

Correlations in the development of the leaves and leaf traces in the shoot of *Actinidia arguta* Planch.

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INTRODUCTION

Several workers have investigated the origin and the organization of primary vascular system in vegetative stems. This problem was treated from different points of view. Esau (1943 b) and Girolami (1953) have studied the origin and the arrangement of vascular bundles in the relation to spiral phyllotaxis. These authors have shown that variation in leaf arrangement in the shoots of two species of *Linum* was associated with variation in vascular organization. The variation in leaf arrangement concerned the numbers of parastichies formed by the adjacent leaves. Explaining of this correlation needs to take the divergence and the number of parastichies into the consideration.

Since the work of Schimper and Braun (Braun 1835) the alternate leaf arrangement have been investigated quite extensively (Bravais 1837; Hirmer 1931, 1934; Fujita 1937, 1938, 1939, 1942; Davies 1939). From these studies it follows that the divergence angles between successive leaves do not fall into the fractions of Fibonacci series, but they are very close to the limiting value of this series. It is found that the commonest angle is 137.5° , i.e. the limiting angle of the primary phyllotactic series: $1/2$, $1/3$, $2/5$, $3/8$, $5/13$, $8/21$ On the contrary the leaf arrangement corresponding to the limiting angle of the subsidiary series: $151^\circ 8' 8''$ ($1/2$, $2/5$, $3/7$, $5/12$, $8/19$...) and this of the secondary series: $99^\circ 30' 6''$ ($1/3$, $1/4$, $2/7$, $3/11$, $5/18$...) appears very seldom.

The relationships between the divergence and parastichies have been studied by Fujita (1939). This author has measured divergence angles in shoots with various parastichy numbers and found that they were always very close to the limiting angle of the corresponding series. For limiting divergence 137.5° , the characteristic numbers of parastichies are: 2, 3, 5, 8, 13, 21 ..., for limiting divergence $151^\circ 8' 8''$ these numbers are different: 2, 5, 7, 12, 19 ..., and for the divergence $99^\circ 30' 6''$ they are still others: 3, 4, 7, 18, 29 These numbers are the successive denominators of the fractions of corresponding series.

From this results it follows that in all shoots of *Linum perenne* described by Esau (1943 b) the divergence is equal to the limiting value of the primary phyllotactic series 137.5° , although some shoots possess 8 parastichies and others 13 parastichies. The difference in the divergence angles occurs however in shoots of *Linum usitatissimum* investigated by Girolami (1953). The shoots with 5 parastichies and these

possessing 8 parastichies belong to the primary series, but the shoots with 7 parastichies belong to the secondary series, the limiting divergence of which is $151^{\circ}8'8''$. Thus, the question is how the changes in the contact parastichies are correlated with those of the vascular organization, and what is the factor determining these changes.

To solve the above question, the development of the primary vascular system was dealt with in the present investigation simultaneously in the axis and in the leaves and the arrangement of the leaves was taken into the consideration.

MATERIAL AND METHODS

The shoot apex of *Actinidia arguta* was used in the present investigation. During the ontogeny of the long shoots of this plant they change the organization of the vascular system and contact parastichies.

The material utilized in the investigation was obtained from a specimen growing in the Botanical Garden of the University in Wrocław.

The shoot apices were fixed in formalin acetic alcohol. The dehydration was accomplished by the ethyl alcohol series and the materials were imbedded in paraffin. Serial transverse and longitudinal sections were cut at 8 and 10 microns in thickness. These were stained with safranin and fast green. The cleared leaves and buds were used too. The material was kept in 2–5 per cent sodium hydroxide for a week or more before clearing was completed.

The procambium was delimited below the shoot apex among the derivatives of the promeristem thanks its dense narrow cells deeply stained. A distinction was made between mature and immature elements of protophloem and protoxylem according to the concept of Jacobs and Morrow (1957, 1958). The sieve tubes were regarded as mature when lacked nuclei and looked like empty. Phloem cells clearly recognizable by their thickened walls, but still retaining cytoplasmic contents deeply stained were regarded as immature. The mature protoxylem had a lignified secondary wall and no cell-contents. Immature protoxylem had a lignified walls but still retained the cytoplasmic contents: such a xylem was easily distinguished by the contraction of its protoplast.

The vascular tissue formed a ring. Each leaf had a single trace.

The leaves were numbered in order of their ages, starting with the youngest one. The leaf trace were numbered according to the leaf with which they were associated.

OBSERVATIONS AND RESULTS

It was found that the arrangement and the connections of bundles in *Actinidia arguta* changed during the ontogeny of shoots. In spring buds the trace of the leaf n was connected with the trace $n+8$, when the shoot began to elongate, the trace

of the leaf n was connected with the trace $n+13$ and still later the connection of the bundles n and $n+21$ was observed.

Fifteen long shoots were studied, five of them of each development stage.

The connections of the bundles n and $n+21$

The organization of the vascular system was exactly the same in all five investigated shoots.

The longitudinal course of differentiation of the first vascular elements was described by the use of serial transverse sections of shoot apex, cut off the 23 May 1960 from the stem measuring about 80 centimetres.

The two diagrammatic drawings were prepared from this series. The first (Fig. 1) illustrates the longitudinal course of the differentiation of vascular bundles in the axis and the second (Fig. 2) the differentiation of midvein and this of principal lateral veins in 29 successive leaves.

Procambium

About 250 microns from the summit of the apex the vascular ring was readily discernible. The individual bundles could be distinguished by their different width and thickness, the ring had therefore an irregular inner outline. At a higher level, the number of leaf traces decreased and the procambium might be observed as discrete individual strands separated by undifferentiated cells. Still higher, the procambium cells were only slightly discernible in transverse sections because they ran obliquely, so that their characteristic shape and small diameter was not clear in this plane of section.

The origin of the trace 1 illustrates the development of a new procambial trace. Its procambium was discernible through 15 internodes above the insertion of the leaf 22 (Fig. 1), and differentiated in continuity with the procambium of the trace 22. The trace 9 was laying on one side of the trace 22 and the trace 14 on the other. The trace 1 connects with the trace 22 on the side of the leaf trace 14.

As the procambium of a new trace n is initiated in continuity with the existing procambium of the older trace $n+21$, the origin of the trace n ought to depend upon the suitable stage of differentiation of the trace $n+21$. To define strictly this stage is the object of the following consideration.

The central strands of the procambium which differentiated at first continued across full length of the trace. New strands, however, began to differentiate on the flanks of these central strands in more and more distance from the point of the connection with the older trace. The leaf trace prolongs into the leaf as a midrib. Some of the midrib procambial strands deflect into the developing lamina and gave rise to the lateral veins. This process proceeds in basipetal sequence and the initiation of every lateral veins interrupts therefore the further acropetal development of the midrib's procambium above them. As a result of such type of development,

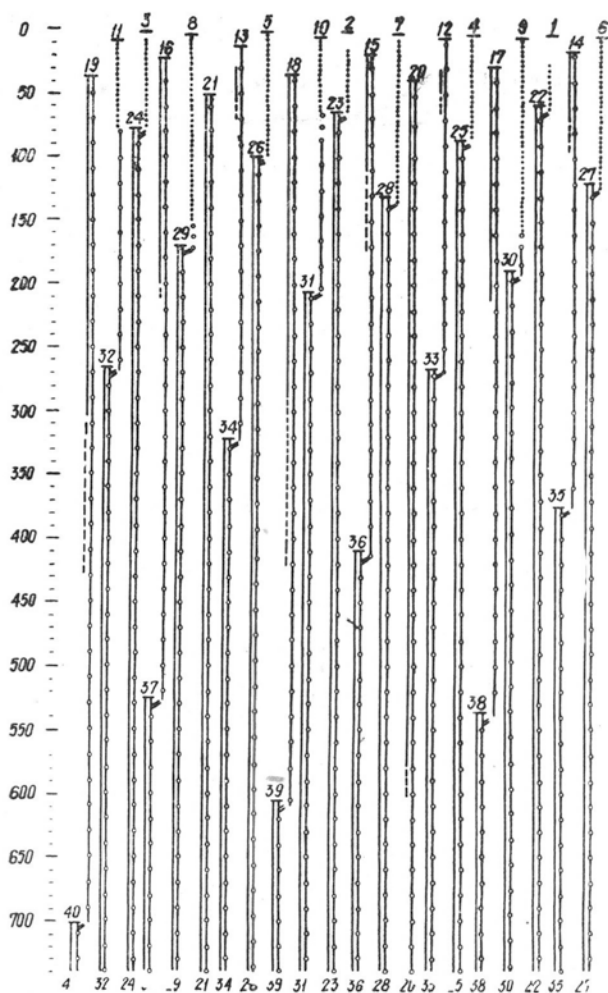


Fig. 1. Longitudinal diagram illustrating the differentiation of leaf traces in the shoot having the connections between the traces n and $n+21$ (shoot 1). The successive sections 10 microns in thickness define a distance below the apex. The marks as in fig. 2.

the leaf trace is the biggest in the region of the node, it is getting thin below in the axis and upward in the leaf (Fig. 3).

Primordia initiated in spring and summer possess a characteristic tip, the differentiation of which comes before that of a proper leaf blade. The initiation of lateral veins in this part of the leaf take place simultaneously with the initiation of lateral veins in the proper lamina, but proceeds in acropetal sequence.

The leaf 15, 850 microns long (Fig. 2), contains one lateral vein just initiated. A further initiation of lateral veins, as shown by a comparison of leaves 15 to 22, occurs basipetally. The leaf 22 is the first to show all principal lateral veins already initiated (Fig. 2).

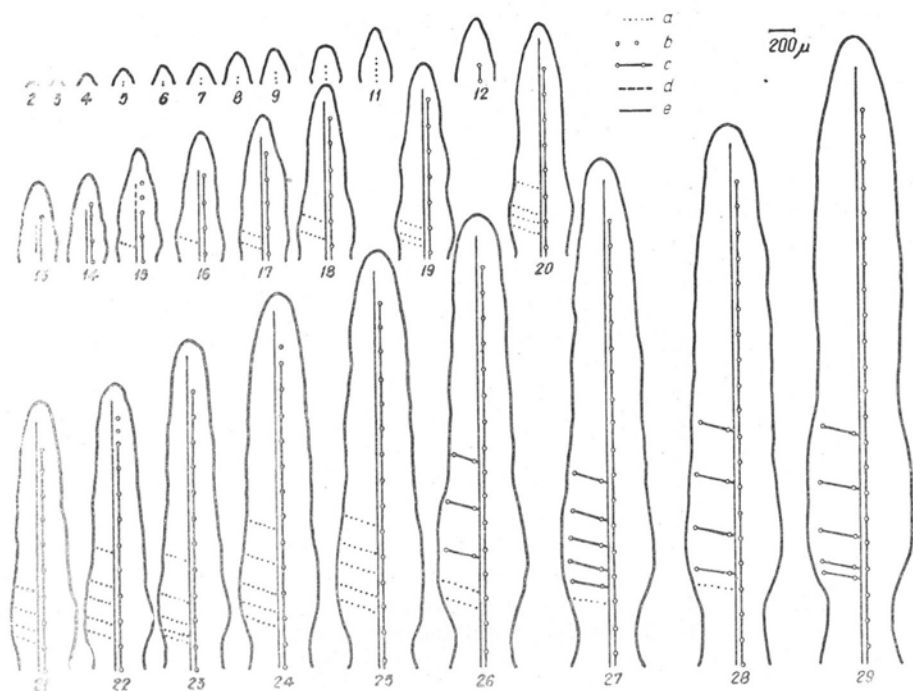


Fig. 2. Diagrams illustrating differentiation of midveins and lateral veins in successive 29 leaves of the shoot.

a — procambium; *b* — immature protophloem; *c* — mature protophloem; *d* — immature protoxylem; *e* — mature protoxylem

The major conclusion which can be drawn from the observations reported here is that the initiation of procambium of the leaf trace 1 is correlated with the initiation of the procambium in principal lateral veins in the leaf 22. It may be said that the trace 1, with regard to the way of its origin, is similar to the lateral veins of the leaf 22, it is namely the lowest branch of the trace 22 developing in the axis in contrast to the lateral veins developing in the leaf.

The appearance of procambium of successively higher levels in successively older traces clearly indicates on its acropetal differentiation. It is difficult to establish the correlation between the initiation of a procambial trace and the initiation of the primordium associated with it. The both processes take place simultaneously or one of them comes before the second insignificantly. In the described shoot the procambium of the trace 1 is initiated as well as the primordium, associated with it. The trace 0 was not found.

The protophloem

The trace 8 is the first to have immature elements of protophloem in its lower part; they develop in continuity with protophloem of the trace 29 (Fig. 1). The initiation of this protophloem is correlated with the differentiation of the proto-

phloem in lateral veins of the leaf 29. As is shown by the comparison of leaves 26—29, the protophloem of lateral veins differentiates in basipetal sequence. The leaf 29 is the first to show the protophloem in all lateral veins (Fig. 2). In the trace 8,

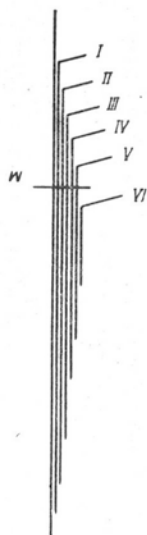


Fig. 3. Diagram of the development of the leaf trace: I, II, III, IV, V — the lateral veins developing in basipetal sequence, VI — a new leaf trace developing below the node (w).

as in the lowest branch of the trace 29, the differentiation of protophloem begins latest.

A comparison of traces 8—12 clearly indicates on acropetal development of protophloem.

The protoxylem

The leaf trace 12 is the first to show the protoxylem as isolated strand 200 microns high. The upper end of this strand is found 300 microns below the region of the node (Fig. 1). This 300 microns correspond to 8 internodes. So, when the length is measured in microns it seems that the differentiation of the xylem begins near to the node, but when the consideration is taken about the number of the internodes, then the xylem is shown to be initiated far below the node nearly to the middle of the trace.

The further differentiation of the xylem, as shown by a comparison of leaves 12—14, occurs acropetally toward the leaf apices and basipetally toward the older trace $n+21$. The acropetal differentiation of the first strand of protoxylem is finished in leaf trace 14. The basipetal differentiation into the axis persists still in the older traces (15—20). In the trace 20, the protoxylem is already differentiated in 19 internodes.

The leaf 13 is the first to have in its midrib the protoxylem elements just initiated. In lateral veins the protoxylem differentiates in basipetal sequence. The leaf 29 is the first to show the protoxylem in the highest lateral vein.

The connections of the bundles n and $n+13$

The longitudinal course of differentiation of the first vascular elements was described by the use of serial transverse sections of stem tip, cut off two weeks after the expansion from the bud (the 15 April 1961).

This shoot apex was designated with the number 2 in contradistinction to the shoot apex described above designated with the number 1.

The longitudinal course of differentiation of vascular bundles in the axis and in the leaves of shoot 2 was illustrated by means of diagrammatic drawings (Fig. 4, 5).

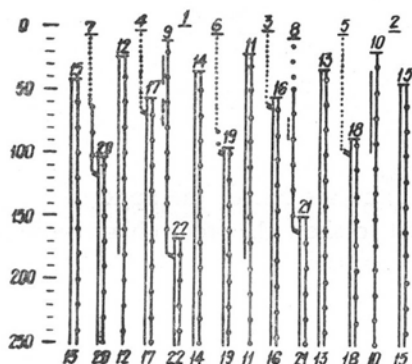


Fig. 4. Longitudinal diagram illustrating differentiation of leaf traces in the shoot having the connections between the traces n and $n+13$ (shoot 2). The successive sections 9 microns in thickness define a distance below the apex. The marks as in fig. 2.

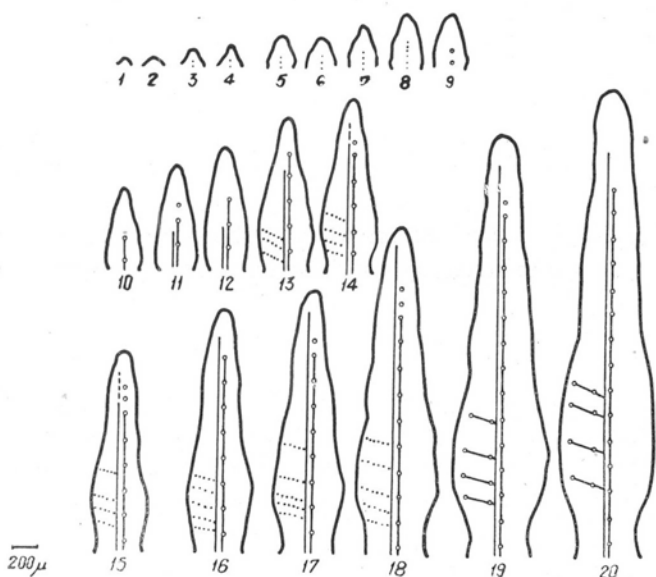


Fig. 5. Diagrams illustrating differentiation of midveins and lateral veins in successive 19 leaves of the shoot 2. The marks as in the fig. 2.

A comparison of the diagrams illustrating the arrangement of the bundles in the axis of the shoot 1 (Fig. 1) and this of the shoot 2 (Fig. 4) indicates on some differences. The arrangement of the bundles in the apex 1 is following: the traces $n+8$, n and $n+13$ run alongside in the lower 8 internodes, the traces $n+8$, n and $n-8$ in the five higher internodes and traces $n-13$, n and $n-8$ in the upper 8 internodes, then the trace $n-21$ takes place of the trace n and the changes are repeated.

In the shoot 2 the arrangement of the bundles is different. The following traces: $n+8$, n and $n+5$ run alongside in the lower 5 internodes, $n-5$, n and $n+5$ in 3 higher internodes and $n-5$, n and $n-8$ in the upper 5 internodes.

The above differences are induced by the variation in the development rate of successive leaves. In the shoot 2, the convergence in the development of the leaves n and $n+13$ occurs, and in the shoot 1 the same convergence occurs between the leaves n and $n+21$. As a consequence, every bundle runs through 13 internodes in the shoot 2 and through 21 internodes in the shoot 1.

Similarly to the shoot 1, the procambial ring in the shoot 2 is readily discernible about 250 microns from the summit of the apex.

The trace 3 is the first to show the procambium on its full longitudinal course. The initiation of this procambium is correlated with the development of the lateral veins in the leaf 16 (Fig. 5).

The trace 6 is the first to have the protophloem just initiated in its lower part. The initiation of this protophloem is correlated with the differentiation of the protophloem in lateral veins of the leaf 19 (Fig. 5). The two diagrams (Fig. 4, 5) illustrate the further longitudinal course of differentiation of protophloem in successive older traces.

Vascularization of the spring buds

The longitudinal course of the differentiation of the vascular bundles in the spring buds differs in some details from this process in the growing stems.

In the buds prior to shoot expansion, the bundles consist of procambium and protoxylem and they do not contain any mature elements of protophloem. The differentiation of the sieve tubes occurs when the buds begin to develop. Then the greater quantity of protophloem appears simultaneously in the full length of the traces.

The differentiation degree of the individual leaf traces in the bud after the beginning of the shoot expansion is illustrated by the two diagrams. The first (Fig. 6) represents the development of the leaf traces in the axis and the second (Fig. 7) that of the midvein and lateral veins in successive 12 leaves.

The trace of the leaf 7 contains the first elements of protophloem being in continuity with the protophloem of the trace 15. The initiation of this protophloem is correlated with the ending of the basipetal differentiation of the protophloem in lateral veins of the leaf 15. In contrast to the growing stems two loci of the protophloem initiation are found in the buds. Except in the axial locus, the protophloem of the trace 8 begins to develop in the midvein (Fig. 6, 7).

The vascular ring at the base of the buds is composed of 13 bundles. Five of these bundles belong to the scale leaves. These traces are minute and prolong to the midvein of cataphylls but the lateral veins do not develop at all or only a little. These bundles do not give rise to any new traces in the axis.

In recapitulation, the pattern of development of the vascular bundles in the shoots of the three stages of ontogeny can be summarized as follows: the procambium of a new trace n is initiated in continuity with the existing procambium of the older

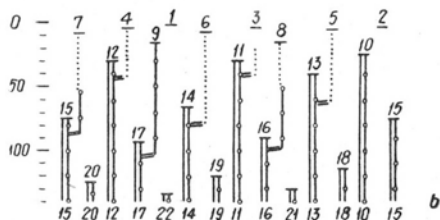


Fig. 6. A longitudinal diagram illustrating differentiation of the leaf traces in the shoot having the connections between the traces n and $n+8$ (the spring bud). The successive sections 9 microns in thickness define a distance below the apex. The marks as in fig. 2.

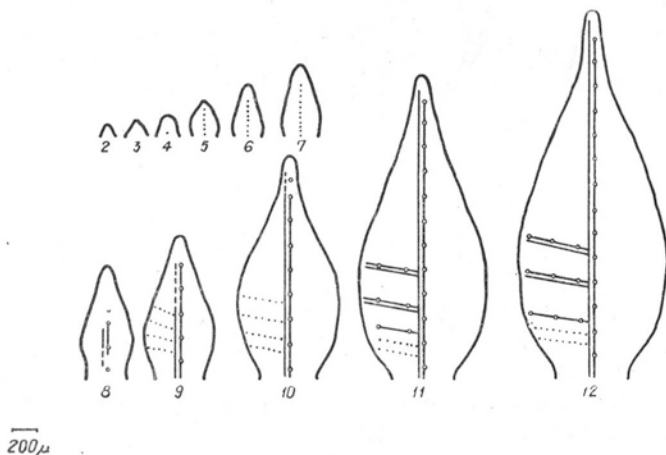


Fig. 7. Diagrams illustrating the differentiation of midveins and lateral veins in successive 12 leaves of the spring bud. The marks as in fig. 2.

trace $n+x$. The initiation of a new procambial trace n is correlated with the differentiation of procambium in the principal lateral veins in the leaf associated with the older trace $n+x$. The initiation rate and the growth of successive leaves change during the ontogeny of the shoots. As a result the different traces and leaves come into the developmental convergence. It was found that the same convergence occur between the traces: n and $n+8$, n and $n+13$, n and $n+21$. The numbers expressing the connections of the bundles belong to the primary phyllotactic series: 3, 5, 8, 13, 21

To explain the relation between the vascular organization and the phyllotaxis, the disposition of leaves in the shoots of different stage of development will be presented.

The leaf disposition

Simultaneously with the changes in the vascular organization, the contacts between the leaves change also during the ontogeny of the long shoots.

In spring buds prior to the beginning of the growth, every second, third and fifth leaf come into the contact (Fig. 8). After the beginning of the expansion every third and fifth leaf come into the contact, but not every second leaf. Among the

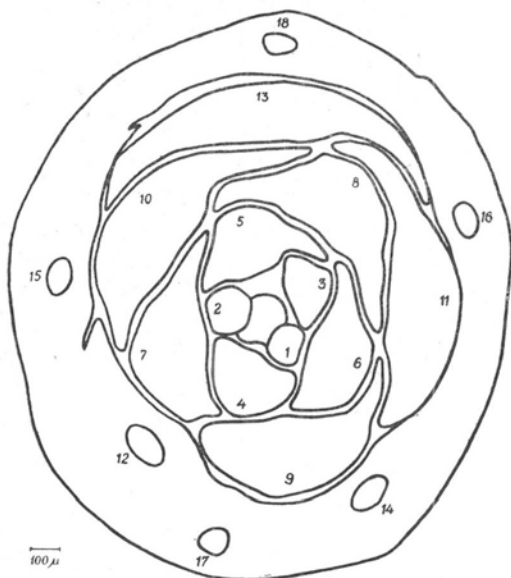


Fig. 8. Transverse section of a spring bud before shoot expansion. The contacts between every second and third leaf.

older leaves of the same buds every second and third leaf come into contact, but not every fifth leaf (Fig. 9). In the shoots of the growing stems come into the contact every third, fifth and eighth leaf (Fig. 10, 11).

The above variation in contact parastichies is characteristic for the primary phyllotactic series (2, 3, 5, 8, 13, 21 ...) and depends upon the relative dimension and form of successive leaves. The existence of such dependence may be easily demonstrated if the divergence is taken into the consideration. The limiting divergence of the primary series is 137.5° . At this divergence the angles between the centres of the leaf $n+2$, $n+3$, $n+5$, $n+8$... and leaf n are the following:

the leaf x	the angles between the centre of the leaf x and n
$n+2$	-85
$n+3$	+52,5
$n+5$	-32,5
$n+8$	+20,0
$n+13$	-12,5
$n+21$	+7,5



Fig. 9. Transverse section of the spring bud after the beginning of shoot expansion. The contacts between every third and fifth leaf among the youngest ones and between every second and third leaf among older ones.



Fig. 10. Transverse section of the growing shoot (the shoot 2). The contacts between every third, fifth and eighth leaf among the youngest leaves, and between every second, third and fifth leaf among the older ones.

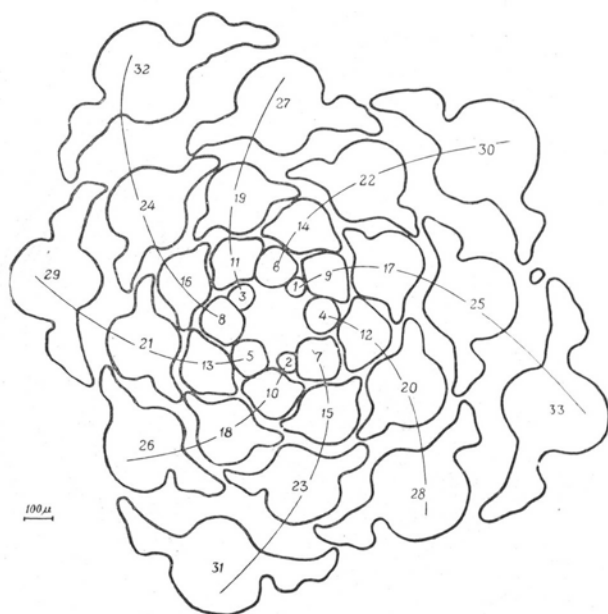


Fig. 11. Transverse section of the growing shoot (shoot 1). Contacts between every third, fifth and eighth leaf.

From the above it follows that the angles between the leaf n and the older leaves are smaller than between them and the younger ones. If the dimension of the shoot apex does not change, the contacts between the leaf n and the leaves initiated later depend upon the dimension of the leaves initiated earlier. E.g. the contact between the leaf n and $n+8$ depend upon the dimension of the leaves $n+3$ and $n+5$. If these leaves are large and their margins overlap, the contact between the leaf n and $n+8$ is not possible. If the dimension of the leaves $n+3$ and $n+5$ are, however, smaller and their margins do not overlap, the leaf n come into the contact with the leaf $n+8$. The comparison of the shoot apices 3 and 1 (Fig. 9, 11) clearly demonstrate the existence of such dependence. On the shoot 3 the margins of the leaves 14 and 12 overlap and the contact between the leaf 9 and 17 is not possible. On the apex 1, however, the leaves 12 and 14 are smaller and do not approximate each other and, as a result, the leaves 9 and 17 are adjoining.

The variation in contact parastichies depends upon the dimension and the form of successive leaves, and the both depend upon the rapidity of initiation and growth of leaves. The last factor determinates the variation in the connections of the vascular bundles and therefore the variation in contact parastichies and this in vascular organization occur simultaneously. The divergence, however, does not change.

DISCUSSION

As Esau stated in her detailed review (1942, 1943 a) on the procambium in vegetative shoots of dicotyledons and gymnosperms, procambial strands differentiate in continuity with the vascular system and progress acropetally from the axis into the developing leaves. The same was found in the shoots of *Actinidia arguta* Planch. It was shown in this paper that the initiation of the trace n is correlated with the differentiation of procambium in the principal lateral veins in the leaf with which this older trace $n+x$ is associated.

The longitudinal course of development of the first sieve tube in the shoots of *Actinidia arguta* Planch. occurs acropetally and continuously from the base upward in both the axis and in the leaf. Several investigations (Esau 1942, 1943 a, b, 1945, 1961; Reeve 1942; Crafts 1943 a, b; Sterling 1945; Gunckel and Wetmore 1946 a, b; Girolami 1954; Sloover 1958) have shown that acropetal differentiation of protophloem in vegetative shoots of dicotyledons and conifers is universal.

It was found also that in *Actinidia arguta* Planch. initiation of protophloem in the trace n is correlated with the development of protophloem in the principal lateral veins of the leaf with which the older trace connecting with trace n is associated.

According to the most references (Esau 1942, 1943 b; Reeve 1942; Girolami 1954; Sloover 1958) xylem is initiated in seed plants, with some variations in details as isolated elements in the region of the node or within the primordial leaves and then differentiates acropetally toward the apex of the leaf and basipetally into the axis until it unites with the xylem of the older traces.

It was found that the protoxylem in spring buds of *Actinidia arguta* Planch. is initiated within the leaf in contrast to the axial locus of xylem initiation in the growing stem.

The first phloem elements appear usually in the trace before the first xylem elements. However, Bond (1942) and Kundu and Datta (1944, cited after Sloover) have reported that in spring buds of *Camelia thea* and *Hibiscus sobdarifera* the first sieve-tubes become recognizable later than the first tracheids. In spring buds of *Actinidia arguta* Planch. the xylem appears in traces also before the first phloem.

The rate of the initiation and growth of the successive leaves changes during the ontogeny of the shoots of *Actinidia arguta* Planch. As a result, the different traces and leaves come into the developmental convergence. During the growth of shoots the developmental correlation occurs between the traces n and $n+8$, than between the traces n and $n+13$ and later n and $n+21$.

Simultaneously with the changes in the vascular organization change also the contacts between the leaves in the shoot apices of *Actinidia arguta* Planch. This variation in contact parastichies is characteristic for the primary phyllotactic series (2, 3, 5, 8, 13, 21 ...) and depend upon the relative dimension and form of the successive leaves. The dimension and form of the leaves depend upon the rapidity of their initiation and growth. As the same factor determines the changes of bundle's

connections, the variation in the connections of the vascular bundles and in contact parastichies occur simultaneously. However, the limiting divergence does not change.

SUMMARY

The pattern of development of the vascular bundles in the shoots of *Actinidia arguta* Planch. can be summarized as follows:

1. The procambium of a new trace n is initiated in continuity with the existing procambium of the older trace $n+x$. The initiation of the trace n is correlated with the ending of basipetal initiation of procambium of the principal lateral veins in the leaf with which this older trace $n+x$ is associated. The above correlation was also found in the development of the protophloem.

2. During the ontogeny of the long shoots the rate of the initiation and growth changes in the successive leaves. As a result, different traces and leaves come into the development convergence. The developmental correlation is established between the traces n and $n+8$, than n and $n+13$ and later n and $n+21$.

The relationship between the vascular organization and the phyllotaxis can be summarized as follows: the variations in contact parastichies depend upon the relative dimension and form of the successive leaves. The dimension and form of the leaves depend upon the rapidity of their initiation and growth. As the same factor determines the connections between the bundles, the variations in contact parastichies and in vascular organization occur simultaneously. The limiting divergence, however, does not change.

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Korelacje w rozwoju wiązek i liści na długopędach *Actinidia arguta* Planch.

Streszczenie

Na podstawie badań nad rozwojem wiązek w wierzchołkach długopędów *Actinidia arguta* Planch z trzech stadiów ontogenezy oraz na podstawie analizy układu liści na tych wierzchołkach uzyskano następujące wyniki:

1. Początek rozwoju pasma prokambialnego nowej wiązki skorelowany jest z rozwojem głównych nerwów bocznych w liściu należącym do starszej wiązki, z którą się owa nowa wiązka łączy. W ten sposób powstanie nowej wiązki zależy od osiągnięcia przez liść, należący do starszej wiązki, odpowiedniego stadium rozwojowego. Podobną korelację stwierdzono w rozwoju protofloemu.

2. Podczas ontogenezy długopędów wzrasta szybkość powstawania i wzrostu kolejnych liści. W związku z tym wzrasta również liczba plastochronów, dzielących te same stadia rozwoju liści. Wobec zaś zależności rozwoju wiązek od rozwoju liści wzrasta liczba międzywęzli między odgałęzieniem nowej wiązki a nasadą odpowiadającego jej liścia. Pociąga to za sobą zwiększenie liczby wiązek w łodydze i zmianę połączeń między nimi. Stwierdzono połączenia między wiązkami n i n+8, n i n+13 oraz n i n+21.

3. Równolegle ze zmianami w połączeniach między wiązkami na wierzchołkach zmieniają się kontakty między zawiązkami liści. Połączeniom wiązek n i $n+8$ odpowiadają kontakty między co 2 i co 3 liściem, połączeniom wiązek n i $n+13$ odpowiadają kontakty między co 3 i co 5 liściem, a połączeniom między n i $n+21$ kontakty między co 5 i co 8 liściem. Wykazano, że przyczyną zmian kontaktów między liśćmi są różnice w ich wielkości i kształcie. Wielkość zaś i kształt kolejnych liści zmienia się w zależności od szybkości ich powstawania i wzrostu. Od tego samego czynnika zależą również zmiany połączeń między wiązkami, prowadzące do zmiany liczby wiązek w międzywęźlach. Dlatego w czasie rozwoju pędu kontakty między liśćmi zmieniają się jednocześnie ze zmianami połączeń między wiązkami. Dywergencja zaś pozostaje taka sama.