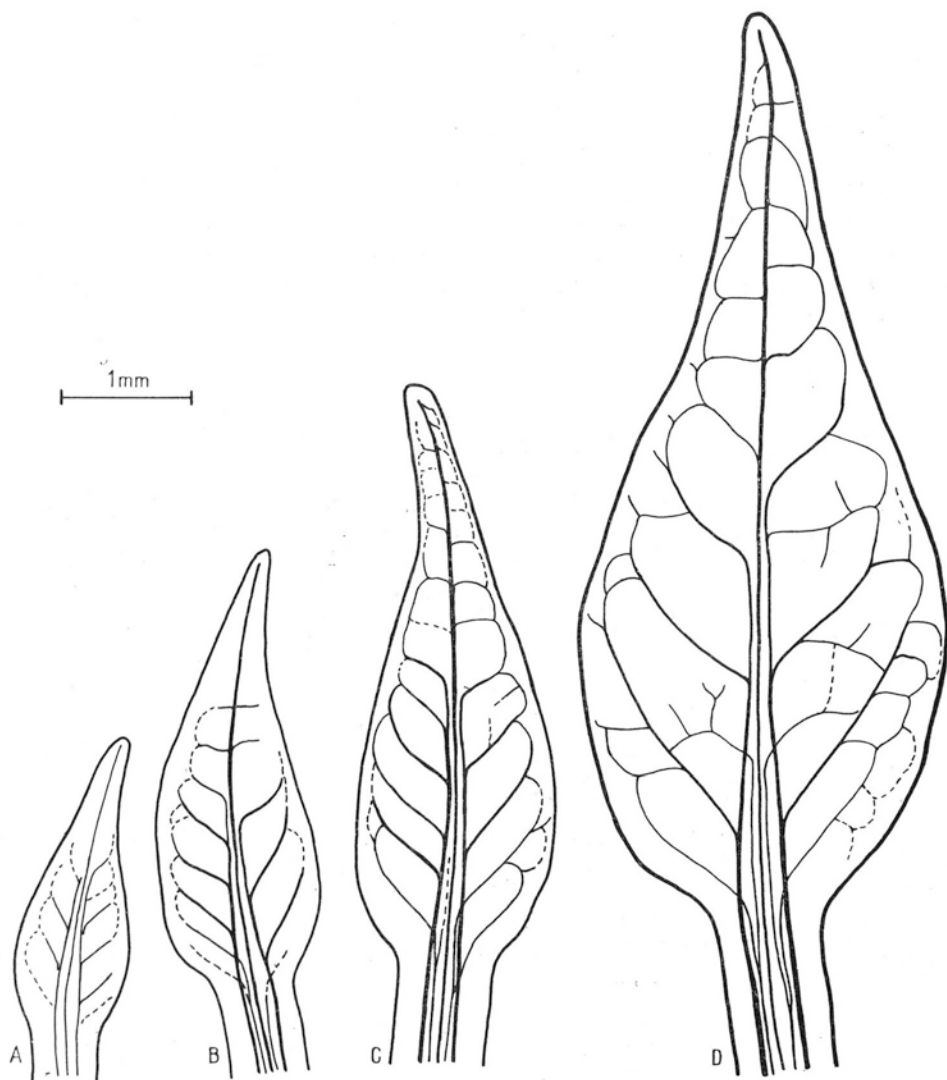


Fig. 9. Development of lateral veins in leaves. The continuous line represents the nerves in which conducting elements of phloem and xylem are differentiated, interrupted line denotes veins in which there are as yet no xylem elements

n-5 leaf and unites with the bundles of leaf n-2. For instance in node 38, with the bundles of leaf 36 the median of leaf 33 is connected. In the same or a similar way the bundles of every 3rd leaf are secondarily united in the whole stem. On the other hand, the bundle which is included into the inner ring on the left side of node n runs to leaf n-3, usually as its right lateral bundle; for instance the right lateral bundle of leaf 35. Sometimes this bundle is connected with the bundles of the n-5 leaf. Thus,

Plate I

Course of bundles in axis of an adult leaf. Cross sections through axis (A—K') and drawing of whole leaf with levels shown to which the cross sections correspond. The cross sections with primes refer to the levels between those denoted by letters without primes

Plate II and Plate III

Fragments of cross section through peripheral part of young elongating thick sprout. Bundle differentiation in cylinder of meristematic tissue; II A — at 0.7 mm, II B — 1.2 mm, II C — 1.8 mm, II D — 2.1 mm, II E — 3 mm; III A — 0.7 mm, III B 3 mm distance from tip.

Plates II A and III A, II E and III B show the same fragments. Magnification: Pl. II $\times 230$, Pl. III $\times 570$

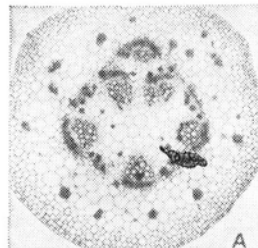
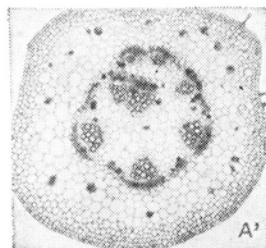
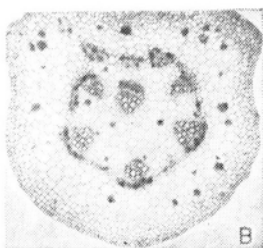
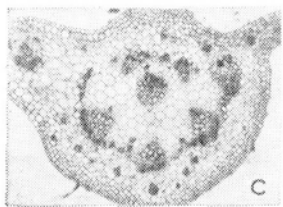
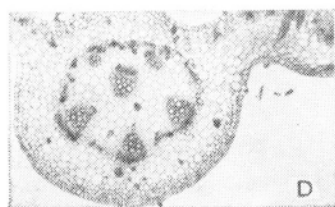
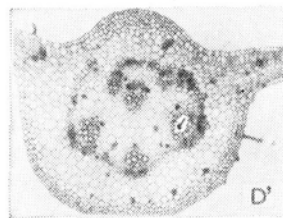
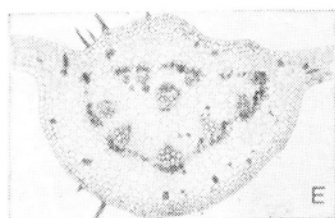
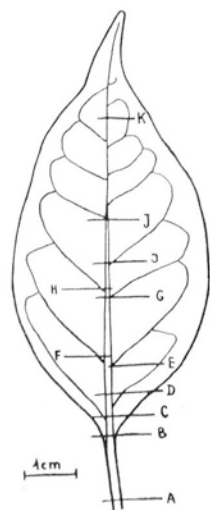
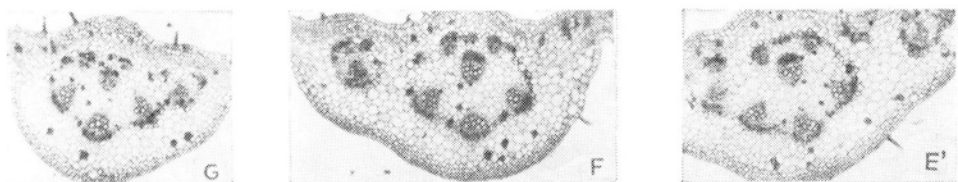
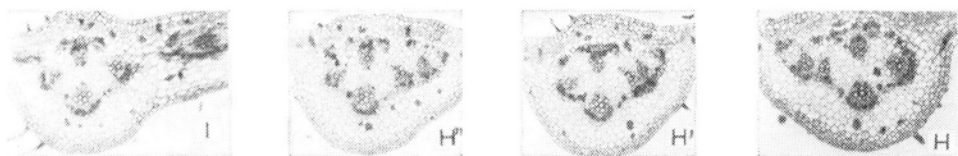
Plate IV and Plate V

Fragments of cross section through peripheral parts of thin shoot at the border of the zone of elongation growth and below. Differentiation of bundles in meristematic zone; IV A — 4 cm, IV B — 6 cm, IV C — 8 cm, IV D — 10 cm, V A — 6 cm, V B and C — 8 cm, V D and E — 10 cm, V F — 12 cm below tip: IV B and V A, IV C and V B and C and IV D and V D present the same fragments. Magnification: Pl. IV $\times 230$, Pl. V $\times 570$

Plate VI

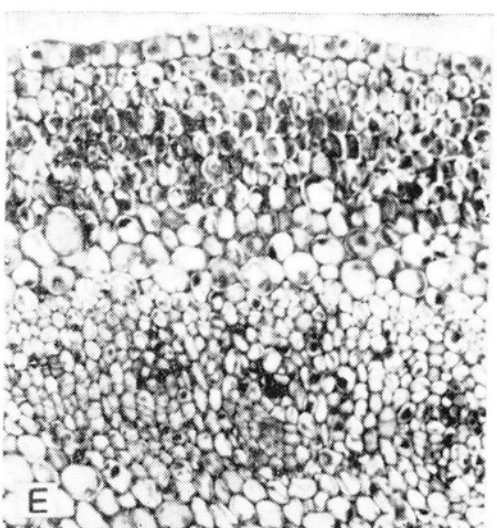
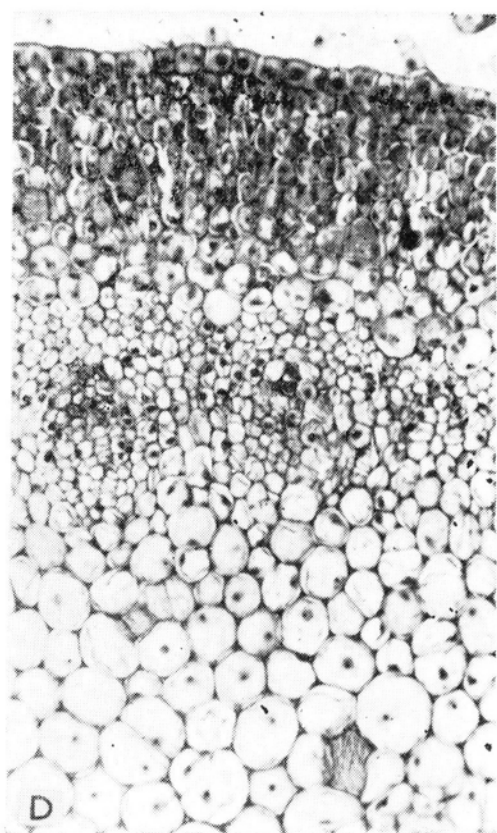
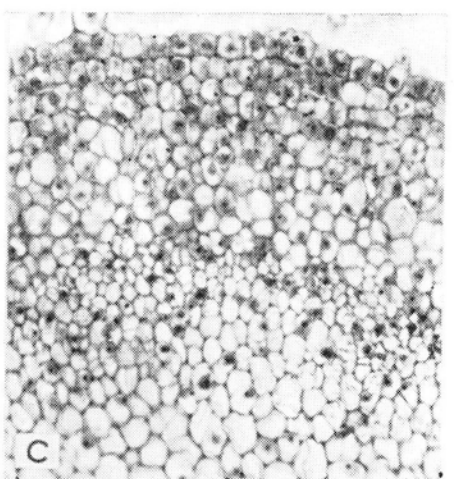
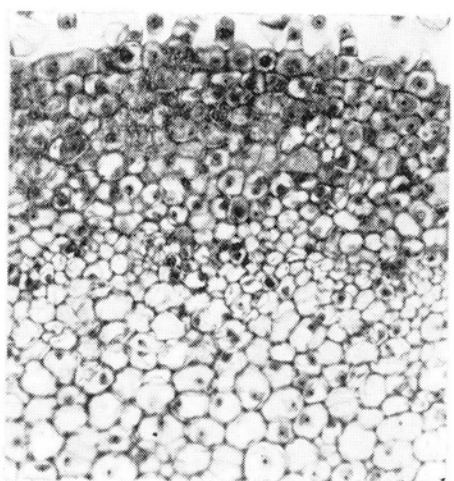
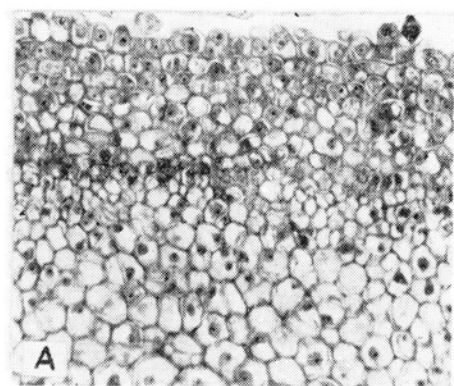
Differentiation of inner ring bundles. Cross section through inner ring bundles at various levels of elongating sprout: VIII A — 0.07 cm, VIII B — 0.1 cm, VIII C — 10 cm, VIII D — 18 cm below tip

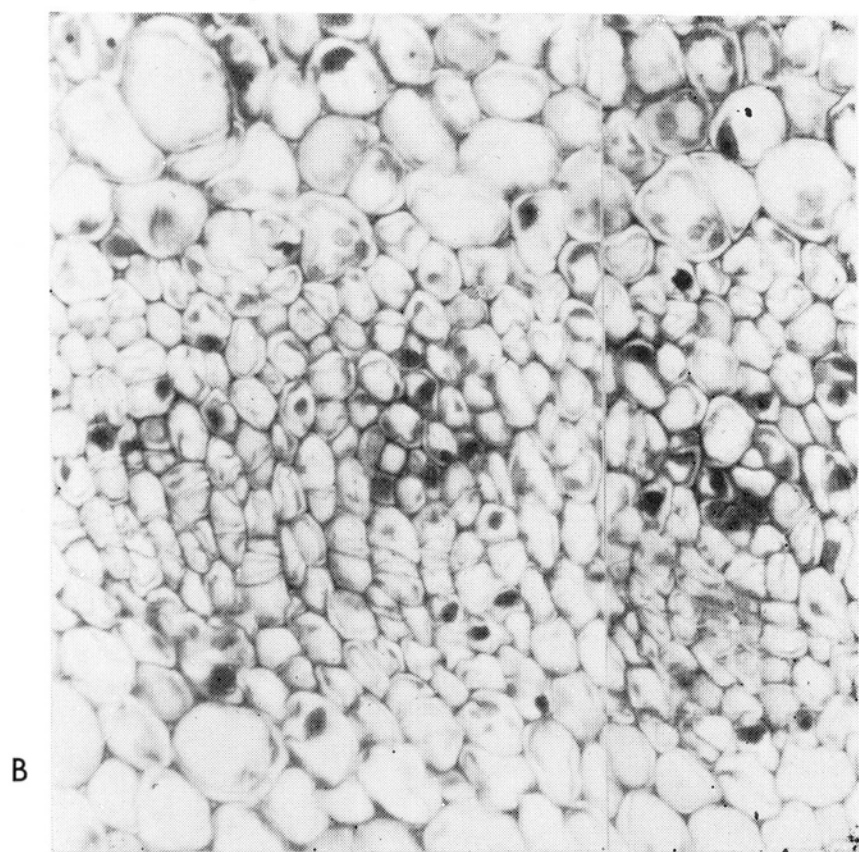
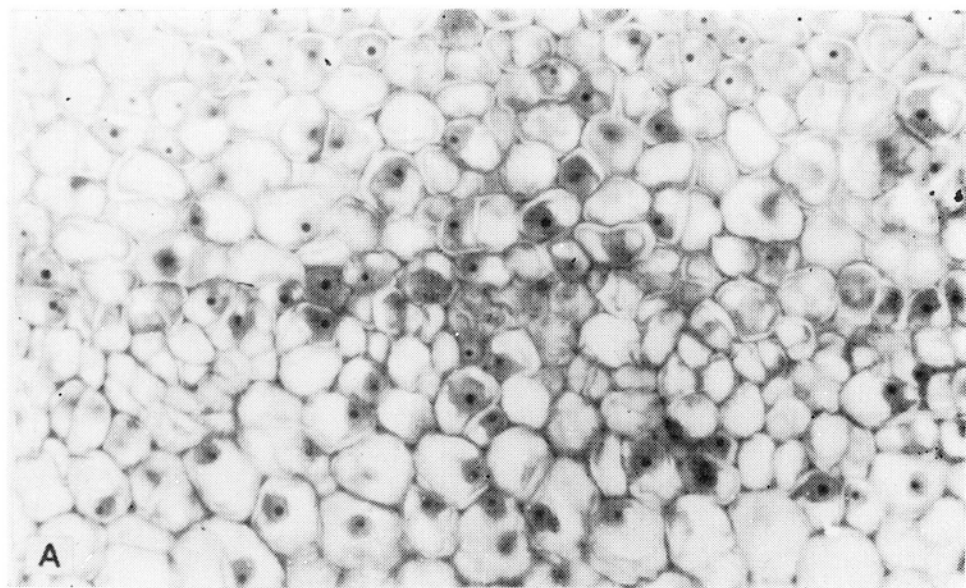
Plate I

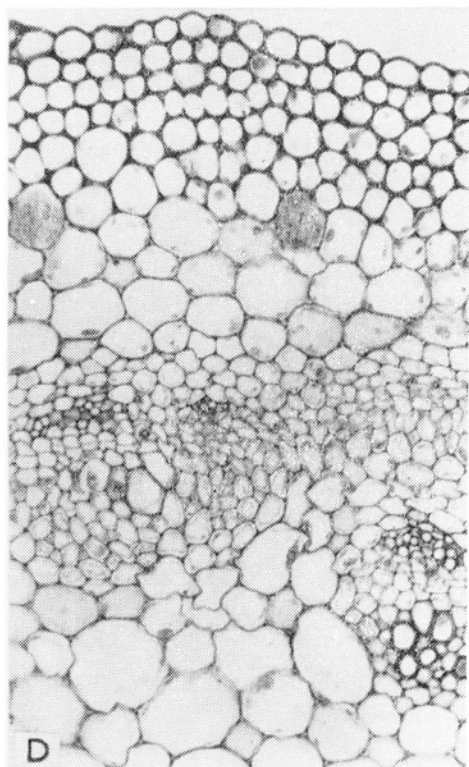
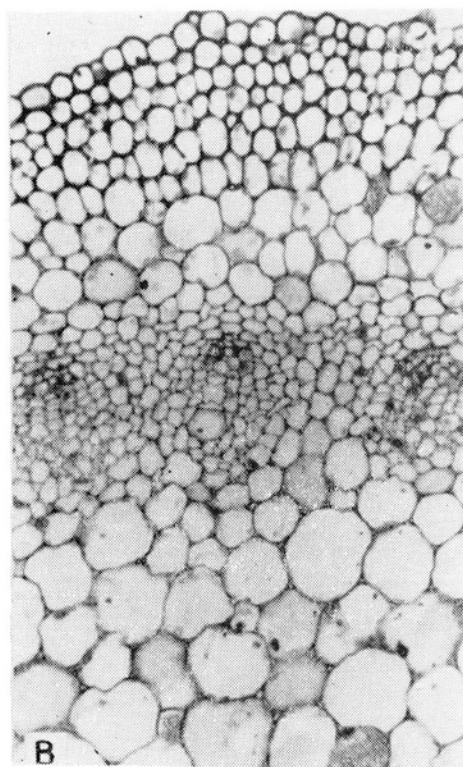
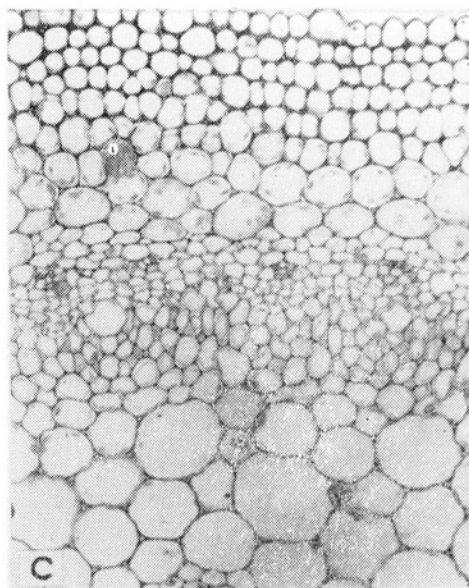
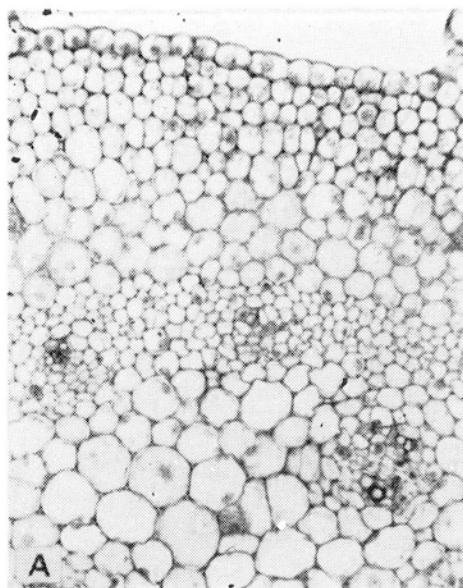


1mm

Plate II







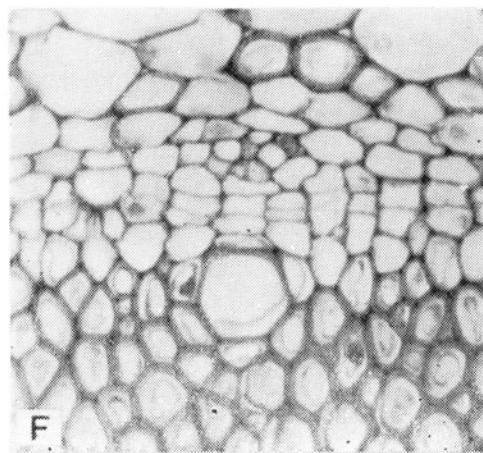
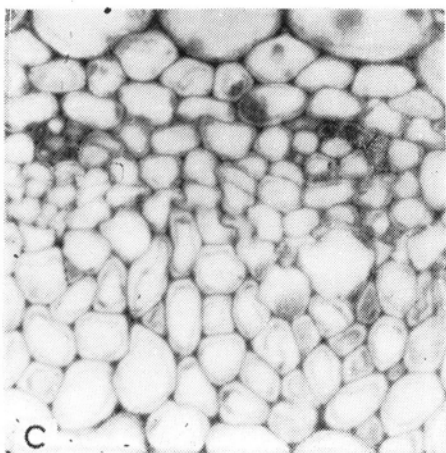
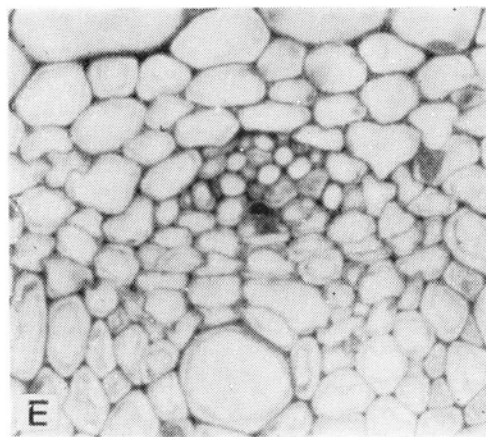
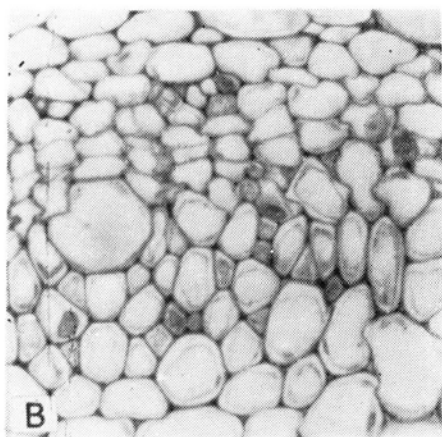
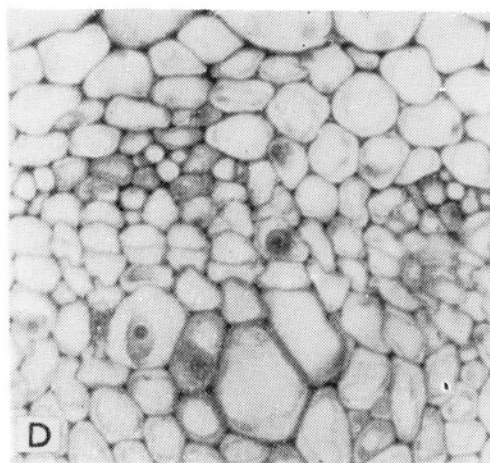
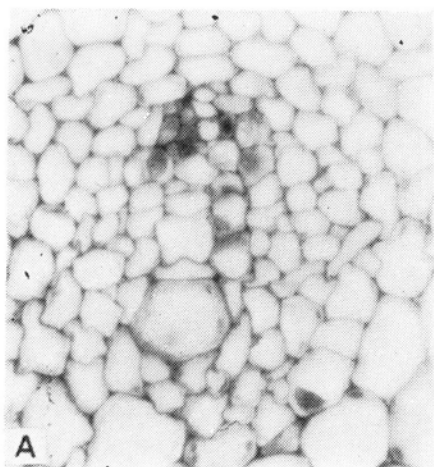
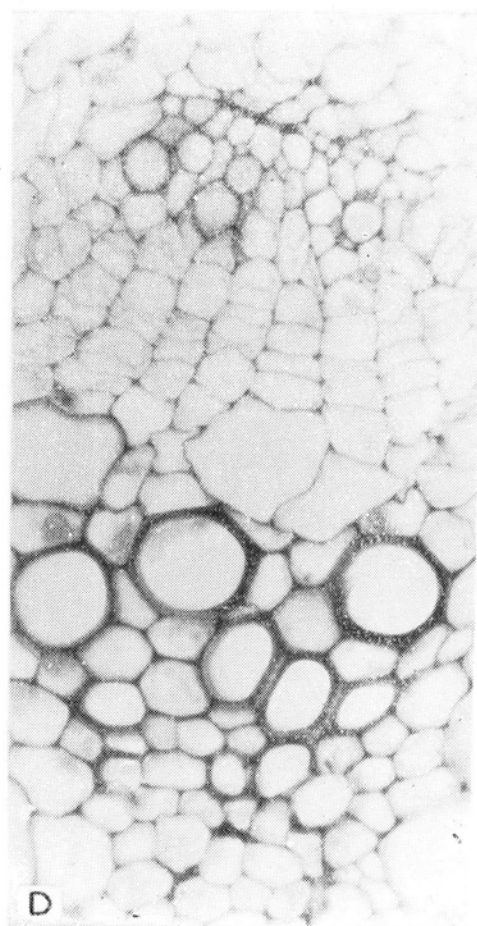
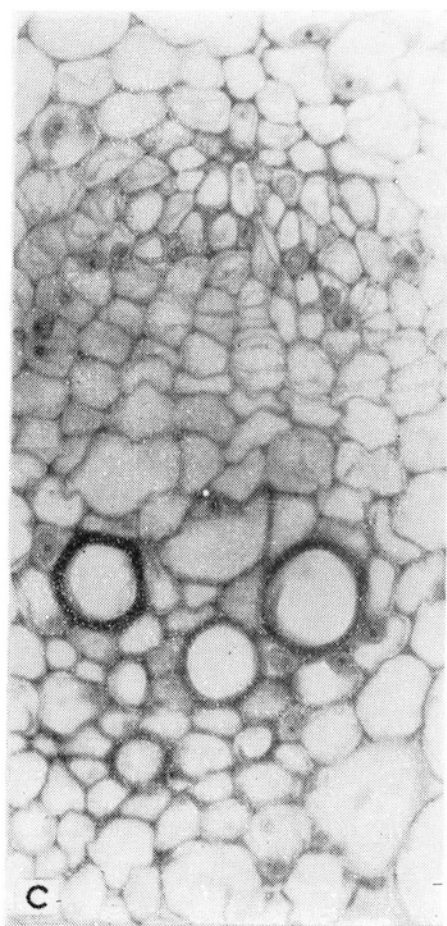
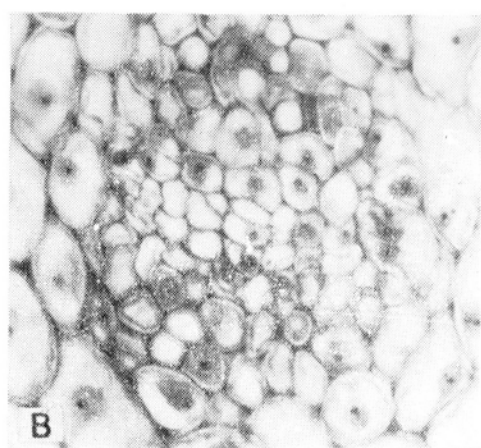
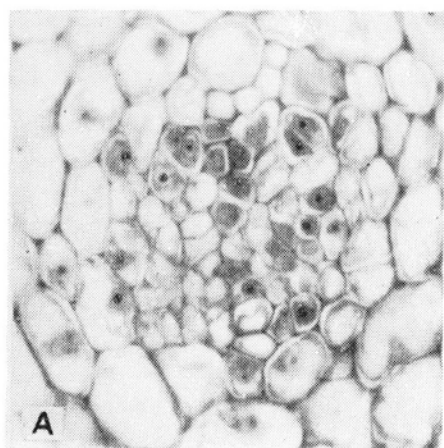


Plate VI



the right lateral bundle of leaf 38 joins the bundles of leaf 36. In this way the bundles of every second leaf are secondarily connected.

The general principles of the longitudinal course of the bundles in the apical parts of four other lateral shoots, examined in detail were the same. In the thinnest shoots the bundles of the nearest leaves unite, thus the bundles of every 2nd or 3rd leaf.

The lateral shoots are always thinner than the sprouts. The differences in shoot thickness run parallelly with those in the quantitative characteristics of the longitudinal course of bundles. In the lateral shoots the bundles of the leaves pass through a smaller number of internodes than in the thick sprouts. Therefore, in the lateral shoots the total number of bundles on the cross sections is smaller than in the thick sprouts, and when the bundles are less numerous the shoots are thinner.

III. Course of bundles in the axis of the adult leaf

Each of the lateral bundles passing from the stem to the leaf divides in two. Just above the base of the petiole all the bundles are arranged as follows: the median bundle runs on the lower side of the petiole, and on its sides one part of the left and right lateral bundle. On the upper side of the petiole the bundles departing from the lateral ones pass and also undergo division. On their outer side lie the extreme bundles united into one (Pl. I, phot. A).

The median bundle does not change along the leaf axis up to its upper part; here it is joined by the lateral veins of this part of the blade (Pl. I, photos J, K). The tissues separating from the lateral petiolar bundles run to the major lateral veins of the lower and middle part of the blade (Pl. I, photos E, F). The extreme bundles are connected with the vein network in the region between the neighbouring lateral veins. They depart from the leaf axis together with the lateral veins and separate from them in the blade (Pl. I, photos E, F) or less frequently they depart running to the blade independently of its major lateral veins.

The course and differentiation of the bundles in several young leaves are shown in fig. 9.

The development of vascular system

The bundles in the lower part of their course differentiate in the meristematic cylinder, and in their upper part they run at a distance from the meristematic cylinder and differentiate in the subapical region of the stem from the procambium.

Longitudinal acropetal differentiation of the procambium occurs in the subapical part of the stem. This procambium differentiated from cells deriving from the apical meristem. In the lower part of the shoot where

the radial and lateral extension of the bundles occurs, the number of procambial cells increases by division of the already existing ones. The lateral expansion of the bundles leads to the formation of new bundles from the older ones. The procambium of the new bundle separates, namely, from the side of the older one and differentiates acropetally. For instance in the thick sprout with 137.5° divergence (Fig. 5A), both extreme bundles of leaf 13 are procambial and separate from bundles in which the first elements of protophloem have differentiated. We find an illustration of a similar situation in the sprout with 99.3° divergence (Fig. 6A) in the left extreme bundle of leaf 20, and in the lateral shoot (Fig. 8A) both extreme bundles of leaf 9. It is characteristic that the procambium of the extreme youngest bundles of the given leaf most frequently separates from the older, protophloem containing bundles of another younger leaf.

In the particular bundles the protophloem begins to differentiate first and is followed by the protoxylem. There are numerous bundles in all shoots in which only protophloem is present (Figs. 5, 6, 8). The process of differentiation of the first elements of protophloem passes from older to younger bundles, and runs acropetally.

Differentiation of the first protoxylem elements also passes from the older bundles to the younger ones and occurs acropetally. In the apical part of the stem, in the bundles isolated protoxylem elements appear, moreover, in the leaf or in the stem below the base of the corresponding leaf, and they differentiate thereafter acropetally and basipetally. In one lateral shoot (Fig. 8A') in the upper segment of the median bundle of leaf 6, the protoxylem is isolated, the middle segment has only protophloem, and the lower segment has acropetally differentiating protoxylem. An illustration of similar situation in a thick sprout is the right lateral bundle of leaf 10 (Fig. 5A).

The particular bundles show extension growth mainly in radial direction and grow but little to the sides (Pl. VI, photos A–D). In the bundles of the inner ring the oldest protophloem and protoxylem elements at the border of the zone of elongation are crushed (Pl. VI, photo D). The meristematic cells between the phloem and xylem show a regular radial pattern already in the elongating parts of the stem (Pl. VI, photos C, D).

On the cross section through thick sprout the meristematic cylinder is distinguishable at a distance of 700–800 μ below the shoot apex (Pl. II, photo A, Pl. III, photo A). Lower, 2–3 mm below the apex, bundles are adjacent to the cylinder of meristematic tissue. The youngest of them are not yet distinctly separated from the meristematic zone, but only form a distinct group of cells in it (Pl. II, photos D, E, Pl. III, photo B). In these bundles only the first sieve elements are differentiated, while the conducting xylem elements are absent.

When the stem ceases to elongate, metaphloem (sieve-tube members and companion cells) and metaxylem elements differentiate in the bundles adjacent to the meristematic cylinder. The metaxylem elements are in these bundles the first conducting elements (Pl. IV, photos *B, C, D*; Pl. V, photos *A–F*). Protoxylem elements are differentiated in older bundles further removed from the meristematic cylinder (Pl. IV, photo *D*). Between the bundles adjacent to the meristematic zone fibres begin to differentiate so that a ring of fibres is formed with the bundles embedded in it (Pl. IV, photos *C, D*; Pl. V, photo *F*). Simultaneously, a single layer of fibers begins to differentiate on the extern border of the meristematic cylinder (Pl. IV, photos *C, D*; Pl. V, photo *F*).

Coordination of leaf and stem development

If we superpose two cross sections through the stem from different levels but analogous sites, one can indirectly conclude on the basis of the relations between the inner bundle rings and the meristematic cylinder on these two sections how the primary increase in thickness of the stem occurs (Fig. 10, *A, B*). In fig. 10 *A* both the cross sections from the older and the younger part of the thick sprout are separated by a segment of about 2 cm, in fig. 10 *B* they are distant by about 1 mm. On the cross section of the older part of the stem the bundles forming the inner ring are slightly shifted more outwards as compared with analogous bundles on cross sections of the young part of the stem. The distance however, of the cylinder of meristematic tissue from the inner ring of bundles increases. It results therefrom that the centre of the stem increases in diameter but minimally, whereas the peripheral parts expand.

In the lateral shoots the circumference of the shoot increases less, and the distance of the inner ring of bundles from the meristematic zone is small.

In thick sprouts a larger number of leaves grow simultaneously than on the lateral shoots. In connection with this a larger number of bundles arises and differentiates simultaneously in the former than in the latter. Owing to this the circumference of the sprouts increases more under the influence of the larger number of leaves than it does in the lateral shoots.

The circumference of this shoot is composed of sectors belonging to different-aged leaves. Therefore the periphery of the shoot increases at a given time nonuniformly, in some parts more and in others less.

If we superpose drawings of the cross section through the bases of three successive leaves from the thick sprout preserving their natural position, the nonuniform increase of the stem in diameter will be visualised (Fig. 10 *C*).

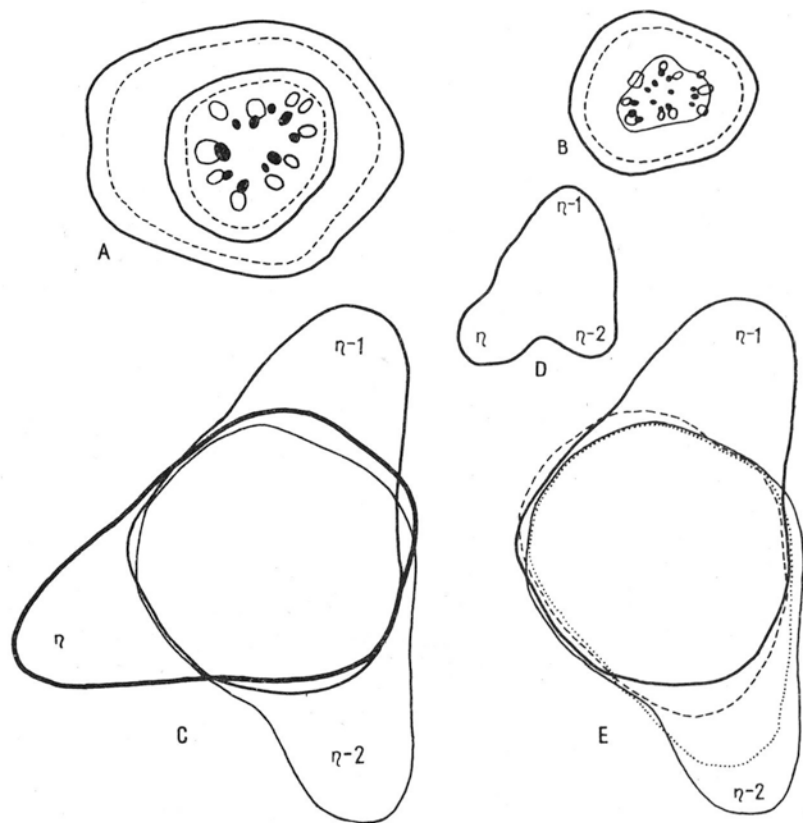


Fig. 10. Primary thickening of stem:

A, B — cross sections from analogous sites on older and younger parts of shoots superposed. In fig. A both cross sections 2 cm and in fig. B 1 mm distant from one another. The bundles from younger parts of stem are darker. C — cross sections through the bases of three successive leaves, n, n-1 and n-2 are superposed. The base of leaf n is ca. 3 mm distant from the base of leaf n-1 and the base of leaf n-1 ca. 5 mm distant from the base of leaf n-2. The base of leaf n is ca. 18 mm below the tip, D — cross section through stem ca. 1 mm below tip, E superposed cross sections through bases of two successive leaves and the internode between them

The outline obtained from the superposed cross sections, through the bases of three successive leaves in the older part of the shoot is very similar to a single cross section from a younger part of the shoot (Fig. 10D). The convexities below the bases of three successive leaves lying close to one another meet here, namely, at the same level. Therefore, in the youngest part, the outline of the shoot circumference is irregular on all cross sections. On the other hand, in older parts of the shoot there is a convexity only below the base of the nearest leaf, and the convexities below the bases of several successive leaves do not meet at the same level (Fig. 10E). This is probably due to the fact that, firstly, during elongation

growth of the stem the most convex earlier expanded sectors below the older leaves grow less intensively at later periods than the sectors below younger leaves between them, and, secondly, each sector ceases to grow acropetally and expands longest below the base of each leaf. Owing to this, in the older parts of the shoot the internodes are, at least at the base less or more rounded. The older the shoot part the longer segment of the given internode is rounded.

DISCUSSION

A. Construction of the vascular system in shoots of *Bougainvillea glabra* Choisy and other members of *Nyctaginaceae*

In the annual shoots of *Bougainvillea glabra* Choisy collateral bundles are scattered in the parenchymatous tissue within the cylinder of meristematic tissue. The oldest ones are close to the centre of the shoot forming the inner ring. The youngest bundles lie close to the meristematic zone or are embedded in it and form the peripheral ring. Between the inner and the peripheral ring the intermediate bundles are disposed.

In each node three bundles excluded from the inner ring depart to a leaf: a median one and two lateral ones. Each lateral bundle is, besides, joined to an intermediate one. These are the extreme bundles of the leaf which never are incorporated into the inner ring. The remaining bundles of the leaf, or those from which they arise run below as peripheral bundles, then as intermediate ones, finally to be included into the inner ring from which they depart to the leaf.

The particular bundles may separate at a definite point of their longitudinal course into two new ones. The bundles arising by this separation either belong to the same leaf or to two different ones. In this way primary connections arise between the bundles of the same leaf and the bundles of different leaves. The bundles of one leaf unite with those of other leaves both from the left or from the right side of the ontogenetic spiral. The bundles of each leaf are connected mostly with those of two other leaves generally in the lower and middle segments of their longitudinal course, thus, beyond the inner ring. In this way a closed system of primary connections between the bundles, determined by the limiting divergence of leaves arises.

One or two intermediate bundles which are incorporated in each node into the inner ring usually unite with each other and also with a definite bundle of the inner ring. These united bundles separate higher and run to definite leaves. In shoots with a 137.5° divergence the bundles are

connected secondarily every three leaves, and in the shoots with a 99.3° divergence every four leaves.

Balfour and Philipson (1962) described the development and arrangement of bundles in a $400\text{-}\mu$ segment of the subapical part of a *Bougainvillea spectabilis* Willd. shoot. They established a classification of the vascular systems of dicotyledones and included the system of *Bougainvillea* into what they called the modified open type. Such an open system is composed of independent not interconnected series of bundles — sympodia. Since in the shoot here the bundles of every third leaf unite, there arise three independent sympodia.

The above named authors classified the system of *Bougainvillea* to the open type taking into account only the upper segments of the longitudinal course of bundles. This was because they investigated the development and arrangement of the bundles in the too short apical part of the shoot.

The vascular system in shoots of other representatives of *Nyctaginaceae* examined is similar to that in *Bougainvillea*. Inouye (1956) described the course of bundles in the shoots of *Mirabilis jalapa* L. Here too the three main bundles are joined from outside by additional (extreme) ones. Pant and Mehra (1961) described the anatomy of the node of a adult stem shoot of *Boerhaavia*. Its similarity with the structure of the *Bougainvillea* shoot concerns all characteristics.

B. The development of vascular system

1. Role of the meristematic cylinder in the development of bundles. Interconnections of primary and secondary tissues along the stem and in relation to the leaf to which they belong

In studies concerning the anatomical structure of shoots in representatives of *Nyctaginaceae*, the view prevails that only the inner-ring bundles are of primary origin, and all the others situated outside this ring are secondarily derived. Only Inouye (1956) demonstrated on the example of *Mirabilis jalapa* L. that the peripheral bundles are of primary origin. On the other hand, Balfour (1962), and Esau and Chandle (1969) assume that in *Bougainvillea* the cylinder of meristematic tissue is active only in older, secondarily thickening shoots, and that it arises independently of the primary bundles and outside them.

It results from the present study that the lower segments of the bundles differentiate in the meristematic zone, and the upper segments of the same bundles run at a distance from this zone and differentiate in the subapical part from procambium. When the upper segments of given bundles are in the growing parts of the stem, their lower segments lie in the parts not subject to elongation. In this connection, in the lower

segments elements typical for secondary tissues, metaphloem and metaxylem differentiate simultaneously in the middle segments, and so do protophloem, protoxylem and procambium in the upper segments.

Such interconnections of primary and secondary tissues along the stem are quite similar to the observations of Thoday (1922). This author described the successive phases of primary and secondary differentiation of the vascular system in the stems of *Heliantus*. In this plant there are three traces and the node is trilacunar. In the stem all the bundles are arranged circularly. At every level can be distinguished median and lateral bundles, which have still preserved their separateness and synthetic bundles resulting from the running together and union of median and lateral bundles of definite leaves. In the parts of the stem showing secondary growth, fascicular and interfascicular cambium is differentiated. The activity of the cambium is not uniform on the entire periphery, this finding its expression in that at the same level some bundles exhibit large quantities of secondary xylem, while others have none. The synthetic bundles may be composed of secondary xylem exclusively or contain it in large quantities, and the median and lateral bundles which still are independent contain much less of it, or contain exclusively primary xylem. The higher the leaf is situated in relation to the level considered the more secondary xylem is contained in the bundle belonging to it. At the base of a full grown stem, the complexes consisting of the union of bundles of the highest situated leaves contain exclusively secondary xylem, and the middle and lateral bundles of the lowest situated leaves exclusively primary xylem.

Similar interconnections of primary and secondary xylem have been described by Col (1904) on the example of *Phyteuma hemisphericum* Hill.

Balfour and Philipson (1962) described in the shoot of *Casuarina* two rings of bundles. Each bundle after separating from an older one runs through one internode in the inner ring and through higher one in the extern ring. The lower part of each bundle is the site of initiation of secondary growth, and the upper part does not take part in this process. The same investigations report that in *Phytolacca dioica* L., the median bundle runs down from the leaf through about six internodes as the medullary bundle and only then runs outside in a normal ring of bundles. In this way a medullary ring is formed composed of median bundles and an inner ring of lateral bundles and lower segments of median bundles. The cambium is active only in the inner ring.

Numerous authors found that in woody forms of dicotyledones primary xylem does not differentiate in the lower parts of the particular bundles in the period of shoot elongation (Esau, 1945; Ball 1949; Sloover, 1958; Benzing, 1967). These are probably the parts of the

bundles in which cambium begins to function earliest, and it is the secondary xylem that forms the missing link between the xylem of the particular bundles.

In monocotyledones, analogously, the lower segments of the bundles contain exclusively metaxylem, and the upper segments of the same bundles exhibit both protoxylem and metaxylem. The higher up the stem and the closer to the leaf the more protoxylem is found in the bundle (Prionium, Zimmerman and Tomlinson, 1968).

It results from the here described examples that in dicotyledones, both with a normal vascular system (e.g. *Helianthus*, *Phyteuma*) and with an atypical vascular system in various varieties (*Bougainvillea*, *Casuarina*, *Phytolacca*), in woody as well as in herbaceous plants, secondary tissues form in the lower segments of the particular bundles, whereas the upper segments of the same bundles are deprived of these tissues.

In dicotyledones with an anomalous vascular system this regularity is particularly pronounced, since the upper segments of the bundles run beyond the site where secondary tissues arise.

2. Limited expansion of bundles

In *Bougainvillea* the bundles expand mainly radially, whereas laterally they grow but little. In dicotyledones with a limited secondary growth the bundles separate from one another and are isolated by parenchymatous tissue like in *Bougainvillea*, but on their whole length they run next to one another, thus, differently than in this plant. In dicotyledones with a marked secondary growth, the bundles do not separate but adhere to one another by their sides, and then their expansion to the sides and radially is unlimited owing to the meristematic tissue contained between phloem and xylem.

The bundles in *Bougainvillea* have a limited growth and are scattered in the parenchymatous tissue. Therefore the meristematic tissue capable of renewed divisions is localised independently of the already existing bundles. It lies outside from them in the form of a peripheral cylinder. A further consequence of this is a different than in most dicotyledones and in all gymnosperms mode of secondary thickening. The secondary vascular tissues arise, namely in the form of bundles. Therefore in older shoots the number of bundles increases internally to the meristematic cylinder.

In the bundles of *Bougainvillea* the parenchyma cells are scarce as in monocotyledonous plants. In dicotyledones with a normal vascular system, on the other hand, particularly in the woody forms, parenchyma cells are numerous in the bundles between the primary conducting elements both in the phloem and the xylem.

Can this small number of parenchyma cells be the factor limiting expansion of the bundles? The hypothesis of Sheldrake and Northcote (1968) concerning the origin of auxins suggests an interesting answer to this question.

In cut and explanted *Nicotiana* internodes, auxin production continues. Their presence is indicated by the callus forming on more and more cut surfaces through the morphologically lower end of the internode. Sheldrake and Northcote (1968) demonstrated that there exists a direct relation between auxin production and the formation of callus, and the activity of cambium and xylem differentiation. They advanced the suggestion that the differentiating xylem in the internode is the source of auxins or their precursors. If cambium is active in the cut off internodes, new auxins form from the decomposed cellular content of the differentiating xylem elements. Part of them is transported down the internode producing callus on the cut surface, while the rest remains in the internode stimulating cambial activity and xylem differentiation. Owing to this differentiation new auxins arise and in this way both these processes automatically regulate and maintain themselves.

If this hypothesis is correct, both the differentiating fibres and the conducting elements of xylem are the source of auxins. If, however, the auxin precursors formed owing to the differentiation of the conducting elements of xylem are at the same time utilised in them and transported to other parts of the plant, then what happens with the auxins which form owing to fibre differentiation? It is possible that they pass to living cells and stimulate their divisions. When the fibres in the bundles do not differentiate, and the parenchyma cells are scarce and irregularly distributed, the auxin precursors are transported to the sites of the same bundle which are in different stages of differentiation. In this case, the auxins would be utilised mainly for differentiation of the bundles in longitudinal direction, and less for extension growth of the bundles laterally or radially.

The limited growth of the bundles, particularly laterally, is perhaps an essential trait of *Bougainvillea* shoots distinguishing this genus and similar ones with an atypical secondary growth from most dicotyledones with a normal primary structure and typical secondary growth. This is an essential and fundamental difference associated with: atypical for dicotyledones distribution of the bundles, the presence of a cylinder of meristematic tissue surrounding all the vascular bundles existing at the given time and atypical secondary growth. All or some of these characteristics occur in monocotyledones in which the bundles also have a limited growth. The organisation and development of the vascular system in the shoots of some monocotyledones e.g. *Prionium* (Zimmermann and Tomlinson, 1968) has many traits in common with the system of *Bougainvillea*. The lack of similarity as regards all these

characteristics with many other monocotyledones, is, maybe, connected with the different mode of elongation and growth in thickness of the *Bougainvillaea* shoots on the one hand, and the stems of monocotyledones with intercalary meristem on the other.

The above quoted suggestions are attractive since they stress the common features of the organisation and development of the vascular system in plants in general. The general regularities of the development of bundles — the basic units of the vascular system — are attained in particular plants in different systems, therefore the final form of this system is not uniform. Any biological variability, namely, is based on what is invariable.

C. Coordination of leaves and stem development

On the basis of the restricted but spectacular experimental studies it may be affirmed with certitude that the development of the stem and of the leaves are closely coordinated.

It is probable that in these interrelations the vascular system plays an essential role.

When a young not fully developed leaf is removed, the growth of a certain segment of the stem below this leaf is inhibited. The limitation of growth is the more pronounced the younger the leaf in question. Experiments of this kind were carried out mainly on plants with decussate phyllotaxis (sunflower seedlings — Wetmore and Garrison, 1966; *Coleus* — Jacobs and Bullwinkel, 1953). In such phyllotaxis only one internode was inhibited in growth below the pair of removed leaves. On this basis Wetmore and Garrison (1966) consider that the leaf and the internode below it constitute a physiological growth unit. Probably, however, even in plants with decussate leaf arrangement, this unit does not always comprise only one internode. Proof of this may be found in the studies of Wangermann (1967). This author described the influence of leaf removal on the differentiation of primary xylem in the shoots of *Coleus*. She removed one of the pair of youngest leaves exposed in the bud. For the first 10 days after its removal, new vessels did not appear in the internode beneath this leaf. At the same time number of vessels below the control leaf doubled. New vessels differentiate below the removed leaf between the 11th and 22nd day. Their differentiation, however, is influenced by the leaf of the younger pair which develops above the removed one. The influence of a leaf, therefore does not extend to one, but to two internodes beneath it. This is due to the fact that in *Coleus* the bundles of each leaf run down the shoot through two internodes and then unite with others and lose their individuality.

It would seem, therefore that the physiological growth unit is the

leaf and a segment of the stem below it difficult to define, which even in plants with decussate phyllotaxis does not always correspond to one internode as Wetmore and Garrison believed. In plants with spiral phyllotaxy, however, one internode is never such a growth unit. As proof of this may serve the experiments on *Gleditschia triacanthos* (Neville 1961). They consisted in that a very young leaf primordium (100—300 μ) was destroyed in the seedling bud. On the grown seedling, the scar lay lower than the base of the leaf older than the one removed.

If in some plants one internode is included in the growth unit, it is not because it is the segment between the bases of two successive leaves, or between the bases of two successive leaf pairs, or else between two successive leaf whorls. The growth unit of the stem is probably identical with a repeatable unit of the vascular system in the longitudinal course.

This supposition may be referred to the views of Priestley and Scott (1933). According to these investigators the growth unit in shoots of dicotyledones depends on the phyllotaxy. In $1/2$ phyllotaxy, the stem consists of units occurring along two orthostichis. In connection with this, on the cross section of the shoot at any level two different-sized units can be distinguished: a larger one which is the prolongation of the nearest leaf, and a smaller one — the prolongation of the successive higher lying leaf on the opposite side.

In $1/3$ phyllotaxy three leaf primordia grow simultaneously at the apex. The shoot then consists of substituable units every three internodes along three orthostichis. When the leaves are disposed according to the $2/5$ or higher fractions, the number of growth units increases correspondingly.

Priestley and Scott (1933) considered that the growth units distinguished on the basis of phyllotaxy should find their reflection and confirmation in the anatomical structure, particularly in the vascular bundle arrangement. Thus, the growth units of the stem should correspond to the units of the vascular system. This most probable suggestion was not proved, however, either by its authors or by other investigators owing to the simple reason that, when the phyllotaxy is the same, the arrangement of the bundles may differ, and therefore the growth units of the stem cannot be defined solely on the basis of leaf arrangement. The same phyllotaxy may be associated with several definite modes of bundle union (Pulawsk a, 1965). The growth units of the stem and of the vascular system change with the stem growth rate, whereas phyllotaxy remains the same. On the thick sprouts of *Bougainvillea* more leaves grow simultaneously than on the thinner lateral shoots. Thus in the former bundles from more distant leaves unite than in the latter, in spite of the same limiting divergence.

A change of limiting divergence from 137.5° to 99.3° causes the development of the thickest sprouts.

SUMMARY

The chief result of the present study was the elucidation of the developmental relations between the peripheral cylinder of meristematic tissue and the vascular bundles in the young parts of shoots, and of the relation between these bundles from the young elongating parts of the stem and those formed during secondary thickening in the older parts. The lower segments of the bundles of the leaves differentiate in the meristematic zone, and the upper segments of the same bundles run upwards into its interior and differentiate in the subapical part of the stem from procambium. The middle and upper segments of the bundles which run inside of the meristematic cylinder have exclusively primary tissues, and the lower segments of these bundles have mainly or exclusively secondary tissues. This combination of primary and secondary tissues along the shoot is a general regular characteristic which is particularly pronounced in *Bougainvillea*, since the upper segments of the bundles run beyond the site where secondary tissues arise. The youngest bundles of each leaf have on one side connections with the finest network of the blade veins, and on the other side in the stem they unite with secondary tissues closer to the base of the given leaf than the older ones. This kind of connection is probably a general rule and is justified by physiological reasons.

Lateral extension growth of the bundles is limited. This is probably an essential specific trait associated with: nontypical for most dicotyledones arrangement of the bundles, occurrence of the cylinder of meristematic tissue outside all the bundles and atypical secondary growth.

In the thick fast-growing sprouts bundles of more distant leaves unite than in the thinner slowly-growing lateral shoots with the same leaf arrangement (limiting divergence 137.5°). In connection with this, on the cross sections through sprouts there are more bundles than on the cross section through lateral shoots, and when the bundles are more numerous the stem is thicker. When the leaf arrangement is the same, but the rate of growth of the stem different, the units of vascular system and those of stem growth are correspondingly changed. The changes in the mode of uniting of the bundles are the expression of a close morphological harmonization of the entire shoot, and particularly of its entire vascular system.

The authoress gratefully acknowledges professor Henryk Teleżyński for his helpful comments on the manuscript.

REFERENCES

- Balfour E., 1965, Anomalous secondary thickening in Chenopodiaceae, Nyctaginaceae and Amaranthaceae, *Phytomorphology* 15: 111—122.
- Balfour E. and Philipson W. R., 1962, The development of the primary vascular systems of certain dicotyledons, *Phytomorphology* 12: 110—143.
- Ball E., 1949, The shoot apex and normal plant of *Lupinus albus*, *Amer. Jour. Bot.* 36: 440—454.
- Benzing D. H., 1967, Developmental patterns in stem primary xylem of woody Ranales. I. Species with unilacunar nodes, *Amer. Jour. Bot.* 54: 805—813, II. Species with trilacunar nodes, *Amer. Jour. Bot.* 54: 813—820.
- Col A., 1904, Recherches sur la disposition des faisceaux dans le tige et les feuilles de quelques Dicotyledons, *Ann. Sci. Nat. Bot.* 8 série, 20: 1—285.
- Esau K., 1945, Vascularization of the vegetative shoots of *Helianthus* and *Sambucus*, *Amer. Jour. Bot.* 32: 18—29.

- Esau K. and Cheadle V. I., 1969, Secondary growth in *Bougainvillea*, Ann. Bot., 33: 807—819.
- Inouye R., 1956, Anatomical studies on the vascular system of *Mirabilis jalapa* L., Bot. Mag., 69: 555—559.
- Jacobs W. P. and Bullwinkel B., 1953, Compensatory growth in *Coleus* shoots, Amer. Jour. Bot., 40: 385—392.
- Neville P., 1961, Influence de la feuille à ses premiers stades sur a morphogenèse végétative chez *Gleditschia triacanthos*, Bull. Soc. Bot. Franc., 108: 120—127.
- Pant D. D. and Mehra B., 1961, Nodal anatomy of *Boerhaavia diffusa* L., Phytomorphology 11: 384—405.
- Priestley J. H. and Scott L. I., 1933, Phyllotaxy in the dicotyledons from the standpoint of developmental anatomy, Biol. Rev. 8: 241—268.
- Puławska Z., 1965, Correlations in the development of the leaves and leaf traces in the shoot of *Actinidia arguta* Planch. Acta Soc. Bot. Pol. 34: 697—712.
- Sheldrake A. R. and Northcote D. H., 1968, The production of auxin by tobacco internode tissues, New Phytol. 67: 1—13.
- Sloover J. De, 1958, Le sens longitudinal de la différenciation du procambium, du xylème et du phloème chez *Coleus*, *Ligustrum*, *Anagallis* et *Taxus*, Cellule 59: 55—202.
- Thoday D., 1922, On the organization of growth and differentiation in the stem of the sunflower, Ann. Bot. 36: 489—510.
- Wangermann E., 1967, The effect of the leaf on differentiation of primary xylem in the internode of *Coleus blumei* Benth., New Phytol. 66: 747—754.
- Wetmore R. H., and Garrierson R., 1966, The morphological ontogeny of the leafy shoot, in Trends in plant morphogenesis, London pp. 187—199.
- Zimmermann M. H. and Tomlinson P. B., 1968, Vascular construction and development in the aerial stem of *Prionium* (Juncaceae), Amer. Jour. Bot. 55: 1100—1109.

Ogólne i swoiste cechy organizacji i rozwoju waskularnego systemu w pędach *Bougainvillea glabra* Choisy (Nyctaginaceae)

Streszczenie

Głównym rezultatem niniejszej pracy jest wyjaśnienie jaki jest związek między peryferycznym cylindrem merystematycznej tkanki a rozwojem wiązek w młodych częściach łodyg, oraz w jakiej relacji pozostają wiązki z młodych rosnących na długość części łodygi do wiązek powstających podczas wtórnego grubienia w starszych jej częściach. Dolne odcinki wiązek poszczególnych liści różnicują się w merystematycznym cylindrze, górne zaś odcinki tych samych wiązek biegną do wnętrza od niego i w subapikalnej części łodygi różnicują się z prokambium. Środkowe i górne odcinki wiązek, które biegną do wnętrza od merystematycznego cylindra mają wyłącznie pierwotne tkanki, a dolne odcinki tych samych wiązek mają głównie, lub wyłącznie wtórne tkanki. Tego rodzaju połączenie pierwotnych tkanek z wtórnymi wzdłuż łodygi jest powszechną prawidłowością, która u *Bougainvillea* jest szczególnie wyrazista, ponieważ górne odcinki wiązek biegną poza miejscem powstawania wtórnych tkanek. Najmłodsze wiązki każdego liścia z jednej strony mają połączenie z najdrobniejszą siatką unerwienia blaszki, a z drugiej strony w łodydze łączą się z wtórnymi tkankami najbliższej nasady danego liścia. Tego

rodzaju połączenie jest prawdopodobnie powszechną prawidłowością i jest uzasadnione względami fizjologicznymi.

Rozrost poszczególnych wiązek, zwłaszcza na boki jest ograniczony. Jest to prawdopodobnie zasadnicza swoista cecha, z którą z konieczności współistnieje: nietypowe dla większości dwuliściennych rozmieszczenie wiązek, obecność cylindra merystematycznej tkanki na zewnątrz wszystkich, aktualnie istniejących wiązek, oraz nietypowy wtórny przyrost.

W grubych, szybko rosnących odnawiających pędach łączą się wiązki dalszych sobie — określonych graniczną dywergencją — liści, niż w cieńszych, wolno rosnących bocznych pędach o takim samym rozmieszczeniu liści (graniczna dywergencja $137,5^\circ$). W związku z tym na poprzecznych przekrojach przez roczne odnawiające pędy jest wszystkich wiązek więcej, niż na poprzecznych przekrojach przez roczne boczne pędy. A gdy więcej jest wiązek, grubsza jest również łodyga. Przy takim samym rozmieszczeniu liści, ale niejednakowym tempie wzrostu pędu, niejednakowe są zarówno jednostki układu wiązek, jak i odpowiadające im jednostki wzrostu łodygi. Zmiana w sposobie łączenia się wiązek jest wyrazem ścisłego morfologicznego szarmonizowania całego pędu, a w szczególności całego jego waskularnego systemu.

*Instytut Botaniki Uniwersytetu
Wrocławskiego
Wrocław, Kanonia 6/8, Poland*