The Production of Adventitious Roots and their Relation to Bird's-Eye Formation (Maser-Holz) in the Wood of Various Trees.

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With Plates VIII.-XI.

In the spring of 1903 my attention was called by the Regius Keeper to the fact that many cherry-laurel shrubs (*Prunus Laurocerasus*, Linn.) in the Royal Botanic Garden, Edinburgh, as well as elsewhere, were prone to produce an abundance of adventitious roots, and under his direction I began an examination of the phenomenon with the object of determining what conditions brought about their formation.

While searching in the Garden for material showing roots in various stages of development I came across three young maple trees, each of which had produced numerous adventitious outgrowths somewhat resembling those on the cherry-laurel, and subsequently the Regius Keeper showed me two young apple trees which were literally covered with outgrowths of a similar nature. After that I commenced a systematic search throughout the Garden in the hope of discovering other examples, with the result that similar formations were found on several specimens of wych-elm, Lawson's cypress, and *Thuja gigantea*.

A few microscopical sections soon confirmed the original impression that those adventitious structures were in reality roots. They could be traced back as round cylindrical prolongations through several year-rings of the wood until they ultimately merged into normal medullary rays, from which, as subsequent investigation proved, they took their origin ; and although differing in some minor details, the adventitious roots in the different species to be described in this paper agree in one important point, that is, they all originate from medullary rays, which, by a process of cell-division, have become abnormally broad, so that they appear like cylinders running through the wood and phloem, whence by a process of apical growth they are continued out as root-rudiments into the cortex, through which these ultimately force their way to the exterior. Their increase, especially in the tangential direction, causes the elements of the xylem and phloem to assume a bent and twisted or wavy course, such as is found in the so-called Curled or Bird's-eye Maple.

A search through the literature indicated that the subject would repay further investigation, hence a detailed examination of each specimen was undertaken. My results, so far as they have gone, are in entire accordance with, and confirm those of, previous authors, but they will be allowed to speak for themselves. Before proceeding, however, to the detailed description of the species examined, a brief resumé of some of the more recent literature on the subject is given. I may mention that it has been my special endeavour to confirm the statements made in this paper by means of photographs.

According to Strasburger[1], Curled or Bird's-eye Maple owes its origin to "the unusually sinuous course taken by the elements of the wood," which he attributes to the production of numerous adventitious buds, and also to the formation of abnormally broad medullary rays round which the wood elements are forced to bend, and thus to deviate from their usual course. No mention is made of these rays being rhizogenous.

Frank[2] points out that bird's-eye formation in wood is not due to adventitious buds alone. He finds that medullary rays may become round and enlarged, thus displacing the elements of the xylem and phloem, so that they must assume the characteristic wavy irregular course seen in this kind of wood. He further states that recent authors are fairly unanimous in the view that

[1] Strasburger, Text-book of Botany, 2nd Eng. Ed., 1903, p. 143.
[2] Frank, Die Krankheiten der Pflanzen, 2nd Ed., Vol. I (1895), p. 81.

bird's-eye formation in wood is directly caused by the presence of numerous adventitious buds, and that bird's-eye maple occurs principally where such buds have been formed in numbers, especially such as result from wounding. These buds are developed from small groups of meristematic cells produced by the cambium. Some develop into short-lived shoots, others persist as small woody cones. In either case they form cylindrical interruptions in the cambium, and the newly-formed elements of the wood and bast are forced to deviate from their usual course and form the characteristic convolutions round these centres or "eyes," which can be always recognised in the net-work formed by the vasa.

The late Professor R. Hartig[1] also proved that not only adventitious buds but also remaining pieces of old tissues, when they occur at a place over which callus is being formed, can offer the same local hindrance to the course of the newly-formed wood-elements, so that they become surrounded and isolated like islands in the callus. He observed in occlusions where the wood-body was covered with old bark still adhering to it by means of the medullary rays and remains of cortical tissue that the grain of the wood was interrupted by those remains, the newly-formed elements being forced to deviate round them.

In anatomical structure the burred wood agrees in all essential points with normal wood, and Frank definitely states that it may be produced by a broadening of certain medullary rays without any accompanying adventitious buds or other foreign bodies, and he points out that, among former authors, Schacht alone mentions that burred wood can occur without any accompanying adventitious buds, and that the same author found very beautiful bird's-eye formation on the outer year-rings of smooth stems of specimens of *Abies* and *Castanea* which were several hundred years old.

A curious case of burr-formation in the apple is mentioned by Sorauer[2], who describes and figures certain groups of conical outgrowths, which may arise either on one side or all round the stem. Those groups occur principally at the base of the shoot

[1] Hartig, Zersetzungserscheinungen des Holzes (1878), p. 136. Taf. XIX. Figs. 5 to 8.

[2] Sorauer, Schutz der Obstbaume (1900), p. 139.

or at the junction of a new shoot with that of the former year, but seldom in the middle of the shoot. He ascribes their origin to a growth-peculiarity in some trees in which the medullary rays have been unusually broad from the first, or become broad later, and project as wedge-shaped protrusions into the cortex which is ruptured. He states "that the majority of these projecting "medullary rays are covered by a woody-cone which is in "continuity with the last year-ring of the branch. Neither buds "nor leaf-rudiments can be recognised on these new formations, "so that they are to be regarded as wood-pegs, and the phenome-"non is to be explained as 'Kropfmaserbildungen.'"

There is a strong resemblance between the *Pyrus* described by Sorauer and the one to be described in this paper. They seem indeed to be identical if one compares the illustrations and descriptions, although Sorauer's interpretation differs from mine.

The formation of adventitious roots on the stem is not uncommon in willows and poplars, but in most cases some damage to the main root-system has preceded their production.

According to Frank[1], when the main root-system suffers injury, by any cause whatever (fungus, insects, physical conditions of soil), there occurs a production of new adventitious roots above the injured part, especially on the normally subterranean stem-portion of the perennating plants, but even also on the under part of the stem near the surface of the soil.

Further, according to R. Hartig[2], when the free access of air to the roots is prevented by too deep planting, the roots are killed. The tree either dies straight off, or may die off gradually, without being able to form new roots or replace the asphyxiated ones. Only a few trees, for example, willows, poplars, but more frequently shrubs, can develop numerous adventitious roots near the surface of the soil, and, like rootless slips, may form a new root-system. Similar conditions occur where earth is piled up round old trees, as often happens by the sides of roads and railway cuttings.

That the willow can produce numerous adventitious roots even on fairly thick-barked trees may be seen in Plate VIII., Fig. 1.

[1] Frank, Die Krankheiten der Pflanzen, 2nd Ed., Vol. I (1895), p. 91.

[2] R. Hartig, Lehrbuch der Pflanzenkrankheiten, 3rd Ed., (1900), p. 265.

This tree stands near the pond in the Royal Botanic Garden. Its rate of growth has been carefully recorded by Dr. Christison[1]. It is in a well-sheltered position and grows in fairly damp soil. Incidentally, it may be mentioned that in this specimen many of the earth-roots were projecting with their free ends above the ground. Directly they reached the soil-surface they became thick and fleshy, with a deep red colour, very much resembling, in fact, the adventitious roots produced on the stem. They could be followed down in an oblique direction into the soil, in which they branched copiously till they joined the main system.

Following that of the willow is a figure (Plate VIII., Fig. 2) of a gean-tree (*Prunus avium*) situated on the western border of the Garden, at the base of which an abundant production of adventitious roots has taken place. The tree is in a fairly sheltered situation and appears to have been severely pruned some years ago. On a recent botanical excursion Professor Bayley Balfour called my attention to a similar tree on which he found, in addition to the basal adventitious roots, dense patches of such structures (see Plate VIII., Fig. 3) formed on the stem up to a height of from five to eight feet above the ground.

A paper, accompanied by a plate containing eight figures, by H. Klebahn[2], "Ueber Wurzelanlagen unter Lenticellen bei Herminiera Elaphroxylon und Solanum Dulcamara," and another paper by Terras[3], accompanied by six figures, "On the Relation between the Lenticels and Adventitious Roots of Solanum Dulcamara," give interesting accounts of the production of adventitious roots in those species.

Many points of resemblance are to be found between the figures accompanying those articles and the figures which accompany this one, although they do not agree in all details. For example, Klebahn does not find a connection between the adventitious roots and the medullary rays, while Terras finds that in *Solanum Dulcamara* the phellogen is stimulated to active division in front of the protruding root-rudiment. This species, therefore, seems to differ from those examined by me; since in

[1] Christison, in Notes from the Royal Botanic Garden, Edinburgh, No. 3, Dec. 1900, p. 60.

[2] Klebahn, in Flora, Vol. LXXIV (1891), p. 125.

[3] Terras, in Trans. Bot. Soc., Edinburgh, Vol. XXI (1900), p. 341.

few cases did the phellogen show any unusual activity. Again, in all cases I found a connection between the cambium of the stem and that of the root—a fact which is not figured or mentioned by the above authors in the species examined by them.

Geyler[1] has shown that the production of aerial roots is a common occurrence on *Laurus canariensis*. Their time of vegetation lasts from the end of autumn to the beginning of summer in the following year, when they turn blackish, dry up, and fall off. They occur at varying heights on the stem and are especially abundant near branch-wounds, around which they occur in circles. They seem to occur more abundantly in moist, shady gullies where many laurel-trees are thickly crowded together, while they are not to be found on single standing or isolated trees. The author ascribes their formation to the action of a parasitic fungus, and it would seem that here the production of aerial roots is purely pathological.

Lawson's Cypress and Thuja gigantea.

There are many specimens of *Cupressus Lawsoniana* and *Thuja gigantea* in the Royal Botanic Garden which show numerous papilla-like projections standing out at right angles to the shoot-axis. These are frequently of a bright green colour and vary in shape from that of a cone to that of a sphere. They seldom exceed 3mm. in length or diameter; they may occur all over the shoot, on the leafy twigs as well as on older shoots from which the leaves have fallen. Externally they appear merely as raised portions of the periderm and are irregularly distributed all over the shoot-axis (Plate VIII., Fig. 12).

If a section is made so as to pass either in a transverse or in a radial longitudinal direction through the stem-axis, the protuberance is seen to be in organic connection with the wood-body of the mother-stem. Such sections are shown in Plate VIII., Figs. 4 and 5, in both of which it is clear that the wood-cambium of the stem passes into the outgrowth and further, that in the outgrowth two distinct regions may be recognised—a central axile portion and a peripheral cortical one. It will also be seen that the cortex of the stem takes no part in the formation of the papilla, but that it is merely passively stretched.

[1] H. Th. Geyler, in Bot. Zeit., Vol. XXXII (1874), p. 322.

The origin, method of growth, and morphology of those structures is illustrated by the accompanying series of figures.

The first changes, which ultimately lead to the formation of those outgrowths, are found to take place in a medullary ray, the cells of which become very rich in protoplasm and develop large conspicuous nuclei. They then begin to divide by radial walls, so that the ray gradually increases in breadth till it ultimately loses its flattened plate-like character and becomes more like a cylinder in shape.

Plate VIII., Fig. 7, shows a ray in which this process had begun two or three years previously. It appears as an attenuated wedge with the thin end towards the pith, becoming gradually broader on its outward course through the xylem and dilating in the extra-xylar and cortical portion of the stem in a club-like manner. Throughout its whole length it consists entirely of parenchyma-cells. Those of the swollen apex are in an active state of division and growth, and are readily distinguished from the cells of the surrounding phloem and cortex by their large well-marked nuclei.

A further stage of development is shown in Plate VIII., Fig. 8. Here may be seen curving into the ray the cells of the wood-cambium which proceed to lay down, in a centrifugal manner, tracheids, the long axis of which is in a plane more or less at right angles to that of the wood-body. The first trace of this in-arching of the cambium may be seen in Plate VIII., Fig. 7, to the right of the ray where it passes through the cambium-zone. From this stage onwards the central portion of the ray consists of parenchyma plus tracheids.

In Plate VIII., Fig. 6—an older papilla in transverse section—the parenchyma-cone has become much larger, the central cylinder which is in connection with the wood-body of the stem makes a downward curve towards its apex—see Plate VIII., Fig. 5—hence this portion is not included in the section, but the preparation serves to illustrate how the parenchyma-cone has developed and has almost totally obliterated the cortical cells lying in its line of growth. It also indicates that the phellogen does not take any part in the formation of the protuberance. Whether the phloem-parenchyma participates in its formation or not I cannot say, but from an examination of all my sections I am strongly inclined to believe that this parenchyma-cone is derived by growth from the medullary ray, and that it is an exaggeration of the rudimentary cone seen in Plate VIII., Fig. 7.

The section (Plate VIII., Fig. 11.) is transverse to the medullary ray as it passes through the wood-body, and being tangential to the stem near the periphery of the wood the centre is occupied by xylem, and to the right and left of this occurs a narrow strip of phloem cut obliquely. In the wood-body the medullary ray appears circular in outline. The figure also illustrates how the tracheids of the wood have become curved and twisted on their passage into the medullary ray. Those tracheids, which lie immediately above and below the ray, do not reveal any twisting in the section, but that they do bend into the ray is apparent in Plate VIII., Fig. 5 ; as they are curved, however, in the median plane we merely see them cut at various angles, more or less oblique. On the other hand, the lateral tracheids, or those lying to the right and left of the ray, show distinctly this incurving and torsion, which we would expect to find after an examinatinon of Plate VIII., Fig. 8. The passage of the ray was traced through the phloem, whose elements were found to twist the curve into the ray, much in the same manner as those of the xylem. The bending aside or lateral displacement of the bast-fibres and the radial arrangement of the xylem in the developing root was very conspicuous in this region. A section made in the cortex of the stem and therefore nearer the apex of the papilla shows a surrounding sheath of parenchyma which belongs to the cone seen in Plate VIII., Fig. 6. Near the apex of the papilla an outer ring of tissue belonging to the cortex of the parent axis becomes visible, but it is very narrow, and its cells, which abut on the parenchyma-cone of the medullary ray-root, are very much compressed, and the apical meristem of the root occupies the greater part of the section.

Plate VIII., Fig. 13, illustrates the appearance of a similar outgrowth formed on *Thuja gigantea*. The section is transverse to the mother-axis and therefore longitudinal to the papilla which is cut in median section. At its apex is seen an undifferentiated mass of meristematic cells in which no trace of the central axis-cylinder can as yet be detected. Further down, the central cylinder appears and its basal connection with the xylem, cambium, and phloem of the stem is quite evident. A series of transverse sections showed that those papillæ were undoubtedly the beginnings of adventitious roots which spring from rhizogenous medullary rays. Their passage through the wood and bast presents the same features as those already seen in Lawson's cypress. In the wood-portion the characteristic incurving of the tracheids was very marked. The cortical cells to the side of the protruding cone (see Plate VIII., Fig. 13) are stretched and elongated, while those in front are crushed and flattened. There is also a striking difference between the size of the cells in cone and cortex. The appearance of a transverse section through the middle of one of these adventitious roots of *Thuja gigantea* is shown in Plate VIII., Fig. 10. The axile portion is surrounded by an endodermis outside of which lies the relatively broad cortex. The vascular bundle is tetrarch, being composed of four patches of primary xylem between which are placed the phloem-bundles. An enlarged view of the central portion of this root may be seen in Plate VIII., Fig. 9, where the structure can be made out better. A section through the tip of this root merely showed an undifferentiated mass of small-celled parenchyma-tissue.

Maple.

Three young maple-trees growing in the Botanic Garden exhibit a similar phenomenon. They occur in the midst of a clump of other trees and shrubs of various kinds. The soil in which they grow is well supplied with water, and the shade and shelter afforded by the other trees keep the lower portion of their trunks fairly moist. Their ages, as ascertained by Pressler's increment-borer, vary from 12 to 15 years. The only one which was sufficiently isolated to photograph is shown in Plate IX., Fig. 14. This photograph was taken about the beginning of April. The foliage-buds were then well advanced, and a fortnight later the lower part of the tree was covered with leaves, which, however, subsequently suffered severely from late frost. Plate IX., Fig. 15, is a nearer view of the limb of this tree to the right, just where it makes a bend to the left, and on it may be seen an abundant development of conical protuberances.

Plate IX., Figs. 16 and 17, are portions of the other two trees, while Plate IX., Figs. 18 and 19, are nearer views of parts of Plate IX., Fig. 17. It will be seen from the figures that the protuberances occur irregularly distributed over the surface of the stem and have no definite sequence of development and also that they may occur singly or in dense clusters. Many of the outgrowths on the trees shown in Plate IX., Figs. 14 and 17, have pierced the periderm and protrude as short, white cylinders; whereas, on the specimen in Plate IX., Fig. 16, the periderm has merely been raised into papillæ but has not yet been pierced. Those endogenetic structures do not necessarily make their appearance externally, even as minute papillæ on the periderm, till some time after their formation. When visible from the outside they can be traced back through two or three or more year-rings of the wood. In fact a tangential longitudinal section of the stem at one of those root-clusters shows all the appearance of the so-called Bird's-eye Maple. In Plate IX., Fig. 19, the lower part of a root-cluster has been cut away in order to show this feature.

The specimens shown in Plate IX., Figs. 20, 21, and 22, are instructive and illustrate several important features. The top specimen in Plate IX., Fig. 21, is a short cylinder extracted by means of Pressler's increment-borer, and has one of these conical projections at its apex. The lower specimen of the same figure proves that the core of the cone is in organic connection with the wood-body of the stem, the cap-like covering of the bark having been lifted off. An enlargement of this specimen is given in Plate IX., Fig. 22, in order to show that the woody-cone does not terminate in a single point, but runs out into several fine threads. In the cap-like portion at the top of this figure the outer cork layers are seen to have been ruptured by the emergence of a whitish cylindrical protrusion. The bottom specimen of Plate IX., Fig. 20, is a cylinder split longitudinally. The darker central band is the basal continuation of the protuberance through the wood-body of the stem. The middle specimen is a cylinder in transverse section and shows two such round swollen rhizogenous medullary rays on their passage through the wood; while at the top of the same figure is a part cut out of a stem with scarcely any apical papilla, although a dark streak may be detected running in towards the pith. This is the commencement of one of these outgrowths. Plate IX., Fig. 25, shows, greatly enlarged, a longitudinal section from the surface of the bottom specimen of Plate IX., Fig. 20. It consists of three photomicrographs of different portions taken separately and subsequently pieced together. The inward prolongation of the papilla is distinctly seen passing through the cambium and wood. It will be observed that here again the cambium-cells show the same incurving as do those of Lawson's cypress and *Thuja gigantea.* The apex of the papilla appears hollow and torn. This is due to the resistance offered to its outward growth by one of the bundles of hard sclerenchyma-fibres which occur in the cortex. To the left in the cortex lie a few dark discoloured patches of sclerenchyma which have been displaced by the outgrowth. They have, however, offered a certain resistance which is indicated by the depression formed opposite to them in the protruding cone.

Plate IX., Fig. 24, represents an early stage in the development of a papilla, which, although continued for some distance back through the wood, is not yet visible on the outside. The formation of the papilla commences with the broadening out of a medullary ray round the end of which the wood-cambium spreads. Simultaneously with this a conical cap of parenchyma is formed over the apex, which projects into the cortex of the stem. This parenchyma-mass seems to arise from division of the parenchyma-cells of the phloem. It may be seen in the figure arching out into the cortex and compressing its cells, so that the gradual attenuation of the cortex in front of this developing cone is quite apparent. The line of demarcation between the two tissues is indicated by the dark line of crushed cells. In the middle of the papilla occurs a triangular area consisting of a disorganised mass surrounded by one or two layers of meristematic parenchyma. The central mass is composed of somewhat displaced and crushed-up remains of sclerenchyma-fibres.

A further stage of development is shown in Plate IX., Fig. 23. The parenchyma-cone has now become much larger and has reached the outer cork-layer through which it is about to break. Right and left lie the sclerenchyma-fibres and other tissues of

[1]Sorauer, Schutz der Obstbaume (1900), p. 58, finds that meristematic cells may arise in a similar way round hard sclerenchyma-bundles in the cortex of the apple-tree.

the cortex which have been pushed aside and displaced. The line of displaced sclerenchyma-fibres on the right and the white streak formed by splitting to the left indicate approximately where the protruding parenchyma-cone abuts on the cortex. At its apex is seen a patch of disorganised tissue which is again caused by sclerenchyma. The prolongation of the wood-cambium around the protruding medullary ray is very clearly seen. This cambium-mantle lays down tissue on both sides. The cells deposited on the inside become thick-walled and lignified, while the tissue on the outside retains its parenchymatic character and appears as a light-coloured zone.

A transverse section near the apex of a mature outgrowth shows a central and a cortical mass of tissue surrounded by a peripheral layer of cork. In sections taken lower down it is quite easy to make out endodermis, pericycle, phloem, xylem, and pith. The arrangement of the vascular elements is that characteristic of roots as may be seen in Plate X., Fig. 30, which illustrates the appearance of a transverse section taken through the base of the protruding portion of a root. In it the first traces of xylem may be distinguished, between which lie the three patches of phloem rendered conspicuous by the large white cells which one usually finds associated with the phloem in maples. The pith runs out into three arms, at the ends of which occur the xylem-patches. Outside the pericycle and endodermis comes a relatively broad cortex with its outer layer of cork-cells. Plate X., Fig. 28, shows a transverse section through the basal portion of an older and more mature root. The pith has become thick-walled and sclerosed. The three patches of xylem have become more elongated and the phloem is more pronounced. In other cases, not figured here, however, secondary growth in thickness was found to have taken place. In Plate X., Fig. 28, the outer cork-layer is also more marked than in Plate X., Fig. 30. Although the figures given here show tetrarch construction, diarch and triarch bundles were of quite as frequent occurrence.

A longitudinal section of a mature medullary ray-root with its central cylinder, cortex, and outer cork-layers is shown in Plate X., Fig. 26, but the features of interest to be noted here are the two lenticular patches placed right and left at the base of the protruding root. In Plate X., Fig. 27, we have one of those patches more highly magnified, and in it may be distinctly seen a connection between the cork-cambium of the stem and the cork-cambium of the root. The piece of cork-cambium seen on the left-hand side of the figure belongs to the stem. At the base of the lenticular patch this cork-cambium forks, one branch running round the outside, while the other branch passes round the inside of the patch at the top of which the branches unite and continue round the periphery of the medullary ray-root. This lenticular patch of tissue is a portion of the parenchyma-cone seen in Plate IX., Figs. 23 and 24, which has ultimately been pierced through by the outgrowing root.

These roots are not permanent structures, but die off at a comparatively early period after they have pierced the periderm, but before this happens a cork-layer is formed across their bases by a branch from the cork-cambium of the stem given off shortly before it forks around the lenticular patch of tissue referred to above. This cork-cambium may be distinctly seen in Plate X., Fig. 29. The old root is cut off therefore much in the same way as a leaf. Sorauer gives a figure[1] of a portion of stem of maple on which bird's-eye wood (Maser-holz) has been formed. The bark has been removed to show what the author calls the wooden-pegs (Holz-Spiese). At the top of the figure they are shown in cross section. The structure presented in that figure recalls very strongly what is seen in our Plate IX., Fig. 19, while the projecting woody-cones resemble the one seen in Plate IX., Fig. 22. Whatever other causes may produce Bird's-eye Maple it would certainly seem that lignified rhizogenous medullary rays can bring about its formation.

Apple.

A very curious and striking example of an abundant production of adventitious outgrowths was pointed out to me by the Regius Keeper on two small apple-trees in the Royal Botanic Garden. All their stems and branches were covered by remarkable coral-like excrescences, especially noticeable at the base of both spur-shoots and elongated shoots. Plate X., Fig. 31, gives the

[1] Sorauer, Pflanzenkrankheiten, 2nd Ed., Vol., I (1886), p. 732, Fig. 38.

general impression presented by a portion of one of those trees In Plate X., Fig. 37, we have a detached branch with its spur-shoots ; at the base of each spur-shoot a number of those conical projections may be seen, while at the base of the branch itself their massed arrangement is very apparent. Plate X., Fig. 36, is the basal portion of Plate X., Fig. 37, enlarged.

It may be well to mention here that these outgrowths were evidently in no case the result of previous wounds and had not been preceded by any callus formation.

In order to see how they would behave when brought into heat and moisture, a cutting was taken from one of the trees and placed in a forcing frame of a warm moist glass-house. The conical protuberances in a surprisingly short time (36 hours) had elongated about 6mm. and in two days were 13mm. in length. This specimen is shown in Plate X., Fig. 35. When put into moisture and heat the protuberances were in the same condition as those seen in Plate X., Fig. 37. It will be observed that in their growth the roots have a downward tendency. This is well seen in Plate X., Fig. 34, which is a photograph of a cutting laid horizontally on the fibre of the forcing frame in the hot-house. The roots then grew vertically downwards into the fibre. Moisture, as might be expected, has a great effect on the rate and direction of their growth.

Plate XI., Figs. 39, 40, and 41, illustrate the effect of causing one of the roots to grow into a glass tube filled with sand. Fig. 39 shows the cutting before the tube was attached. Fig. 41 indicates how the tube was attached ; the root is seen growing into it ; while in Fig. 40 we have the root after the tube was removed. That those structures have a strong geotropic tendency is clearly shown in Plate X., Figs. 32 and 33. A cutting was inverted so that its apex pointed in a downward direction ; when the roots developed, their direction of growth was towards the turned-down apex, Plate X., Fig. 33. After being allowed to remain in this position till the roots were about 6mm., the cutting was re-inverted, so that base and apex each occupied its normal relative position ; this was immediately followed by a downward curving of the root-tips (Plate X., Fig. 32.)

When the air-moisture was sufficiently great, a fine felty covering of white silvery hairs was developed. The sandparticles adhering to the root in Plate XI., Fig. 40 are held there by those hairs. The behaviour of the roots when grown in water agreed exactly with what might have been expected, that is, they became very much elongated, with no vestige of root-hairs and assumed the white colour typical of water-roots. Two or three roots of a cutting were kept just above the level of the water, with the result that they did not undergo the same change in character as those which were submerged.

THE STEM.—In a radial longitudinal section which has passed through a bud of the young stem the centre is occupied by a relatively broad pith, bounded on either side by a narrow white strip of young wood, from which the leaf-trace-bundles may be seen to come off and to pass upwards in an oblique direction through the cortex each on its way to a leaf. If, after a leaf has fallen, the scar left be examined, three dark dots may be seen on its surface, which indicate that three leaf-trace-bundles enter the petole; although only one is seen in a longitudinal section.

The vascular system of the axillary bud is also seen to come off from that of the mother-axis, but at a much higher level than the leaf-trace-bundles.

The sequence in which those various branches come off from the main system may readily be made out in transverse sections. In a section which passes across the main axis just at the place where the leaf-traces come off we have three outstanding bundles —a large central one and two smaller laterals which are about to pass through the cortex on their way out to a leaf-base. A section taken a little higher up shows that the lateral leaf-traces pass quicker into the cortex and become free sooner than the central one. In a section taken still higher up, and which passes through the base of the leaf-cushion, all three traces have become quite independent strands. The vascular system of the bud comes off here, interior to but in the same radial plane as the central leaf-trace. The cambium ring of the stem passes in a loop-like manner round its periphery, and the pith is also continued out into it. This semi-circular portion of cambium proceeds to lay down xylem on the inside and phloem on the outside. Further up, when the vascular-system of the bud with its central pith becomes entirely free, this cambium forms a complete ring. This arrangement of the leaf-trace and bud-bundles was carefully studied in the specimens in order to make quite sure that there should be no chance of mistaking any of these several bundles for those of the adventitious roots.

THE ADVENTITIOUS ROOTS.—The microscopical structure of these roots agrees very closely with those in the other species. The transverse series, in fact, presents no new features.

If the axis-cylinder be examined under a high power, Plate X., Fig. 38, the various tissues are found to present very characteristic root-like features. The xylem-strands stand out conspicuously, and between them lie the smaller fine-walled cells of phloem. A well-marked endodermis and pericycle may also be seen. The conspicuous ring of dark-walled cells belongs to the endodermis. The ring just inside it is the pericycle, whose cells, especially those opposite the intervals between the xylem-strands, are in an active state of division. Immediately outside the endodermis ring occur groups of cells with distinctly-marked dot-like cuticularisations on their radial walls.

Those roots originate from medullary rays, which become much broadened out and swollen at their ends (Plate XI., Fig. 42). The cambium of the stem becomes arched in a vaulted manner, and runs round the periphery of the club-headed medullary ray. As the internal protuberance increases in size, the cortex of the twig is raised up into a papilla. The phellogen-layer does not appear to take any part in the formation of this papilla. Ultimately the periderm is ruptured and the root is seen protruding through the torn ragged collar just like an ordinary soil-root (Plate XI., Fig. 43). It will be seen from this figure that the cambium of the stem is directly continuous with that of the root; further, the continuation of the root back into a wedge-shaped medullary ray is quite apparent. To the left of the old root may be seen a younger one in course of development.

In the apple-stem the endodermis is by no means a well-defined layer, but the pericycle may be recognised by the patches of thick-walled sclerenchyma-fibres, which are developed in it. The cells of the pericycle between those patches are of a parenchymatous nature. The hard sclerenchyma-strands offer considerable resistance to the outgrowing root. Those on the flanks of the root become bent out of their course and displaced to one side. Those directly in front are forced outwards to some slight extent, but, being held firmly in position by their long spindle-form and their pointed ends dovetailing into each other, they gradually cut into the soft protruding tissue of the root. Such a patch may be seen to the right in Plate XI., Fig. 43, lying at the bottom of the deep incision which it has made in the cortex of the root.

A comparatively early stage of development is shown in Plate XI., Fig. 42, which is a section transverse to the stem and longitudinal to the root-rudiment. That this structure has nothing whatever in common with the vascular supply to the leaves or buds was easily seen on comparing it with a transverse section of a normal stem. We have here a medullary ray which has become abnormally broad and developed a large swollen apex projecting into the cortex and causing a corresponding papilla to appear on the outside. Over the apex of the protruding medullary ray may be seen a dark semi-circular cap, which is formed by the crushed and flattened remains of cortical cells, against which the apex of the outgrowing protuberance is pressing. The continuation of the cambium round the swollen end of the ray can be traced.

The dense coral-like masses at the base of the shoot (Plate X., Figs. 36 and 37), are formed by closely-packed adventitious roots which branch copiously.

Elm.

There are various elm-trees (*Ulmus campestris*) in the Garden which have likewise thrown out numerous peg-like protuberances which, on microscopical examination, were also found to be medullary ray-roots. Plate XI., Figs. 44 and 45, give a general impression of the appearance and arrangement of those adventitious structures. In a radial longitudinal section of both stem and adventitious root (Plate XI., Fig. 49), the continuation of cambium and xylem of the stem into the papilla can be easily traced. In transverse section those excrescences showed distinct root-like characters.

The aerial roots in this tree had not pierced the periderm or cork-layers of the stem, and it would seem that, for a time at least, the phellogem keeps pace with the outgrowing root. On this tree I have not yet observed any cases where the cork-layer has been broken through.

In addition to this specimen there are two wych elms (*Ulmus montana*), not far from the palm-house, which bear at their bases the large burrs so characteristic on many trees of this species. Numerous water-shoots have sprung up round their bases, forming a thick cover. These water-shoots all bear well-developed protuberances, especially on their under side, which resemble in appearance and agree in structure with those seen in Plate XI., Figs. 44 and 45. However, those adventitious roots were not confined to the branches alone, but were also to be found scattered over the surface of the burrs, which were, as usual, thickly covered with small adventitious shoot-buds, nevertheless a careful examination showed that many root-rudiments which might have been easily passed over for buds were also present. The size and shape of both structures were fairly similar, but the absence of bud-scales soon led to the detection of the root-rudiments which sometimes, though rarely, grow out into aerial roots. (See Plate XI., Fig. 48, which is a piece cut out of one of the burrs.) A radial longitudinal section of a bud (Plate XI., Fig. 48), and of a root-rudiment (Plate XI., Fig. 47), show distinctly the characteristic differences between those structures. The two specimens seen in these two figures were picked off a burr on which they were growing side by side.

Mountain-Ash.

Quite recently I came across the same phenomenon in a mountain-ash (*Pyrus Aucuparia*), which bore several large burrs near the base of its stem. The adventitious roots produced on the burr in this specimen were large, well developed, and abundant.

Cross sections of the burrs (of both elm and mountain-ash) show that the inward prolongations of these roots cause the vascular tissues to assume a very irregular course. In fact the effect of these adventitious roots on the vascular tissues of the burr is very much the same as that of the adventitious buds described by Professor Marshall Ward.[1]

Cherry-Laurel.

There yet remains to be mentioned the occurrence of those adventitious roots in the cherry-laurel.

[1]Marshall Ward, Disease in Plants (1901), p. 224.

I have found that the branches which bear those structures invariably die prematurely. The appearance presented by such a branch is illustrated in Plate XI., Fig. 50, where opposite sides of an abnormal branch are shown.

So far I have found on the dead branches, without exception, the fructification of one and the same fungus, but as yet I do not know whether the fungus may have anything to do with the formation of the aerial roots or not.

In Fig. 50 the part of the stem which produced the roots is dead, but just below the place where the roots ceased to come off were two branches which were still living.

General Remarks.

In discussing the occurrence of abnormally broad medullary rays, Kuster[1] gives, in a foot-note, a reference to an article by Sorauer[2], of which I append an extract.

"The canker-like 'Rindhypertrophe' of the rose, which, according to Sorauer, is probably due to over-feeding, is accompanied by certain abnormalities in the structure of the wood. Those abnormalities consist in the formation of four abnormally broad medullary rays, which run from the pith to the periphery of the wood, dividing it into regular compartments. The tissue of the bands is composed of very porous wood-parenchyma. On two opposite arms of those abnormally broad medullary rays adventitious bud-rudiments were formed in the cambium-zone, which had produced a thick wood-cylinder pointing in an outward direction, but had not pierced the outer tissues. In the neighbourhood of these internal bud-cones all the elements were increased."

Further, Frank[3] mentions the fact that adventitious buds arise on the roots of *Pyrus japonica*, *Rubus*, *Prunus*, and others from primary medullary rays.

It would therefore appear that medullary rays are capable of giving rise to adventitious shoots in some cases, in others to adventitious roots. It would be interesting to know the conditions which determine whether the adventitious organ is to be

[1] Kuster, Pathologische Pflanzen Anatomie (1903), p. 182.

[2] Sorauer, Zeitschrift fur Pflanzenkrankheiten, Vol. VIII (1898), p. 220.

[3] Frank, Lehrbuch der Botanik, Vol. II (1893), p. 52.

root or shoot, because the potentiality of producing either certainly resides in the medullary ray.

The conditions which govern the production of the adventitious roots have, so far as I know, not yet been determined. Certainly moisture plays a very important role in their subsequent development, as it is only in the moistest situation that they persist for any time after they pierce the periderm. This was very well marked in *Thuja*.

Conclusions.

1. The medullary rays of *Cupressus Lawsoniana*, *Thuja gigantea*, *Cupressus pisifera*, *Cupressus pisifera plumosa*, *Acer*, apple, and elm may become broad and cylindrical and be continued out into adventitious roots.

2. Such abnormal medullary rays and adventitious roots may be produced abundantly on the burrs found on elm and mountain-ash.

3. Those adventitious roots may cause, like adventitious buds, bird's-eye formation in wood.

4. In none of the above cases, except possibly the cherry-laurel, did the formation of these adventitious structures appear to be the result of mechanical injury, fungus, or insect attack.

I have to express my indebtedness to the Regius Keeper for much valuable advice and the many facilities afforded to me while engaged in carrying out the investigations of which the above is a record.

Explanation of the Figures in Plates VIII.-XI.

PLATE VIII.

FIG. 1.—Willow tree trunk, bearing numerous adventitious roots.

FIG. 2.—Gean tree stem, with swollen base showing numerous adventitious roots.

FIG. 3.-- Gean tree, piece of bark cut from the stem at a height of several feet from the ground, showing cluster of adventitious roots.

FIGS. 4-12.—*Cupressus Lawsoniana*.

FIG. 4.—Section transverse to stem and longitudinal to adventitious root.

FIG. 5.—Section radial longitudinal to both stem and root.

FIG. 6.—Longitudinal section of papilla caused by medullary-ray root.

FIG. 7.—Rhizogenous medullary-ray as seen in transverse section of stem.

FIG. 8.—Passage of rhizogenous medullary-ray through cambium of mother stem.

FIG. 9.—Axis cylinder of rhizogenous medullary-ray root in transverse section.

FIG. 10.—Transverse section of rhizogenous medullary-ray root showing axis cylinder and cortex.

FIG. 11.—Section longitudinal tangential to wood-body of stem showing rhizogenous medullary ray in transverse section.

FIG. 12.—Twig showing adventitious roots.

FIG. 13.—*Cupressus gigantea.* Section transverse to stem and longitudinal radial to medullary-ray root.

PLATE IX.

FIGS. 14-25.—Maple tree.

FIG. 14.—Tree showing numerous adventitious roots.

FIG. 15.—Part of a limb of the tree seen in Fig. 14 on nearer view.

FIG. 16-17.—Portion of two other trees showing adventitious roots.

FIG. 18.—Portion of stem in Fig. 17 enlarged.

FIG. 19.—Root cluster with portion cut away to show appearance of the wood.

FIGS. 20, 21, and 22.—Cylinders extracted by means of Pressler's Increment Borer to show connection of root with parent stem.

FIGS. 23 and 24.—Young adventitious roots in longitudinal section.

FIG. 25.—Passage of rhizogenous medullary-ray through wood body, cambium and bark of parent stem.

PLATE X.

FIGS. 26-30.—Maple tree.

FIG. 26.—Median longitudinal section of adventitious root.

FIG. 27.—Part of Fig. 26 enlarged.

FIG. 28.—Transverse section near base of adventitious root.

FIG. 29.—Cork layer forming across base of old adventitious root.

FIG. 30.—Transverse section near apex of adventitious root.

FIGS. 31-38.—Apple tree.

FIG. 31.—Branches producing coral-like clusters of adventitious roots.

FIGS. 32 and 33.—Twig which was first inverted so that adventitious roots first grew down towards the tip (Fig. 33). On being reinverted adventitious roots again show positive geotropic curvature (Fig. 32).

FIG. 34.—Twig kept horizantal. Adventitious roots have developed on lower side.

FIG. 35.—Adventitious roots developed in 36 hours in warm, moist chamber.

FIG. 36.—Coral-like mass of adventitious roots developed at base of long branch.

FIG. 37.—Long branch with spur shoots, showing coral-like mass of adventitious roots at their bases.

FIG. 38.—Transverse section of adventitious root.

PLATE XI.

FIGS. 39-43.—Apple tree.

FIGS. 39, 40, and 41.—Twig one of whose adventitious roots was caused to grow into a glass tube filled with moist sand. Fig. 39, before tube was attached. Fig. 41, with tube attached. Fig. 40, after tube was removed.

FIG. 42.—Transverse section of stem showing beginning of adventitious root by dilation of medullary-ray.

FIG. 43.—Section transverse to stem and longitudinal to adventitious root which has pierced the periderm.

FIGS. 44-49.—Wych elm.

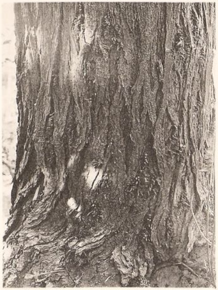
FIGS. 44 and 45.—Stems showing numerous adventitious medullary-ray roots.

FIGS. 46-47.—Longitudinal sections of bud and root-rudiment from burr on which they were growing side by side.

FIG. 48.—Pieces taken from burr showing elongated adventitious roots.

FIG. 49.—Section radial longitudinal to stem and adventitious medullary-ray root.

FIG. 50.—Cherry laurel branch with numerous adventitious roots.



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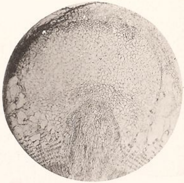

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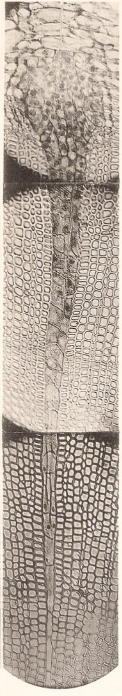

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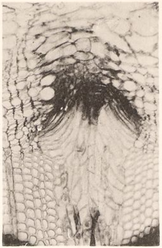

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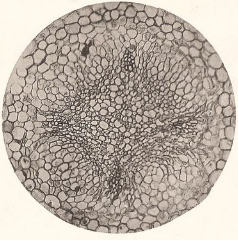

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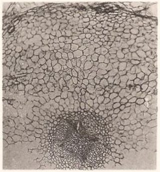

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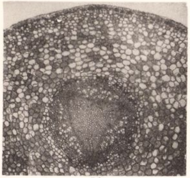

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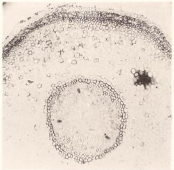

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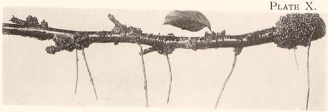

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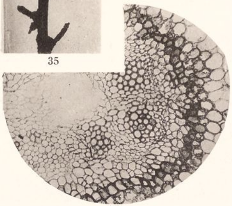

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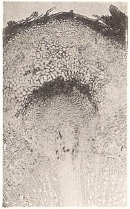

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