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ON THE ANATOMY OF THE WOODY STEM OF THE TWISTED HAZEL, CORYLUS AVELLANA L. 'CONTORTA'

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Abstract

Data are presented concerning the internal structure of the woody stem of *Corylus avellana* L. '*Contorta*', the twisted Hazel. In the primary state the pericycle is noteworthy because of its poor development, which is in striking contrast to the situation in the normal Hazel.

Because the primary shoot is twisted from the very beginning, the cambial cylinder is also twisted. In the loops, unequal amounts of secondary xylem are formed, with a larger quantity at the inner bends than at the outer bends.

The changes in the cambial areas—decrease at the inner and increase at the outer bends—are almost completely parallel to the changes observed in the dimensions of wood vessel elements—decrease in length from the pith towards the inner bends of twisted parts of branches and increase in length towards the outer bends.

In the majority of cases tension wood proved to be present at the outer bends. A method for localizing tension wood using fluorochromes is described.

1. Introduction

In the horticultural literature, forms or varieties of woody plants distinguished by the possession of remarkable twisted twigs have occasionally been described. Among the well-known examples of such plants are *Corylus avellana* L. '*Contorta*', the subject of the present publication, *Salix matsudana* Koidz. '*Tortuosa*', *Robinia pseudacacia* L. '*Tortuosa*', and *Crataegus monogyna* Jacquin '*Pink Corkscrew*' (Meyer, 1961). As far as the authors are aware, no data are available concerning either the anatomy of these bizarre plants or the cause of the phenomenon.

In addition to the contorted stems, the leaves are also more or less abnormal. In the contorted Hazel, the leaf veins are undulated in planes perpendicular to the leaf surface with the result that the leaf surface is very uneven.

The material used in the present investigation was obtained from a twisted Hazel cultivated since 1941 in the Leyden Botanic Garden. In all probability all twisted Hazels in cultivation derive from a plant discovered in 1863 in England in the neighbourhood of Gloucester and shown for the first time in 1894 (Anonymous, 1894; Bean, 1898, 1914; Wakefield, 1962).

2. General appearance and gross anatomy

Plate I gives a good impression of the general appearance of the plant in winter. It will be observed that the one year old shoots are already heavily contorted. As a matter of fact, the phenomenon can be seen from the very beginning in young, tender shoots. Sometimes the loops or coils are so narrowly wound that older branches show massive knots formed as a result of secondary growth.

In transverse sections of the curved parts of twigs and branches, the pith is situated eccentrically in the majority of cases. The amount of secondary tissue measured from the pith towards the periphery is in such cases much larger at the inner bend than in the outer one. This holds especially for the amount of secondary xylem, but the same situation can also be observed in the tissues outside the cambium. This is all the more remarkable because as a result of the formation of secondary xylem in the inner bend, the space available for cambium, secondary phloem, pericambial tissue, cortex and secondary cork is considerably decreased.

The extent to which this occurs is obvious from a simplified diagram of a longitudinal section through a three year old shoot (Fig. 1). The simplifications introduced are based on the assumption that secondary growth is regular in both space and time, the result being a twig with centric pith, constant seasonal increment, and a semi-circular bend.

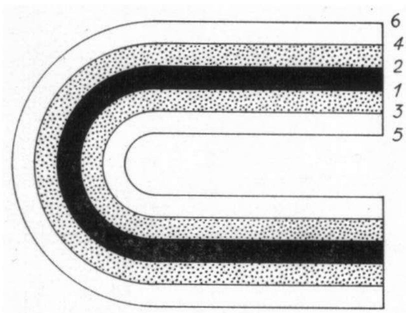


Fig. 1. Schematic drawing of a longitudinal section of a 3 year old bent shoot. See text, page 190.

Table 1 shows clearly that the lengths of the successive inner bends during the period of three year's growth, indicated by the numbers 1, 3, and 5 respectively, are proportional to those of the respective radii, i.e. 100, 70, and 40. This means that the inner bend during one year's growth must reduce its length by 30 %. On the other hand, the lengths of the successive outer bends, numbered 2, 4, and 6, are in the proportion 100:123:146. Therefore, in the course of a year the outer bend must increase its length by 23 %.

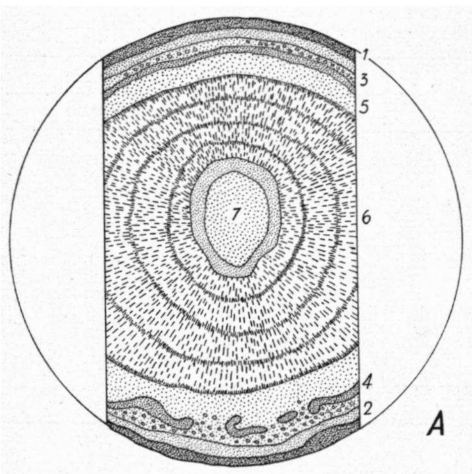
It is evident that especially the loss of space in the inner bends forces changes in the arrangement and very probably in the dimen-

TABLE 1

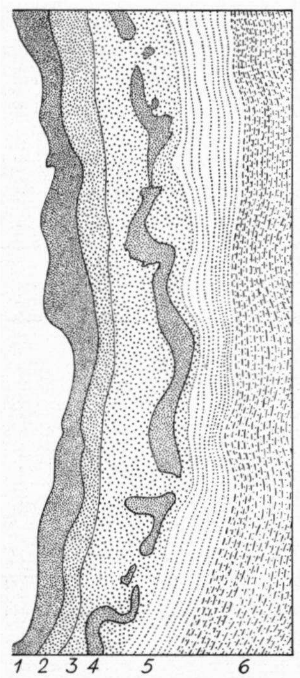
Relative length of inner and outer bends.

No.	r in mm	length in % of No. 2	length in % of No. 1
6	19	146	
4	16	123	
2	13	100	
1	10		100
3	7		70
5	4		40

sions of the cells already present in this region. In reality, the reduction of space in the inner bends is far greater and the increase in space of the outer bends is less than that shown in the diagram, the pronounced eccentricity being due to the production of much more secondary xylem at the inner bends. (Fig. 2a).



A



B

Fig. 2a. Transverse section through a bend of a 4 year old branch, the inner side of the bend below. 1: periderm; 2: collenchyma; 3: parenchyma; 4: pericambium; 5: phloem; 6: xylem; 7: pith.

Note the eccentrically-situated pith and the disrupted pericambial zone at the inner side of the bend.

Fig. 2b. Longitudinal section of the inner side of a strongly bent part of a 4 year old branch. The non-parallel folding of the involved tissues is evident.

As to the gross anatomy, the straight parts of twigs of the twisted Hazel are very much like those of normal Hazel. Especially in sharp inner bends of older, twisted twigs, however, the secondary xylem and all tissues distal to the xylem are heavily folded and often show a disrupted or more or less chaotic structure (Fig. 2b).

3. Pericycle

Although the authors are well aware of the fact that the fibres mentioned in this paragraph may be phloem fibres (Esau, 1950), the term pericyclic fibres is used because the origin of the object under observation is as yet unknown. There appears to be a characteristic difference between the pericambial zones of normal and contorted Hazel-twigs, as can be seen from Plate II, 1 and 2. Whereas in normal Hazel the pericambial zone of the one year old shoot consists of extensive bundles of fibres alternating with groups of sclereids, this zone is very much less developed in the twisted variety. As a matter of fact, in the latter the radial extension is only one or two cells thick and, especially along the outer side of the bends is in addition interrupted to a considerable degree by parenchymatous tissue. In a number of sectors of one year old twigs measuring 200 μ tangentially, sclerenchyma fibres and sclereids were counted in the pericambial zone; the data are given in Table 2.

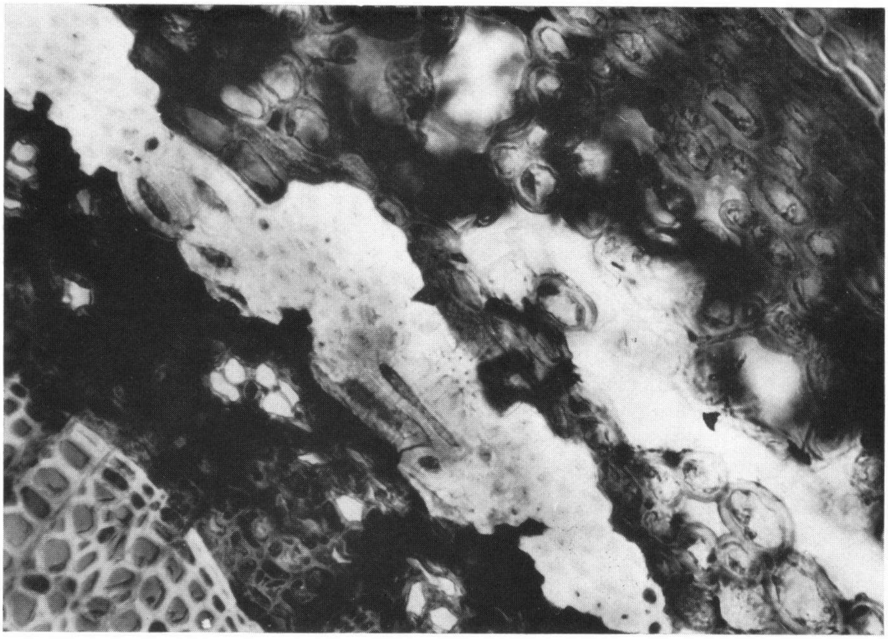
Table 2

Number of sclerenchyma fibres and sclereids.

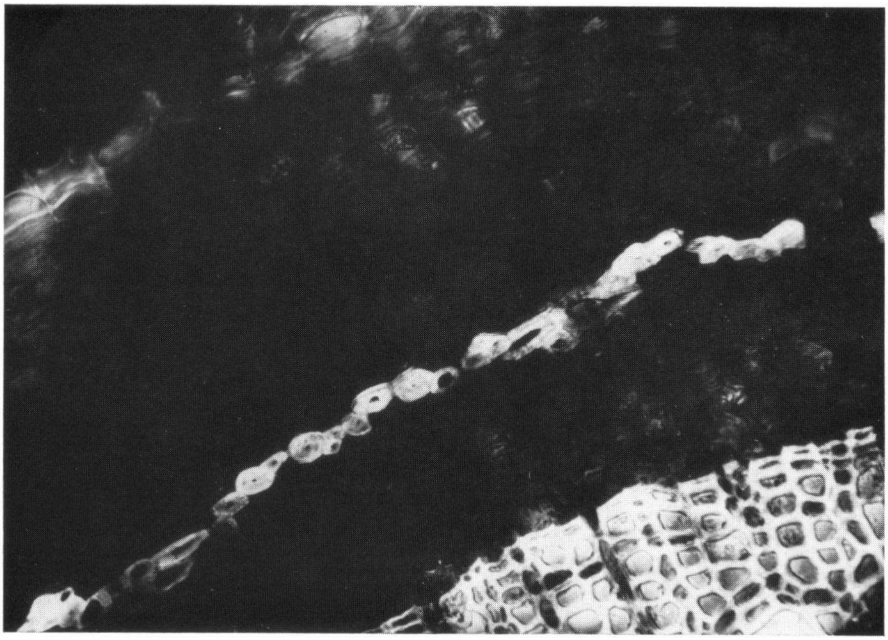
Normal		Twisted	
Fibres	Sclereids	Fibres	Sclereids
119	—	25	1
72	10	22	2
108	5	18	1
67	7	17	2
93	5	15	4
121	2	17	1
113	2	21	3
85	3	31	—
153	—	18	7
		18	1
103.4 ± 25.6	3.8 ± 3.1	20.2 ± 4.5	2.2 ± 1.9

From the data in Table 2 the arithmetical means (A.M.) and the standard deviations (S.D.) (Feldman, 1935) have been calculated for the two categories, fibres and sclereids, in both normal and twisted Hazel. The values for the fibres of normal and twisted twigs are 103.4 ± 25.6 and 20.2 ± 4.5 respectively, those for the sclereids 3.8 ± 3.1 and 2.2 ± 1.9 respectively. The difference in fibre-content of the two stem types is highly significant. This is not the case for the

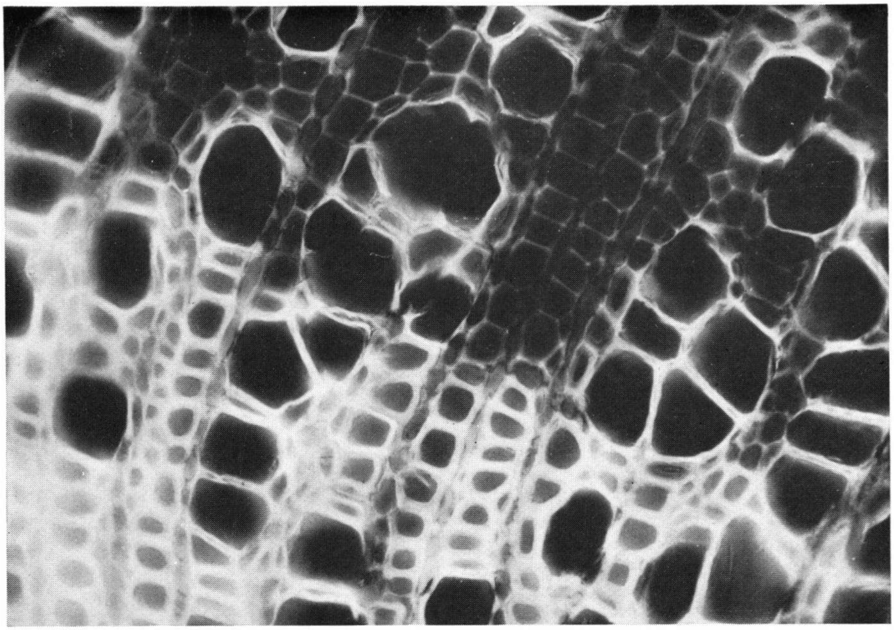
Corylus avellana 'Contorta' General appearance in winter.



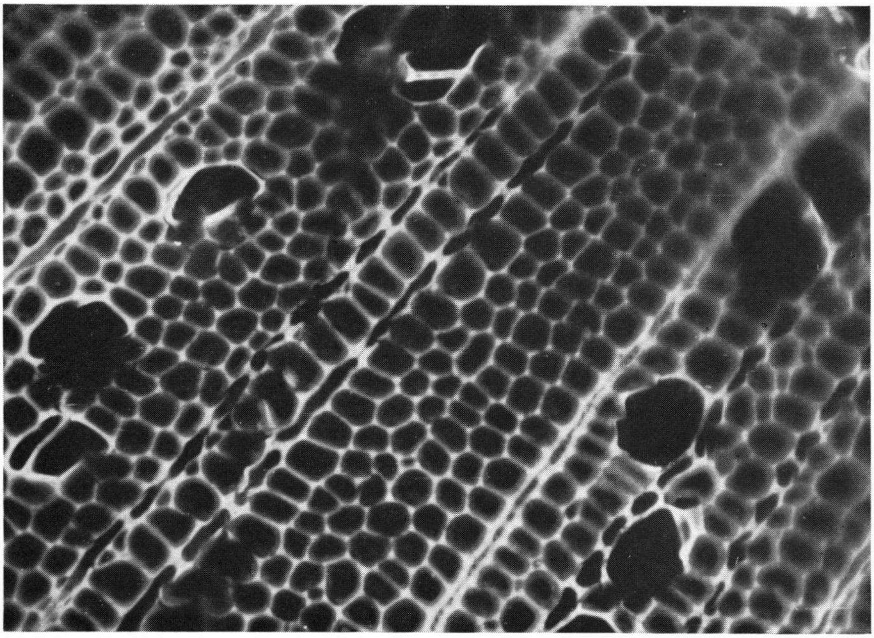
1. *Corylus avellana* normal. One-year old twig; transverse section. Hematoxylin.



2. *Corylus avellana* 'Contorta'. One-year old twig; transverse section of the outer side of a bend. Hematoxylin.



1. *Corylus avellana 'Contorta'* Normal wood at the bottom, tension wood at the top. Transverse section. Coriphosphin. Ultraviolet illumination.



2. *Corylus avellana 'Contorta'* Tension wood. Transverse section. Titan yellow. Ultraviolet illumination. Secondary cell walls hardly visible.

sclereids. It is obvious that the pericambial zone of the normal Hazel is much more developed than that of the twisted Hazel.

It is interesting to mention here, but without drawing any inferences, the results of an investigation done by Löwe (1917) on the anatomical difference between normal and weeping forms of a number of trees. The pericambial fibres of the twigs of the pendulous forms proved to be present in a much thinner layer.

4. Structural elements of the secondary xylem

4.1. *Introductory remarks*

The work of Greguss (1947) and Metcalfe and Chalk (1950) discusses the structural pattern of the secondary xylem and of the constitual elements in normal Hazel. The twisted Hazel, however, is not mentioned. The only reference found in the literature with any relation to our work is the publication by Löwe (1917) on differences in the anatomy of twigs of normal trees and their weeping forms. She reports the differences between normal Hazel and its weeping form to be insignificant and inconstant.

4.2. *The horizontal system*

In agreement with Greguss and Metcalfe and Chalk, we found the horizontal system to be composed of rays, predominantly of the uniseriate type. Multiseriate rays up to two or three cells wide and aggregated ones composed of more than three cells, as described by these authors, were also encountered.

We could not detect any difference in this respect between normal and twisted Hazel. Also as to the height of the rays, up to eighty cells according to Greguss for normal Hazel, we were unable to establish any difference between the two types. As a matter of fact, an aggregate ray seventy-five cells high was encountered in the twisted form.

The same appears to be the case in respect of the number of rays per mm width. Metcalfe and Chalk mention ten to seventeen rays per mm, whereas we found a value of 15 ± 3 for both normal and twisted Hazel.

Concerning the composing elements, the latter authors describe the rays of Hazel wood as "composed wholly of procumbent cells or with single marginal rows of square cells". This description comforms very well to the structural pattern of the wood of normal Hazel at our disposal. The wood of the twisted Hazel, however, sometimes exhibits quite a different picture, very long procumbent ray-cells sometimes being found along the margins of the rays.

4.3. *The vertical system*

With respect to the distinction between the different types of elements present, no difficulty arises in the case of the vessels. In radial sections the scalariform perforation plates, with six to twelve bars according to Greguss and "with fewer than 20 bars" according to Metcalfe and Chalk, are very distinct. For the length of these elements, TIPPO (1938) gives an average of 550 μ, Metcalfe and Chalk 650 μ, while Greguss does not give any value at all. For the twisted Hazel we found deviating values. In straight portions the length of the vessels averaged 500 μ, while in heavily twisted parts a decrease to a length of only 250 μ and an increase to 670 μ were observed for inner and outer bends respectively. More details concerning this phenomenon will be found in the next section.

Some difficulties arise in classifying the different fibre-like elements. Metcalfe and Chalk are not very explicit in distinguishing between different types of fibrous elements in Hazel wood. According to Greguss, the bulk of the wood of *Corylus avellana* consists of libriform wood fibres and parenchyma. We did not attempt to distinguish between different types of fibrous elements such as libriform wood fibres and fibre tracheids, which will be called wood fibres here. This simplification is even advisable in the case of the twisted Hazel because of the occurrence of curiously misshapen fibres in the inner bends of extremely twisted portions of twigs and branches. (Fig. 3).

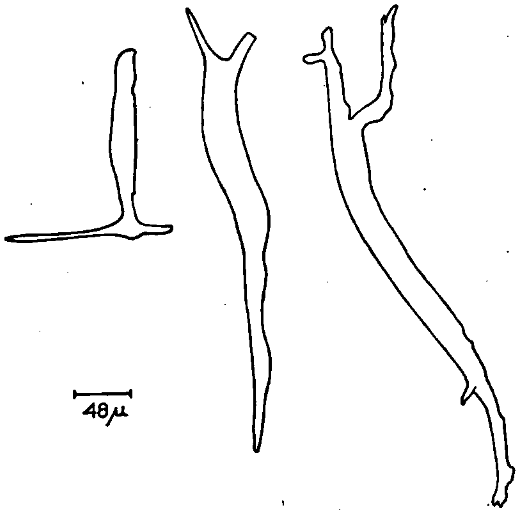


Fig. 3. Wood fibres from the inner bend of an extremely twisted portion of a 16.5 mm thick branch.

A third type of element in Hazel wood is wood parenchyma, according to Metcalfe and Chalk usually present in strands of eight cells. We encountered this situation in normal Hazel, but in this respect the twisted Hazel again exhibits a deviating picture. Especially in the inner bends of very twisted stem portions, many elements can be found that are morphologically intermediate between so-called substitute fibres, i.e. non-subdivided wood parenchyma fibres, and normal wood parenchyma cells, i.e. strands of cells produced by subdivision of fibre-shaped elements. Such elements are much longer than common wood parenchyma cells. It may be noted that one of the illustrations of *Corylus avellana* given by Greguss and described as a wood parenchyma cell might represent one of the apical cells of such a scantily-divided parenchyma fibre.

5. Quantitative analysis of the secondary xylem

5.1. *Introductory remarks*

In section 2 attention was drawn to the fact that the formation of secondary tissues by the cambium meets certain "difficulties" because of the decrease and increase in area at the inner and outer bends respectively of twisted stem portions of *Corylus avellana* '*Contorta*'.

5.2. *The horizontal system*

In the foregoing section a description of the structural elements of the wood of *Corylus avellana* and its twisted form was presented. By means of counting and measuring certain elements, we tried to detect possible features related to the remarkable phenomenon of twisting. Comparable areas of secondary xylem were investigated to this end. It appeared that in tangential sections the number of rays per mm width in both normal and twisted Hazel amounts to 15 ± 3. This is in agreement with Metcalfe and Chalk, who for normal Hazel give values of between 10 and 17. For the twisted form we could find no differences between straight and curved portions of the twigs; for the curved portions in both the inner and the outer bends the same values were again encountered.

If, however, in equal areas ($480 \times 480\ \mu$) of tangential sections the number of uni- and multiserial rays are counted, the results differ. According to Greguss and Metcalfe and Chalk, the majority of wood rays in the Hazel is uniserial, with only a small number of multiserial rays present. This holds for straight portions and for outer bends of branches of the twisted Hazel, but not for the inner bends.

Table 3

Number of the two types of rays for equal areas ($480 \times 480\ \mu$) in wood of twisted Hazel.*)

Portions of the branch	Number of uniseriate rays	Number of multiseriate rays
straight portion	17–25 (22 $\pm$ 3)	3–5 (4 $\pm$ 1)
outer extreme bend . .	18–24 (21 $\pm$ 2)	1–4 (3 $\pm$ 1)
inner extreme bend . .	13–14 (13.5 $\pm$ 0.5)	7–9 (8 $\pm$ 0.5)

*) The data in Tables 3–7 represent minimum and maximum values. The numbers in brackets are the arithmetical means (A.M.) and the standard deviations (S.D.).

It is evident that the inner bend of extremely twisted portions of the branches shows a much larger proportion of multiseriate rays. The same trend appears to be present as to the number of ray cells in comparable areas (480 × 480 μ) of tangential sections (See Table 4).

TABLE 4

Number of ray cells in wood of the twisted Hazel.

Portion of the branch	Number of ray cells
Straight portion	193–221 (206 ± 12)
Outer portion of extreme bend	201–220 (211 ± 8)
Inner portion of extreme bend	262–315 (283 ± 23)

A third point we investigated concerns the height of wood rays expressed in the number of the composing cells. Because the number of multiseriate rays is quite appreciable in the inner portions of bends and practically negligible in the outer portions of the bends and in the straight parts, data concerning the number of cells of multiseriate rays are given only for the inner bends (See Table 5).

TABLE 5

Height of rays expressed in number of cells.

Portion of the branch	Number of cells in uniseriate rays	Number of cells in multiseriate rays
Straight portion	3–20 (8 ± 5)	
Outer portion of extreme bend	3–75 (22 ± 18)	
Inner portion of extreme bend	1–21 (7 ± 5)	3–28 (12 ± 6)

The data in Table 5 indicate that in respect of the height of the uniseriate wood rays expressed in the number of the composing cells, the outer portions of extreme bends are exceptional. Concerning the dimension of ray cells in the longitudinal sense, the few cells measured average for straight portions, outer bend portions, and inner bend portions, 19.2, 16.9, and 12.1 μ respectively.

Although they do not belong to the horizontal system, something may be said here about the number of longitudinally-oriented elements separating the wood rays. No difference could be detected between normal Hazel and its contorted form. Furthermore, close to the pith in both plants the number of cells between two successive rays is smaller than in the region bordering on the cambial zone.

5.3. *The vertical system*

In order to obtain more information, the vertical system of the wood was also investigated. Besides data derived from transverse, radial, and tangential sections taken from straight and bent portions of twigs and branches, information was obtained by measuring vertically-oriented elements in macerates of wood fragments. These measurements were done for pitted vessels and wood fibres. As already mentioned (see p. 194), no distinction was made between fibre tracheids and libriform wood fibres.

To prepare macerates, samples of wood measuring 1 mm in the radial sense, 2 mm in the tangential sense, 3–4 mm in the longitudinal sense, and of known position, were macerated with the phenolhydrochloric acid method. The schematic drawings in Fig. 4 elucidate this. From a curved part of a branch (Fig. 4, A) a 3–4 mm thick slice is

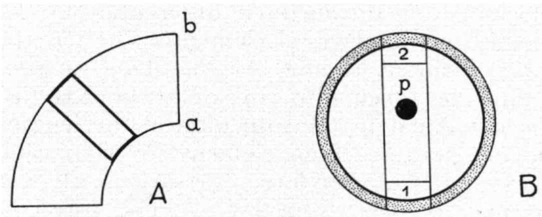


Fig. 4. Schematic drawing indicating the original situation of the wood samples investigated. A. From a bent part of a branch with a diameter ab of 8 mm, a slice 3–4 mm thick is cut (heavy outline); B. Subdivision of the same slice. The dotted area is situated outside the cambium, which is represented by the heavy line. p: pith; 1 and 2: the investigated wood samples. B. 2 × scale of A.

cut with the aid of a small, very fine-toothed hacksaw. From this slice a 2 mm wide strip is cut (Fig. 4, B) to provide the wood samples (Fig. 4, B 1 and 2). Thus, sample 1 was originally situated in the inner bend and sample 2 in the outer bend of a contorted branch.*) The loop shown in Fig. 4 was 8 mm thick, while the inner and the outer radii measured 7 and 15 mm respectively. Since the bark was 0.4 mm thick, samples 1 and 2, measuring 1 mm in the radial sense, were originally situated in parts of the loop with radii between 7.4–8.4 mm and between 13.6–14.6 mm respectively (mean values 7.9 and 14.1 mm). Using macerates of samples 1 and 2 and a sample situated in the immediate neighbourhood of the pith (p), measurements were made of the length of a number of wood vessel elements (31, 30, and 55 respectively) and of wood fibres (in all three samples, 60). (See Table 6).

It is evident that a relation between the length of the elements in the bend and their localization is present. It is impossible, however, to conclude on the basis of these data alone that the reduction and augmentation in the length of inner and outer bends of contorted branches are caused exclusively by modification in length of the constituting elements.

In the first place, it must be kept in mind that wood fibres undergo

*) For a loop with a radius x for the inner bend, radius y for the outer bend will be x + the diameter of the branch loop.

TABLE 6

Length of wood vessel members and wood fibres in a branch loop of the twisted Hazel.

Fragment	Wood vessel elements, length in μ	Wood fibres, length in μ
No. 1	338–600 (440 ± 70)	375– 953 (675 ± 126)
No. 2	525–900 (623 ± 85)	360–1575 (818 ± 191)
Close to pith . .	375–788 (548 ± 101)	360–1200 (675 ± 179)

an important elongation during their differentiation. This is not the case for the length of wood vessel elements. The length of the latter is, therefore, better suited for study of the above-mentioned relation. However, it must be taken into consideration that the length of a wood vessel is not equal to the sum total of the lengths of the constituting elements because those elements overlap each other to a considerable extent. It is therefore necessary to allow for a certain correction, as may be seen from Fig. 5. The corrected values are kl minus ml, mn minus on, etc. In the present case this correction amounts to about 100 μ.

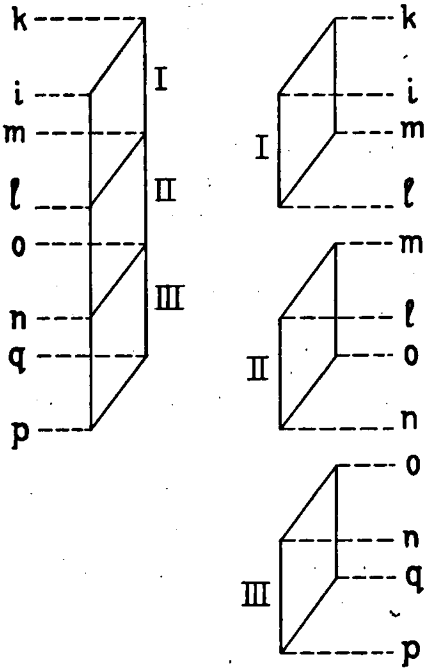


Fig. 5. Schematic representation of three vessel elements (I, II, and III) in relation to a necessary correction. The exact length of I is not kl but kl minus ml. Thus, the total length of the three elements is km + mo + oq.

If the difference in length of the constituent elements—taking the above-mentioned reservations into consideration—causes the difference in length of inner and outer bends of contorted branches, the ratio between the corrected values of the length of vessel elements situated at the inner and outer bends must be equal to the ratio between the radii of those bends (See Fig. 6).

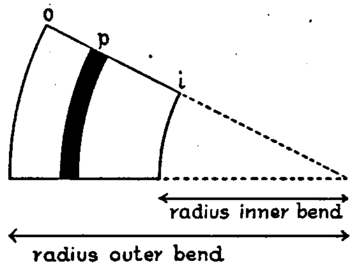


Fig. 6. Schematic illustration of the direct proportion of the length of the inner and outer bends to their respective radii. i: inner bend; o: outer bend; p: pith.

The corrected values of the length of vessel elements at the inner bend, around the pith, and at the outer bend are 340, 448, and 523 μ respectively. The radii corresponding with the inner and outer bend measure 7.9 and 14.1 mm respectively. For the two radii corresponding with the localization of vessel elements of 448 μ length on both sides of the pith, the values are 11.9 and 13.2 mm.

At the inner bend, the vessel elements decrease in length from 448 to 340 μ (ratio 0.8), while the corresponding radii measure 11.9 and 7.9 mm respectively (ratio 0.7). For the outer bend, the vessel elements increase in length from 448 to 523 μ (ratio 1.2), while in this case the corresponding radii measure 13.2 and 14.1 mm respectively (ratio 1.1). These results appear to be satisfactory because there is a fair agreement between the two ways of approach. Similar ratios were established in another case.

In order to obtain more precise and more detailed information, a much thicker branch was chosen. In this case the diameter of the branch was 16.3 mm. The layer of wood at the inner bend was 7.6 mm thick, that at the outer bend 5.1 mm, while the eccentric pith measured 2.8 mm in diameter, leaving 0.8 mm for the two layers of bark. The loop was, in this particular case, nearly closed. Eight samples from different positions and of the same dimensions as those mentioned before, were isolated and macerated, after which the length of a number of vessel elements and fibres was measured. In the sample from the extreme inner bend adjacent to the cambial zone, no wood vessels or fibres could be distinguished; the component elements resemble parenchyma cells. Their length amounts to only 49 $\pm$ 13 μ. It must be kept in mind that cambial activity was so extensive that the bend was nearly closed. The cambial zone at this site was, therefore, in the longitudinal sense, reduced to almost zero.

Table 7 gives the data. Data for the wood vessel elements are given in non-corrected form, i.e. the value of the total length. For comparison, data are given in addition for adcambial and admedullar fragments of wood from a straight portion of the same branch.

It is very enlightening to study the data from Table 7 in graphical form. (Fig. 7). The abscissa is divided according to the areas occupied

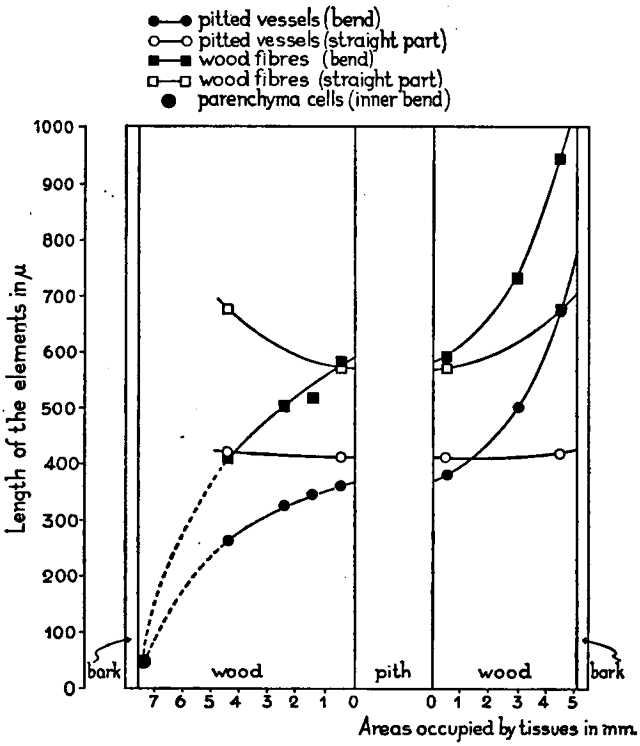


Fig. 7. Presentation of the data from Table 7. The abscissa is subdivided according to the areas of wood, pith, and bark found in the median section of the bent twig under discussion. The various elements are plotted along the ordinate according to their length.

by the various tissues in the median section of the bend; the ordinate shows the length, expressed in μ, of the elements under investigation. To simplify matters we show the mean values of each set of two distances from the pith between which the wood samples were taken. The dispersion of the values for the length of the elements concerned is not expressed in the graphs, only the mean values having been used.

The slight increase in length of the wood elements from pith to cambial zone observed in straight parts of the branch is probably due to a lengthening of cambial fibres as described by BAILEY (1920). Especially in Gymnosperms and relatively primitive Dicotyledons —*Corylus avellana* belongs to the latter category—Bailey observed a

TABLE 7

Length of wood vessel elements and wood fibres in a nearly closed branch loop of the twisted Hazel.

Location of the fragment	Parenchyma cells, length in μ	Number measured	Vessel elements, length in μ	Number measured	Wood fibres, length in μ	Number measured
Inner bend adcambial	30–100 (49 ± 14)	50				
Inner bend 4–5 mm from pith			210–338 (263 ± 46)	15	188–750 (413 ± 118)	70
Inner bend 2–3 mm from pith			210–420 (323 ± 47)	25	285–825 (503 ± 113)	70
Inner bend 1–2 mm from pith			240–488 (345 ± 51)	50	240–735 (518 ± 109)	70
Inner bend 0–1 mm from pith			218–510 (360 ± 78)	35	360–863 (585 ± 107)	70
Outer bend 0–1 mm from pith			270–525 (383 ± 58)	36	383–825 (593 ± 162)	40
Outer bend 2.5–3.5 mm from pith			375–750 (503 ± 77)	45	458–1013 (735 ± 119)	60
Outer bend adcambial			465–900 (668 ± 107)	64	465–1275 (968 ± 159)	62
Straight portion admedullar			230–540 (413 ± 20)	50	390–788 (578 ± 98)	50
Straight portion adcambial			285–563 (420 ± 22)	34	315–938 (675 ± 150)	50

gradual increase in length of cambial fibres until a certain age is reached.

From the graphs pertaining to the inner and outer bends of a contorted portion of the branch it is evident that the extreme lengthening of wood elements towards the cambial zone in the outer bend cannot be ascribed to Bailey's phenomenon except to an insignificant extent. For the inner bend the inverse phenomenon is clearly demonstrated by the gradual decrease in length of the elements towards the short nondescript cells situated adcambially.

6. Tension wood

6.1. *Occurrence and localization*

The remarkable twisting of the branches of the twisted Hazel might show some relation to special features in the structure of the wood. Straight parts alternate with more or less sharp bends in all sorts of positions, so that in certain areas reaction wood might be present.

Two kinds of reaction wood have been described in the literature: tension wood occurring in hardwood species and compression wood in plants with so-called softwood, belonging to the Angiosperms and to the Gymnosperms respectively. Tension wood is always found at the upper side of branches, compression wood at the lower side. It is evident that in the case of the twisted Hazel only tension wood need be considered. Macroscopically, tension wood is often recognizable in transverse sections as pale-coloured, more or less shining areas in otherwise darker-coloured wood. Under the microscope, the libriform fibres are characterized by the presence of a so-called gelatinous or mucilaginous layer belonging to the secondary wall. The layer in question consists of relatively pure cellulose and contains no lignin (Wardrop and Dadswell, 1955).

Twigs and thicker branches of *Corylus avellana* and its cultivar '*Contorta*' were cut into pieces about 5 mm long and fixed in a mixture of 70 parts 95 % ethanol, 5 parts glacial acetic acid, 5 parts of a 40 % formalin solution, and 20 parts distilled water. They were then cut into sections 15–20 μ thick with a freezing microtome. The sections were stained according to Dadswell and Wardrop (1949) but using fast green in combination with safranin instead of the less stable light green. After washing with distilled water, the sections were stained with a solution of 1 % safranin in 50 % ethanol for 18 hours, washed with 50 % ethanol, counterstained with a 1 % solution of fast green in 96 % ethanol for 30 seconds, washed with 96 % ethanol, and mounted in Caedax after dehydratation in a series of ethanol, tertiary butanol, and xylene. After staining, in tension wood a green-coloured secondary wall contrasts nicely with a red-coloured primary wall; in normal wood both primary and secondary wall are red.

The result of the present investigation shows that tension wood does occur in *Corylus avellana* and its cultivar '*Contorta*'. Normal Hazel shows the presence of tension wood at the upper side of horizontal branches, the vertical shoots of course never possess tension wood. Moreover, the formation of tension wood can be induced by bending a vertical shoot into a vertical loop. This method was introduced by Ewart and Mason–Jones (1906). Our results are in agreement with their finding that tension wood is found at the upper side of the horizontal parts of the artificially-made loops, but we also found tension wood at the outer side of the vertical part of the loop.

Dadswell and Wardrop (1949) state that tension wood (so-called "white wood") in Angiosperms is always found at the adaxial side of branches grown in a horizontal position. A still more important question is whether horizontally-grown branches always show tension wood at their upper side. Sato (1956), from his experiments on stems of *Corchorus* and *Cannabis*, gives a positive answer to this question. One of his conclusions is that the position in which these stems had grown could be deduced from the anatomy of the plants.

The results of our investigation on the presence and the location of tension wood in naturally-occurring loops of the twisted Hazel, combined with some data on the normal Hazel, are given in Table 8. Most of the symbols used are explained in Fig. 8.

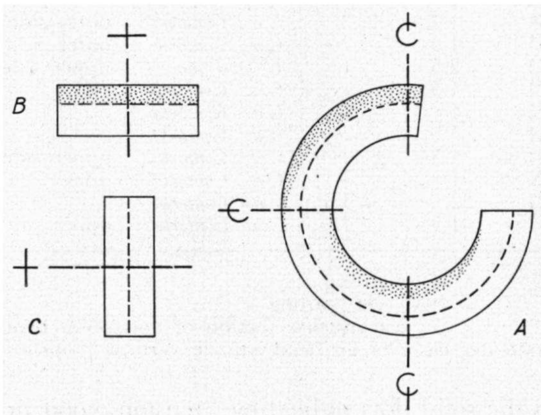


Fig. 8. Schematic drawing of longitudinal sections of: A: part of a vertical loop; B: part of a horizontally-growing shoot; C: part of an upright-growing shoot. Dotted areas: tension wood; dotted line: pith; +, -+-, ¢, -€, and ç symbols for transverse sections prepared from the indicated spots.

At first sight these results are not satisfactory because various data do not seem to agree. In order to better reflect the situation, the data have been divided into two categories according to whether tension wood is present or absent. For each case in Table 8 it must be considered whether tension wood might be expected or not. According to the literature and our own observations (see pp. 202 and 203), tension wood might be expected at the upper side of horizontal portions of shoots and in the outer bends of loops. Table 9 summarizes the results.

TABLE 8

Location and degree of development of tension wood.

Symbol	Sample No.	Diameter of loops in cm	Age in years	Object	Location of tension wood	Degree of development of tension wood cell walls
+	V		1	*C. avellana*	upper side	++
+	VII		1	*C.a. 'Contorta'*	upper side	++
+	XIV		4	*C.a. 'Contorta'*	upper side	+
+	IV		1	*C. avellana*		—
+	VIII		1	*C. avellana*		—
¢	III	2	1	*C. avellana* A	upper side	++
¢	VI	2	1	*C.a. 'Contorta'*		—
¢	XVI	2.5	1	*C.a. 'Contorta'*	upper side	+
¢	IX	3–4	2	*C.a. 'Contorta'*	upper side	++
¢	XIII	1.5	2	*C.a. 'Contorta'*	upper side	+++
¢	X	1	3	*C.a. 'Contorta'*		—
-€	III	2	1	*C. avellana* A	outer side	±
-€	VI	2	1	*C.a. 'Contorta'*		—
-€	XVI	2.5	1	*C.a. 'Contorta'*		—
-€	IX	1.7	2	*C.a. 'Contorta'*	outer side	++
-€	XIII	1.5	2	*C.a. 'Contorta'*	outer side	±
Ç	III	2.5	1	*C. avellana* A	upper side	++
Ç	VI	1.5	1	*C.a. 'Contorta'*		—
Ç	XI	1	2	*C.a. 'Contorta'*		—
Ç	XII	1	2	*C.a. 'Contorta'*		—
Ç	XIII	1.5	2	*C.a. 'Contorta'*	upper side	++
Ç	X	1	3	*C.a. 'Contorta'*	sides	±
-€	II	2	3	*C.a. 'Contorta'*		—
-€	I	1.5	4	*C.a. 'Contorta'*	upper side	+

— none ++ strong
± slight +++ very strong
+ moderate -€ transverse section of horizontal bend
C. avellana A indicates cases of artificially-made vertical loops.

Adding up the solid dots indicating "tension wood present" shows that they outnumber by 14 to 8 the open circles which indicate the cases in which, contrary to expectation, no tension wood could be found. This contradiction at first sight seems deplorable. However, the possibility remains that some of the "open circle" cases might have "some excuse" for their "behaviour". One of us (Siebers) observed that tension wood may be absent in the first year's wood cylinder of a branch which in later years very clearly shows this particular type of wood. The absence of tension wood might thus be explained for four of the eight cases in which tension wood is absent contrary to expectation (Twigs VI and XVI). Similar relationships might also be sought between the position of twigs and branches and the situation of the pith, (eccentric or centric), on the one hand, and correlations between the presence or absence of tension wood and the eccentricity or centricity of the pith on the other.

TABLE 9

Object	Tension wood present	Tension wood absent
Corylus avellana		
+	●	
+		●
+		●
Corylus avellana A		
¢	●	
-€	●	
ç	●	
Corylus avellana 'Contorta'		
+	●	
+	●	
¢	●	
¢	●	
¢	●	
¢		○
¢		○
-€	●	
-€	●	
-€		○
-€		○
ç	●	
ç	●	
ç		○
ç		○
ç		○
-€	●	
-€		○

● cell wall structure according to expectation
○ cell wall structure contrary to expectation.

Because the cambial activity in the inner bends of contorted twigs and branches is greater than in the outer ones and is furthermore greater on the upper side of horizontally-growing branches than on the lower side (HABERLANDT, 1929; SCURFIELD and WARDROP, 1962), situations can be imagined in which tension wood combines with centric pith. Our investigations on this point are not sufficiently extensive to justify any conclusions.

6.2. *The use of fluorochromes for the detection of tension wood*

One of us (SIEBERS, 1960) has stated that fluorochromes can be succesfully used for the detection of tension wood. It was found that in a series of different types of fluorochromes in contradistinction to the primary cell walls of both normal and tension wood and to the secondary walls of the former type of wood, the secondary walls of tension wood exhibit no fluorescence at all or only a very slight amount. Studying cross-sections of fluorochrome-treated wood in ultra-violet light under the fluorescence microscope reveals dark areas

TABLE 10

Fluorochromes used	Staining	Prim. N. Sec. N. Prim. T.	Sec. T.	Pericycle	Phloem	Fluorescence colour	Prim. N. Sec. N. Prim. T.	Sec. T.	Pericycle	Phloem
Fluorescein	none	—	—	—	—	greenish yellow	+	—	+	—
Uranin	orange	—	—	—	±	greenish yellow	+	—	+	—
Titan yellow	none	—	—	—	—	blue	+	—	+	+
Magdala red	pink	—	—	—	+	yellow	+	—	+	—
Congo red	none	—	—	—	—	green and pink	+	—	+	+
Anilin blue	blue	—	+	±	—	blue	+	—	+	—
Rhodamin-B	violet	+	—	+	±	orange	+	—	+	—
Fuchsin red	violet	+	—	+	—	rose red	+	—	+	—
Coriphosphin	brownish yellow	+	++	+	+	yellow	+	—	+	—
Acridin orange	brownish yellow	+	++	+	+	orange yellow	+	—	+	—

— very weak or no colouration or fluorescence
±, + and ++ moderate, strong, and very strong colouration or fluorescence

Prim. N., Sec. N. Primary and Secondary cell walls of Normal wood
Prim. T., Sec. T. ditto of Tension wood

of tension wood next to areas of strongly fluorescent normal wood.

Since the above-mentioned publication gave no details about the colour of the different types of cell walls after staining with a number of fluorochromes or any data on elements other than those of the secondary xylem, some further results are presented here. (See Table 10).

It is evident that apart from Titan yellow and Congo red, the fluorescence pattern is uniform, however different the staining of the different types of cell walls may appear in visible light. Especially the lignified cell walls of the elements from the primary and secondary xylem and from the pericycle exhibit strong fluorescence.

Discussion

The authors are well aware that the data presented here give no information about the cause of the abnormal structures described. These structures must be traced to the very young stages of development of the shoots because they are heavily contorted from the very beginning. Possibly, the stem apex itself shows some abnormal features and the observed phenomena may be a direct or indirect consequence of certain apical abnormalities.

The former may hold for the differences observed in the pericyclic regions of normal and contorted twigs. An indirect consequence is certainly the case for the way secondary xylem is formed in the contorted parts of the twigs. Because of the twisted shape of the primary shoot, the cambium does not form a straight cylinder but is also twisted. In the twisted portions, during secondary growth the cambial area increases at the outer bends but decreases at the inner portions of the bends. This has its repercussions in the anatomical structure of the secondary tissues. Quantitative analysis of the secondary xylem reveals that the greater part of the observed changes can be explained by a gradual alteration of the pattern of the cambial areas in question and by changes in shape and proportion of the cambial elements themselves.

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