Seedling Anatomy of certain Amentiferae.

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With eighteen Figures in the Text.

THE present paper deals with the seedling anatomy of those forms somewhat loosely classified as Amentiferae, an investigation of which was suggested by Dr. E. N. Thomas and carried out under her direction at Bedford College.

The group Amentiferae has here been regarded as consisting of the earlier cohorts of the Archichlamydeae of Engler up to and including the Urticales.

The only account so far published dealing with seedling anatomy in any of these cohorts is that of the Piperales by Mr. T. G. Hill.¹

The majority of the species to be described are members of the Juglandales and of the Fagales. Forms belonging to Verticillatae, Myricales, and Salicales have been obtained, but in the case of several of the smaller cohorts no material has been available.

Although in point of number of species representation is somewhat inadequate, the available forms in the larger cohorts Juglandales and Fagales cover a wide range as regards size of seed and habit of seedling. In addition to the difficulty of obtaining seeds the work has been much hindered on account of the long germination periods required by many of those which have been secured.

With the exception of a few individuals of British species collected in the field, most of the seedlings described have been raised at Bedford College.

The material has been examined chiefly by means of microtome series for which the best staining combination was found to be Bismarck brown and gentian violet. For hand sections a method of staining with Bismarck brown after treatment with sodium hypochlorite and acetic acid (recommended by Chauveaud² for early stages of phloem differentiation) has been found very useful.

¹ Hill, T. G.: Seedling Anatomy of the Piperales. *Ann. of Bot.*, vol. xx, 1906.

² Chauveaud, G.: Sur l'évolution des tubes criblés primaires. *Compt. rend. Acad. des Sc.*, t. cxxv, 1897.

The chief aim of the investigation has been to record the earlier phases of primary differentiation of vascular tissue in the seedlings. To this end the material has been cut as far as possible in the youngest stage in which such differentiation could be demonstrated. Owing to differences in habit and rate of growth, correlated with differences in the rate of succession of the phases of vascular development, it is not possible to fix or exactly define any one stage which shall be equally applicable to all the seedlings.

The types of seedling include, on the one hand, slender epigeal forms in which the cotyledons are elevated above the soil by intercalary elongation of the hypocotyl, development of the plumular bud being meanwhile retarded (e.g. *Alnus*, *Carpinus*, &c.) ; and, on the other hand, massive hypogeal forms (e.g. species of *Fagians*, *Castanea*, &c.) in which the axis of the plumule may be more or less well developed in the seed. In these forms growth at first takes place almost simultaneously in both hypocotyl and epicotyl, but subsequently the latter elongates rapidly while the former remains very short.

In the first case there exists a well-defined stage during which the plumular strands are not sufficiently differentiated to exert any influence on the essential structure of the vascular system of the hypocotyl, and description of transition phenomena involves only the vascular strands in primary root, hypocotyl, and cotyledons.

In the second case there is no stage in which the plumular influence can be thus non-existent, since the earliest primary differentiation of vascular tissue will extend throughout the root, hypocotyl, and epicotyl. 'Transition' here includes the connexion of the vascular system of the root and of the hypocotyl with the early leaves, both cotyledonary and plumular.

In both cases cambial development may begin so early in the region of the cotyledonary node that primary differentiation is obscured, and in some cases can scarcely be said to exist.

The most striking anatomical feature of the forms under consideration is the absence of that uniformity of structure which has been found to be so pronounced in other groups. The variations which occur relate to number and position (these factors being to a great extent correlated) of the protoxylem poles in hypocotyl and root. All the modifications may be referred to Type 3 of Van Tieghem, in which transition from stem to root structure is brought about by 'movements' of the phloem strands while the xylem centres remain fixed.

In describing the various types of structure the terms *Cruciform* and *Diagonal* (see Fig. 1) will be applied in the sense in which they are used by Dr. Thomas¹ in her recent paper.

¹ Thomas, E. N. : Seedling Anatomy of Ranales, Rhocadales, and Rosales. *Ann. of Bot.*, vol. xxviii, 1914, p. 698.

It will be remembered that there exist two modifications of the Cruciform type: the *tetrarch* as described for *Althaea rosea* and many Rosales,¹ and as occurring also in Leguminosae,² Cactaceae,³ Tubiflorae,⁴ &c., and the *diarch* as described for Ranales and Rhoeadales, and for many other cohorts.⁵ In the former case four root poles are present, two in the cotyledonary and two in the intercotyledonary planes respectively, while in the latter case only the cotyledonary poles are present. Examples of both the above types have been found among the Amentiferae to be described.

In the Diagonal type the root poles occur in planes lying between the cotyledonary and intercotyledonary planes. The following diagonal modifications known to exist in other groups⁶ occur relatively frequently in the Amentiferae: diagonal tetrarchy (e. g. *Alnus cordifolia*), hexarchy, in which the preceding modification is combined with cruciform diarchy (e. g. *Quercus*, *Castanea*), octarchy, a combination of cruciform and diagonal tetrarchy (e. g. *Carya amara*), and in addition a double diagonal octarch type in which eight xylem centres occur on diagonals lying in pairs between the cotyledonary and intercotyledonary planes (Fig. 1, *a*, *b*, *c*, *d*).

This diagonal octarchy appears to be of constant occurrence only in *Fagus sylvatica*. It is shown by some individuals of *Quercus Ilex*, and has been described by Miss W. Smith⁷ in a seedling of *Palaquium petiolare*, a member of the Sapotaceae.

In the published accounts of other groups the greater number of forms are shown to possess one or other modification of the cruciform type, diarchy being by far the most common. The diagonal type is rare, but has been described in Calycanthaceae and in Rosaceae by Dr. Thomas, in Sapotaceae by Miss W. Smith,⁸ and in Ebenaceae by Mr. Wright.⁹

In the Amentiferous forms herein dealt with (exclusive of the Piperales and Urticales), diarchy is comparatively rare, since it is found only in the Salicales and in *Betula* and *Alnus* among Fagales. In the remaining forms cruciform tetrarchy and the various diagonal modifications occur with about equal frequency. Diarchy would seem to be the characteristic type

¹ Thomas, E. N. : loc. cit., p. 698.

² Compton, R. H. : Seedling Structure in Leguminosae. Journ. Linn. Soc. Bot., vol. xli, 1912.

³ de Fraine, E. : Seedling Anatomy of certain Cactaceae. Ann. of Bot., vol. xxiv, 1910.

⁴ Lee, E. : Seedling Anatomy of certain Sympetalae. Pt. I. Ann. of Bot., vol. xxvi, 1912. Pt. II. Id., vol. xxviii, 1914.

⁵ Hill, T. G. : Piperales, loc. cit. Hill, T. G., and de Fraine, E. : Seedling Structure of certain Centrospermae. Ann. of Bot., vol. xxvi, 1912. Chauveaud, G. : L'Appareil conducteur des plantes vasculaires. Ann. Sci. Nat., Bot., 9^e sér., t. xiii, 1911.

⁶ Thomas, E. N. : loc. cit., p. 698.

⁷ Smith, W. : The Anatomy of some Sapotaceous Seedlings. Trans. Linn. Soc., ser. ii, Bot., vol. vii, 1909.

⁸ loc. cit.

⁹ Wright, H. : Genus *Diospyros* in Ceylon. Ann. Roy. Bot. Gard., Peradeniya, vol. ii, pt. 1, 1904, pp. 62-5.

for the Urticales and also for the Piperales described in the works of T. G. Hill¹ and of A. W. Hill.²

FIG. 1. Diagrams illustrating modifications of the diagonal type.

Since, however, so many of the earlier cohorts supply only a limited range as regards number of forms, comparison of this kind with the large groups described by other authors is of little value except perhaps in the case

¹ Hill, T. G. : loc. cit.

² Hill, A. W. : Ann. of Bot., vol. xx, 1906.

of the Fagales, a cohort of considerable size which presents instances of all the above-mentioned modifications.

The Amentiferae furnish interesting examples of the various degrees of connexion between the vascular system of the primary root and hypocotyl with the strands of the plumular leaves, similar to those which have been observed by Mr. Compton¹ in the Leguminosae. The traces of the early plumular leaves may show double bundle or triad structure to a marked degree.

VERTICILLATAE.

Casuarinaceae.

Casuarina. The species examined possessed slender, wiry seedlings; there are two epigeal cotyledons and a relatively long hypocotyl. The plumular axis develops earlier than is usual for this type of seedling. In the youngest individuals obtained, the minute bud enclosed within the short cotyledonary tube possessed three leaf whorls with well-differentiated vascular system. At the first plumular node there is a pair of rudimentary leaves alternating with the cotyledons, while successive nodes bear leaf sheaths, like those on the adult branches, consisting of four to six members. Well-developed buds which expand early are present in the axils of the cotyledons.

Casuarina equisetifolia. The cotyledons fuse into a short tube above the node. In the epicotyl each member of the leaf whorls contributes a single vascular strand. At the cotyledonary node six such strands are present, two in the intercotyledonary plane (from the first pair of leaves) and four diagonally placed (related to the members of the second whorl). These strands close up, forming two groups of three in the intercotyledonary plane. The cotyledons show an extended double bundle in which the medianly placed protoxylem becomes exarch at the node. Two lateral strands are present in the base of the petiole resulting from the union of more numerous ones at higher levels. The laterals sometimes approach the diverging halves of the central strand so that their phloem portions merge. The three strands of each cotyledon enter the axis without change in their relative positions. The central cotyledonary protoxylem continues downwards in the cotyledonary plane, while the metaxylem diverges from it. The metaxylem and protoxylem of the laterals approach the intercotyledonary plane, while elements of an earlier stage of differentiation appear in connexion with it on the sides adjacent to the poles. At a relatively high level in the hypocotyl the lateral metaxylems become united across the intercotyledonary plane, owing partly to contraction of the stele as a whole, and partly to the presence of centrally placed protoxylem which is not differentiated near the node. The phloem of the

¹ loc. cit.

plumular strands in the intercotyledonary plane becomes divided and united to the cotyledonary phloem in the diagonal corners. A few xylem elements from the plumular leaf-trace persist for a time external to the central intercotyledonary protoxylem. The hypocotyl stele now consists of four protoxylem poles, two in the cotyledonary and two in the intercotyledonary planes in connexion with tangentially differentiated metaxylem, and alternating with four phloem groups diagonally placed. An endodermis is present. In passing downwards the pith becomes smaller and tangential differentiation of the metaxylem is gradually replaced by centripetal, so that a typical tetrarch root structure is obtained above the collet.

In *C. tenuissima* and *C. stricta* the anatomical features are similar to those above described. In the latter species an older seedling showed that secondary growth begins very early in the region of the cotyledonary node, but is delayed at lower levels.

C. inophloia, described by Chauveaud,¹ is tetrarch and resembles the above species.

In these forms 'transition' takes place in accordance with the cruciform tetrarch type previously referred to (see p. 577).

PIPERALES.

Mr. T. G. Hill² has described the seedling anatomy of members of this cohort, including several species of *Piper* and of *Peperomia*, all of which appear to conform to the diarch type. *Peperomia peruviana*, a geophytic form described by Mr. A. W. Hill,³ and *Piper excelsum* referred to by M. Chauveaud⁴ are also diarch.

SALICALES.

Salicaceae. Seeds of several species of *Salix* and of *Populus* were obtained, but all except those which were sown immediately after ripening failed to germinate.

Salix caprea, *S. repens*. These have very small epigeal seedlings. In each cotyledon petiole there is an extended strand which is resolved into a double bundle at the node. The two double bundles together constitute in the hypocotyl a diarch stele having central protoxylem in the cotyledonary plane flanked by tangential metaxylem wings, and four phloem groups diagonally placed. Contraction of the stele with fusion of neighbouring phloems in the intercotyledonary plane produces a normal diarch root.

MYRICALES.

Myricaceae. Seedlings of only two species were obtained, and these were almost indistinguishable in external appearance. They are small, wiry, and slow growing. The cotyledons are epigeal. The first plumular

¹ loc. cit., p. 302.

² loc. cit.

³ loc. cit.

⁴ loc. cit.

leaf is prominent at an early stage and causes slight asymmetry in the structure of the node.

Myrica californica (Fig. 18, III). The cotyledon petioles each possess a double bundle whose metaxylem and phloem diverge so as to be laterally placed with respect to the median protoxylem. At the node this protoxylem occupies the cotyledonary plane with metaxylem spreading tangentially on either side of it. In the upper part of the hypocotyl the stele conforms to the diarch type (see p. 577). The central protoxylems with their adjacent metaxylem wings constitute xylem arcs or secants in the cotyledonary plane, while the four phloem groups occupy the diagonal corners. In the intercotyledonary plane are the traces of the first and second plumular leaves, slightly differentiated as regards primary elements,

FIGS. 2 and 3. *Myrica californica*. 2. Transverse section of hypocotyl near cotyledonary node. $\times 280$. 3. Transverse section of root. $\times 320$. *ph.* = phloem; *cot.* = cotyledonary plane; *intercot.* = intercotyledonary plane; *px.* = protoxylem.

but linked with neighbouring cotyledonary traces by cambium which produces two bands of vascular tissue leaving wide gaps outside the protoxylem poles in the cotyledonary plane. In descending the hypocotyl this secondary tissue dies out. The phloem of the plumular trace persists for a time; it becomes divided, and its halves unite with the adjacent cotyledonary phloems. In the intercotyledonary plane feebly differentiated protoxylem elements appear, with metaxylem spreading tangentially on either side of them and increasing in amount as the hypocotyl is descended (Fig. 2). A tetrarch stele results, with protoxylems at the cotyledonary and intercotyledonary poles flanked by tangentially spreading metaxylems which eventually meet so as to form a lignified ring around the pith (Fig. 3). A well-differentiated endodermis is present. The stele

becomes more compact at lower levels, while lignification proceeds centripetally rather than tangentially from the protoxylem centres. In the region of the external collet the walls of the endodermis become much thickened. Tetrarchy persists throughout the root.

Myrica Gale. The structure of the cotyledonary traces and their behaviour on entering the axis resembles what is found in *M. californica*. At the node the cotyledonary and plumular strands unite to form a very compact stele in which the pith soon becomes obliterated by lignified elements. The cotyledonary phloems unite in the intercotyledonary plane in the manner of the diarch type. At a high level the stele shows the structure of a diarch root with a somewhat broad xylem plate, surrounded by a well-differentiated endodermis (Fig. 4). Diarchy extends

FIGS. 4 and 5. *Myrica Gale*. 4. Transverse section of lower part of hypocotyl, showing diarch root-structure. 5. Transverse section of root of same seedling near its apex. *cot. px.* = protoxylem of cotyledon; *ph.* = phloem. Both $\times 480$.

throughout the hypocotyl. In the region of the collet extensions of the xylem mass in the form of metaxylem and exarch protoxylem elements bisect each phloem group in the intercotyledonary plane. The cruciform tetrarch arrangement thus produced is continued downwards throughout the root (Fig. 5).

The above species agree in the possession of a tetrarch root, and also in the diarch structure of their hypocotyls near the cotyledonary node. In *M. Gale* the intercotyledonary protoxylem poles do not extend upwards above the collet, and the hypocotyl structure is that of a diarch root, but in *M. californica* four phloem groups always remain distinct, and the intercotyledonary protoxylem poles extend upwards through the greater part of the hypocotyl.

JUGLANDALES.

Juglandaceae. This family includes both hypogeal and epigeal forms, in all of which the cotyledons are deeply bifurcated, the resulting halves being again divided.

All the species of *Juglans* and *Carya* examined possess large seeds and robust seedlings. The bifurcation of the massive folded cotyledons extends down to where the lamina merges into a broad flattened petiolar region. There is a very short thick hypocotyl and a stout primary root. The plumular axis lengthens at an early stage and bears scales like rudimentary leaves which show gradual transitions to the mature form.

Juglans nigra. The cotyledon petioles each contain a small central bundle flanked by two pairs of large lateral strands which supply the four lobes of the lamina. These lateral strands are extended and somewhat incurved, and smaller branches from the lamina sometimes unite with

FIG. 6. *Juglans nigra.* A. Cotyledonary node. B. Hypocotyl. C. Root. *px.* = protoxylem; *ph.* = phloem. Arrows show direction of cotyledonary and intercotyledonary planes.

them in such a position as to produce inverse orientation. This does not extend into the node.

The central cotyledonary trace enters the axis in the cotyledonary plane and is resolved into a double bundle. The adjacent laterals approach each other and enter as a more or less compact group in the diagonal planes. The intercotyledonary poles are occupied by the traces of the first two plumular leaves. Each consists of a central protoxylem group flanked by metaxylem, beyond which are two divergent phloem groups (Fig. 6). The structure is that of the triad unit considered by Dr. Thomas¹ to be characteristic of cotyledonary and probably also of plumular traces.

The triad arrangement is continued upwards in the epicotyl until the exit of the leaf-traces as double bundles with loss of their central protoxylem. In the short hypocotyl, root poles are organized in the cotyle-

¹ loc. cit., p. 732, and Text-fig. 28, p. 716 (*Draba Aizoon*).

donary plane from the central strands of the cotyledons, their metaxylems being supplemented by that of the lateral groups. Widely extended tangential masses of metaxylem result, as the stele surrounds a very large pith. In the intercotyledonary plane the amount of metaxylem helping to constitute the plumular traces becomes increased, and they continue downwards as root poles with which the cotyledonary strands make no connexion (Fig. 6, A, B, C). In the cruciform tetrarch root all the poles are equivalent, and the differentiation of their primary xylem becomes entirely centripetal. Groups of plumular metaxylem in the diagonal planes also extend into the root, and neighbouring cotyledonary phloem groups do not

FIG. 7. *Juglans nigra*. Part of transverse section of very young epicotyl, showing one of the plumular leaf-traces in cotyledonary plane (*cot. plane*). *px.* = protoxylem; *ph.* = phloem. $\times 360$.

appear to meet, perhaps owing to the large size of the stelar ring, but become linked by phloem developed later in connexion with plumular traces. The hypocotyl stele is surrounded by a well-marked endodermal sheath, portions of which leave the axis with the cotyledon traces. Within the endodermis there is a wide pericycle consisting of several layers of cells. Secondary thickening takes place at an early stage.

In this seedling there has been traced the complete connexion of a plumular leaf with an intercotyledonary root pole by means of a vascular strand showing uniform structure in hypocotyl and epicotyl. Similar connexions have been described by Compton¹ as occurring in *Caesalpinia sepiaria* and in *Pithecolobium Unguis-cati*, members of the Leguminosae.

¹ loc. cit., pp. 9 and 21.

Juglans Sieboldiana. This seedling agrees with the preceding species in the structure of its cotyledon strands and in their arrangement at the cotyledonary node. The traces of the first and second plumular leaves in the intercotyledonary plane show double structure with isolated median protoxylem, but this last feature is not continued into the epicotyl, where the leaf-trace consists of two widely separated endarch bundles. The structure of the hypocotyl and of the root is tetrarch and resembles that of the last species, but some of the xylem of the lateral cotyledonary strands diverges towards the intercotyledonary plane, where it becomes connected with the plumular strands. The greater part of the metaxylem of the intercotyledonary root poles is continuous with that of the cotyledonary strands, but the central portions are continued up into the epicotyl as the traces

FIG. 8. *Juglans Sieboldiana*. Outlines of vascular system. A. At cotyledonary node. B. At a lower level in the hypocotyl. cot. = cotyledonary traces. Arrows indicate cotyledonary and intercotyledonary planes.

of the first two leaves. In other respects, such as the presence of a large pith and early secondary thickening, and also in the fact that metaxylem from later plumular leaves may persist in the diagonal planes, the seedling is similar to that of *Juglans nigra*.

Juglans cinerea. The cotyledon petioles show the usual five strands, but the central one is extremely small, and the constituents of the laterals are not compactly united. These enter the axis as groups of two or three approximated bundles at the diagonal corners. The plumular strands are very slightly differentiated, but show doubleness of their phloem. In the hypocotyl, the cotyledonary poles are supplied by the central strands together with adjacent parts of the lateral groups, the remaining portions of which are connected with the intercotyledonary poles as in the normal tetrarch type. No plumular tissue takes part in the primary organization of root poles.

Juglans regia. This seedling showed tetrarchy in root and hypocotyl

related to central and lateral cotyledonary traces as in *Juglans cinerea*. The material available was so old that secondary thickening in the region of the cotyledonary node prevented the primary structure of the plumular traces from being followed with certainty.

The genus *Juglans* is interesting, since in some species there is complete continuity of a vascular unit similarly constituted throughout root, hypocotyl, and epicotyl. In all the species there is great similarity in the structure of the hypocotyledonary stele.

The seeds and seedlings of the genus *Carya* are not so large as those of the species of *Juglans* described above, but in habit and mode of germination they are similar.

Carya olivaeformis. This seedling is smaller and slenderer than that of the other species described. The hypocotyl possesses eight protoxylem centres surrounded by the customary tangential metaxylem and diverging phloem groups. Passing upwards, six of the xylem poles, four diagonal and two cotyledonary, are continuous with the xylem of the central and lateral cotyledon traces respectively. The two remaining intercotyledonary strands with their related phloems extend up into the epicotyl, forming the traces of the first two plumular leaves exactly as in *Juglans nigra*.

In young seedlings octarchy persists throughout the root, but in one somewhat older individual the intercotyledonary poles diminished in size and became merged with one of the neighbouring diagonal ones by suppression of the intervening phloem group. The cotyledonary poles became less well developed, and were represented at low levels by tangential arcs of xylem. Rootlets arose in connexion with the diagonal poles only.

This seedling shows the combination of diagonal and cruciform tetrarchy, and is further interesting in that it possesses well-developed intercotyledonary root poles organized in connexion with plumular leaf-traces as in *Juglans nigra*.

Carya amara. The only seedling obtained was very old and had produced great length of root with much secondary thickening, although the plumule had not emerged from the seed.

In the hexarch root two of the poles are in the cotyledonary plane, while the remaining four are diagonal. The poles persist in the hypocotyl and are connected with the central and two lateral double bundles in the cotyledon bases. Higher in the cotyledon petiole there are six bundles arranged in pairs, each being surrounded by a single layered sheath of cells. A thick-walled tannin containing endodermis surrounds the stele in both root and hypocotyl. At the cotyledonary node portions of it pass out with the cotyledon traces and are continuous with the bundle sheath in the petioles.

Pterocarya rhoifolia (Fig. 18, VI). This species has a fairly robust epigeal seedling with a long hypocotyl. The cotyledons (deeply four-lobed as in the other genera) are thin and leaflike. Their petioles possess two pairs of lateral strands and a small central one as in *Fuglans*. Near the node the neighbouring lateral strands approach and fuse, while the central strand becomes divided, its halves merging with the laterals. There thus result two large divergent strands which enter the axis at diagonal corners as endarch bundles. At this level there is no central protoxylem. The first plumular leaf-trace shows slight lignification which dies out at the cotyledonary node. The cotyledonary metaxylems become divided, and their halves approach the neighbouring cotyledonary and intercotyledonary planes, where at lower levels protoxylem is differentiated slightly external to the metaxylem. Protoxylem and metaxylem become approximated so as to produce flattened secants about the cotyledonary and intercotyledonary poles. At this stage the stele is very large, and the diagonally placed phloems form much-extended tangential bands. In the region of the collet only centripetal development of the xylem occurs. The root is tetrarch and shows a very large pith. A thin-walled endodermis with the characteristic radial dot is present in the greater part of the hypocotyl.

Fortunea chinensis (Fig. 18). This seedling, although smaller than that of *Pterocarya*, resembles it closely in habit and also in anatomical structure, except for the fact that the central cotyledonary protoxylem of the hypocotyl extends upwards into the minute central strand of the cotyledon.

FAGALES.

Betulaceae. With the exception of *Corylus Avellana* the seedlings of this family are small and slender, having an elongated hypocotyl and epigeal cotyledons. Portions of the cotyledon blades are prolonged downwards as auricles.

Alnus incana, *A. glutinosa*, and *A. cordifolia*. These are slender, wiry seedlings resembling each other very closely. In all three species the cotyledon petiole shows a double bundle, the halves of which diverge widely. The cotyledon traces enter the hypocotyl with isolated central protoxylem in the cotyledonary plane flanked by metaxylem groups, beyond which are the phloems in the diagonal positions.

In *Alnus incana* and *A. glutinosa* normal diarch structure is attained in the hypocotyl by union of neighbouring phloem groups in the intercotyledonary plane together with compacting of the xylem secants in the cotyledonary plane. In *A. glutinosa* the phloem groups remain apart for a longer period than in *A. incana*. In both species the root is diarch.

In *Alnus cordifolia* (Fig. 9) the structure of the node and of the upper part of the hypocotyl resembles that found in the species above

described, but the central cotyledonary protoxylem may be feebly developed. Neighbouring phloems unite in the intercotyledonary plane at a high level. In descending the hypocotyl the central cotyledonary protoxylem gradually dies out, while the metaxylem becomes extended, and exarch protoxylem groups appear in contact with it at the diagonal corners

FIGS. 9, 10, 11. *Alnus cordifolia*. 9. Transverse section of hypocotyl near cotyledonary node. 10. Transverse section of same at lower level, showing indications of six protoxylem centres. 11. Transverse section of same at level of 'collet', showing diagonal tetrarch root. *ph.* = phloem; *px.* = protoxylem; *cot.* and *intercot.* indicate directions of cotyledonary and intercotyledonary planes, respectively. All $\times 360$.

of the stele (Fig. 9). For a time six protoxylem centres may be present, but the original cotyledonary groups cease to be differentiated, while those diagonally placed persist into the root. In the region marked by the external collet, phloem is differentiated in the cotyledonary plane; thus completing a tetrarch root stele (Fig. 11). This method of formation of a diagonal tetrarch root recalls what is described by Chauveaud¹

¹ loc. cit., p. 320.

for *Calycanthus occidentalis*, in which the phloem strands present in the cotyledonary plane of the root die out in the base of the hypocotyl.

Betula excelsa and *B. pumila*. These are very small seedlings, resembling in habit those of *Alnus*. In both species the root is diarch and the transition features are precisely similar to those of *Alnus incana*.

The following features occur in all the above species of *Alnus* and *Betula*. The first plumular leaf is prominent, and vascular traces from this and the succeeding leaf are present at the cotyledonary node in the intercotyledonary plane. These consist almost entirely of secondary tissue and do not extend far into the hypocotyl. At an early stage the cambium develops so as to link the cotyledonary and plumular traces together, producing two bands of vascular tissue extending at right angles to the

FIGS. 12 and 13. *Carpinus Betulus*. 12. Vascular system of hypocotyl showing protoxylem in cotyledonary plane. 13. Root of same. *cot.* and *intercot.* indicate the respective planes.

cotyledonary plane, as in *Myrica*. An endodermis showing the characteristic radial dot makes its appearance at a high level in the hypocotyl.

Carpinus Betulus and *C. Ostrya*. These seedlings are larger than those of *Alnus*. The cotyledons are slightly fleshy and remain within the seed longer than do those of the preceding genera.

The anatomical features of both species are exactly similar. The cotyledon petioles possess each a large double bundle with widely diverging halves which enter the node at the diagonal corners as collateral endarch strands. Centrally placed protoxylem is present in the base of the petiole and at the cotyledonary node, but dies out immediately below it. In descending the hypocotyl each of the four metaxylem strands becomes divided into two by the failure to continue differentiation of its median elements (Fig. 12). The eight groups of metaxylem thus produced gradually 'approach' the neighbouring cotyledonary or intercotyledonary planes by means of the appearance of earlier lignified elements on the side

adjacent to the plane and the dying out of those remote from it. The stele becomes contracted and an endodermis is differentiated (Fig. 13). The central cotyledonary protoxylem reappears in the form of a few feebly lignified disorganizing elements. At lower levels similar protoxylem appears at the intercotyledonary poles. Near the collet the metaxylem makes contact with the protoxylem poles so that four somewhat extended xylem secants are formed, alternating with the phloem groups which have maintained their diagonal position. Below the collet the metaxylem becomes compacted and a tetrarch root stele results.

The first plumular leaf-trace is double at the cotyledonary node, but is differentiated so slightly before secondary thickening ensues that it makes no connexion with the primary structure of the hypocotyl. The cambium at first develops in two bands, as in *Alnus* and *Betula*.

Corylus Avellana. This is a large seedling with fleshy hypogeal cotyledons and a very short hypocotyl as externally limited. There is early elongation on the part of the plumular axis, which bears rudimentary leaves, as in *Fuglans* and *Carya*.

The cotyledon petioles each contain two massive and rather widely separated strands which enter the axis diagonally, as in *Carpinus*. At the cotyledonary node a small group of protoxylem is present between these strands, and can be traced downwards in the cotyledonary plane throughout the hypocotyl. The four groups of metaxylem from the cotyledons become each divided into two, and the resulting portions approach the neighbouring cotyledonary or intercotyledonary planes. Root poles are organized in the cotyledonary plane, as in *Carpinus*. In the intercotyledonary plane there persist the traces of the first and second plumular leaves. Their phloem in each case consists of two groups which diverge and unite with that of the cotyledons, while their xylem forms arcs of small scattered elements linking the adjacent cotyledonary metaxylems. Extended xylem secants consisting of plumular and cotyledonary elements are thus formed, and become compacted at lower levels into the intercotyledonary xylem poles of the cruciform tetrarch root. The replacement of tangential by centripetal development of the xylem takes place so gradually that typical root-structure is attained only at some distance below the collet.

In this seedling the intercotyledonary root poles are connected partly with the cotyledon traces and partly with those of plumular leaves, thus recalling *Fuglans Sieboldiana*. The plumular portion is not so well marked as in the latter species, and is continued into the epicotyl as a double strand without central protoxylem.

Fagaceae. With the exception of *Fagus sylvatica*, the members of this family to be described possess large hypogeal seedlings in which the early plumular leaves are rudimentary. In all the species the cotyledon blades are prolonged downwards below their junction with the petioles.

In the species of *Quercus* examined, the vascular structure of the cotyledonary node and hypocotyl conforms to the hexarch type (Fig. 1, B). The cotyledon petioles contain three massive vascular strands, of which the central one is double near the cotyledonary node, while the laterals are usually not obviously so until they enter the axis. Here the usual triad grouping takes place in connexion with all the strands. The hypocotyl contains six protoxylem centres (two cotyledonary and four diagonal), each flanked by scattered tangentially placed metaxylem. The adjacent phloems of neighbouring triads approach each other. The pith is very large. Plumular traces are present in the cotyledonary node and for a short distance below it, interpolated between the cotyledon strands.

Quercus robur. The hypocotyl and root show hexarch structure related to three strands in each cotyledon.

In one seedling the central strand was very small in one cotyledon and was entirely absent from the other. Five triads were organized in the hypocotyl for a short time, but only the four diagonal ones persisted, and the root was tetrarch.

Another individual showed extreme development of incurved traces in the cotyledon petioles. Irregularly grouped strands from the lamina came together, forming a much-extended central band with incurved ends and a pair of lateral strands in the form of more or less complete rings. Near the node the rings opened out and became organized as double bundles. Central protoxylem was not present above the node. The central band slowly became more compact and was resolved into a double bundle in which central protoxylem elements were present. These bands and rings consisted mainly of secondary tissue, the primary elements being very small and fugitive.

Quercus Ilex. The seeds and seedlings are somewhat smaller than those of the other species described.

In general the seedlings were hexarch, but the following modifications occurred. In some individuals, eight triads were present in the hypocotyl. These were arranged as in the double diagonal type. Each triad was continuous with one of four strands in each cotyledon, and occurred as laterally placed pairs; sometimes, however, the two innermost groups came together to form a single large central strand. A very small central strand was sometimes produced by the union of portions detached from the laterals. The root was diagonally octarch, as in *Fagus sylvatica*.

In a few otherwise normal seedlings there was increase in the number of root poles from six to seven or eight. This always took place at some distance below the collet and was observed only in relatively old seedlings.

Quercus Cerris. All the individuals examined followed the general hexarch type and showed no irregularities.

Castanea sativa. The seed and seedling are larger and more robust than is the case in *Quercus*; except in one instance, where four seeds had

FIGS. 14 and 15. *Castanea sativa*. 14 (outer figure). Half of vascular system of hypocotyl just below cotyledonary node, showing cotyledonary (*cot. 1*, *cot. 2*, &c.) and plumular traces (*pl.*). 15 (inner figure). Vascular system of the same seedling at a lower level, showing 'triads' of xylem and phloem corresponding to cotyledonary and plumular traces. The boundary line of each figure indicates the position of the endodermis. (Xylem, black; phloem, white.)

matured within a single fruit and all germinated. Their structure was similar to that of the larger seedlings.

The cotyledonary petioles possess three large vascular strands which

may be incurved, the laterals occasionally forming almost complete rings. The cotyledonary traces enter the hypocotyl and are continued downwards as triad units in accordance with the hexarch type described for *Quercus*. At the cotyledonary node, plumular leaf-traces in the form of slightly differentiated bundles or desmogen strands are interpolated between the

FIGS. 16 and 17. *Castanea sativa*. Details of vascular units indicated in Fig. 15. 16. A 'plumular' unit. 17. A cotyledonary unit (only one of the constituent phloem groups is shown at *ph.*). *px.* = protoxylem; *mx.* = metaxylem. Both $\times 360$.

cotyledon traces (Fig. 14). In descending the hypocotyl there is increase in the differentiation of the xylem elements of any pair of adjacent plumular strands, while an isolated protoxylem group appears between them. The vascular system of the hypocotyl thus comes to consist of a variable number of triad units, of which only six are related to the cotyledon traces (Fig. 14). The number of additional units may vary from two to eight, but is commonly six. At lower levels the lateral or tangential metaxylem of each triad fails

to be differentiated, while centripetal development proceeds from the central group. The lateral metaxylem of the cotyledonary triads persists downwards to a lower level than does that of the 'plumular' triads (Figs. 14, 15, and 16). Neighbouring phloems are slow in coming together, but in most cases a root stele was attained, showing from eight to fourteen equivalent protoxylem poles alternating with phloem groups. A wide pericycle and a well-defined endodermis are present in the root, and are continued up into the hypocotyl. In the youngest seedlings no root stage was observed, since the triad units persisted downwards independently as far as differentiation could be demonstrated.

It seems clear that the additional units of the hypocotyl and of the root are organized in continuity with the plumular strands found at higher levels; but the feebleness of differentiation in the upper regions of young seedlings, which is rapidly succeeded by cambial development in older stages, renders their exact connexion difficult of observation.

Fagus sylvatica. This is a large seedling of the epigeal type. The cotyledons, which are fleshy and much folded, are slow in expanding, and the elongation of the plumular axis is much retarded. All the plumular leaves are of the normal foliage type, the first two being opposite. The cotyledon petioles contain four lateral strands approximated in lateral pairs. These diverge to form the leading veins of the broad fan-shaped lamina. There is no indication of the central strand either in petiole or lamina. The vascular supply recalls that of the bifurcated cotyledons of Juglandaceae. At the base of each cotyledon petiole the four vascular strands are organized as double bundles. Eight of these enter the hypocotyl in diagonal planes, producing a symmetrical octarch structure. Metaxylem and phloem diverge more widely from the central protoxylem, which gradually assumes the exarch position. Throughout the long hypocotyl and for some distance below the collet the stele consists of eight triad groups; eventually the neighbouring phloems unite and an octarch root results. A large pith extends throughout hypocotyl and root.

The cambium, which begins its development in the upper part of the hypocotyl, is at first active only within the limits of each triad. Metaxylem and phloem become linked by secondary tissue, while the protoxylem disorganizes; so that the stele appears to consist of eight endarch bundles. A well-marked endodermis is present in the root and extends upwards throughout the greater part of the hypocotyl. A large number of seedlings examined at different stages failed to reveal any variations or irregularities such as were found in *Quercus*.

The seedlings of Fagales are of some interest, because they include examples of most of the known types of seedling anatomy together with forms showing transition from one to the other. Diarchy occurs in *Betula* and in certain species of *Alnus*. *Alnus cordifolia* shows diarchy

in the upper part of its hypocotyl replaced by diagonal tetrarchy in the root, a transitory hexarch stage being suggested in the intermediate region. Cruciform tetrarchy is found in *Carpinus* and in *Corylus*. In the latter seedling the intercotyledonary poles are connected in part with plumular strands, but not to so marked an extent as in certain Juglandaceae.

Hexarchy is the fundamental arrangement in the hypocotyl of *Quercus* and *Castanea*, but in the latter genus additional units are present which are probably related to plumular leaf-traces.

Throughout the group the early plumular leaf-traces show double structure in both epicotyl and hypocotyl. In the epigeal forms this usually applies only to the first pair of leaves, and in their case secondary thickening ensues so early that very little primary tissue is differentiated. In the hypogeal forms the growth of the plumule is so rapid that the traces of several leaves may be present at the cotyledonary node. These may extend into the hypocotyl and root, bearing the same relation to root poles as the cotyledonary double bundles.

URTICALES.

In this cohort only a few forms have been examined. All of them possess epigeal seedlings which differ considerably in size. Their anatomical features show striking uniformity.

Ulmaceae.

Celtis australis and *C. occidentalis*. These are moderately robust seedlings. The cotyledons possess a central double bundle, and transition is in accordance with the diarch type.

Moraceae.

Morus alba. The seedling is small and slender. The hypocotyl and root are diarch, transition taking place at a high level.

Maclura aurantiaca possesses a much more robust seedling, resembling those of the species of *Celtis*. Transition follows the diarch type.

Urticaceae.

Urtica cannabina has a small diarch seedling very similar to that of *Morus alba*.

Urtica dioica, *Parietaria officinalis*, and *Humulus Lupulus*, described by Chauveaud,¹ all conform to the diarch type.

General Remarks.

Speaking of the vascular structure of the seedlings of Ranales, Rosales, and Rhoeadales, Dr. Thomas² says that 'the hypocotyl shows a varying number of primary centres of xylem which alternate with two phloem

¹ loc. cit., p. 295.

² loc. cit., p. 732.

groups and from which differentiation proceeds in a more or less tangential direction on either side'. This statement may be applied equally to the Amentiferae at present under consideration, the structure of which, therefore, lends support to the view that the unit of vascular structure in the hypocotyl is the triad unit as above defined. The triads are continued upwards into the cotyledonary strands (and sometimes into plumular leaf-traces), where they constitute the familiar double bundles of so many authors.

In the Amentiferae, examples of the double bundle or triad structure in the traces of earlier plumular leaves are frequent (*Fuglans*, *Corylus*, &c.). At their base in the region of the cotyledonary node these traces usually die out or become merged with cotyledonary strands in the hypocotyl. In certain cases, notably *Fuglans nigra* and *Carya olivaeformis*, the triads of the first and second plumular leaves extend downwards into the hypocotyl as independent strands related to root poles in exactly the same way as the cotyledon traces.

In *Castanea sativa* there are interpolated between the cotyledonary traces a number of additional strands (usually seven or eight), which are well differentiated as triad units in hypocotyl and root, and correspond in position to the plumular leaf-traces or desmogen strands found at the cotyledonary node. It seems that there is continuity of unit strands between hypocotyl and plumular leaf. This would indicate that a large number of units in root and hypocotyl may be differentiated in connexion with rapidly developing plumular leaves. The number of leaves is not so great as might appear, since the three strands which enter the node from any one leaf may remain as independent centres.

In the genus *Fuglans* there are shown varying degrees of relationship of two hypocotyl units with the strands of the first and second plumular leaves. In *Fuglans nigra* the two intercotyledonary poles are in continuity with the triad units of plumular leaves. In *F. Sieboldiana* the central part of the strand is plumular, while the lateral portions diverge into the cotyledons; in *F. cinerea* the poles are entirely cotyledonary.

It is possible that a similar series might be established in the genus *Carya*, in which, so far, only two species have been examined: *C. olivaeformis*, which is octarch with its intercotyledonary poles entirely plumular, and *C. amara*, which is hexarch owing to the absence of poles in this position.

Similar phenomena ¹ have been described by Compton ² as occurring in members of the Leguminosae. Independent plumular intercotyledonary poles like those of the above-mentioned species of *Fuglans* and *Carya* have been found by him in *Pithecolobium Unguis-cati* and in *Caesalpinia sepiaria*.

¹ It is possible that the 'accessory' root bundles described by Miss W. Smith in *Bumelia tenax* (loc. cit., p. 192) may bear the same interpretation.

² loc. cit., pp. 9 and 21.

Of the smaller epigeal seedlings many are tetrarch, but very often the four poles are well differentiated only at low levels in the hypocotyl near the collet. The most extreme instance of this is furnished by *Myrica Gale* (see p. 582). It occurs also in *Carpinus* and *Alnus*. The intercotyledonary protoxylem poles persist upwards to a varying degree, but die out near the cotyledonary node; while the metaxylem diverges and passes out as part of

FIG. 18. Seedlings of Amentiferae (all figs. $\frac{2}{3}$ natural size). I. *Casuarina equisetifolia*. II. *Salix caprea*. III. *Myrica californica*. IV. *Juglans nigra* (IV a. plumule of same, IV b. younger seedling). V. *Carya olivaeformis*. VI. *Pterocarya rhoifolia*. VII. *Fortunea chinensis*. VIII. *Betula pumila*. IX. *Carpinus Betulus*. X. *Alnus cordifolia*. XI. *Corylus Avellana*. XII. *Quercus Ilex*. XIII. *Castanea sativa*. XIV. *Fagus sylvatica*.

the cotyledonary traces. In some cases the whole of the triad strand is divided between the cotyledons.

It is probable that here also the intercotyledonary centres are differentiated in relation to the plumular traces, which are frequently double strands. Since the plumular development is so much delayed, differentiation is not complete at the upper end of the seedling, so that the protoxylem

centre 'dies out' in ascending the hypocotyl, and actual connexion cannot be demonstrated.

Similar distribution of the intercotyledonary vascular units between cotyledons and plumular leaf has been recorded as obtaining in many Leguminosae by Compton, who describes it as a phenomenon of replacement in which the cotyledons are being supplanted by plumular leaves.

The variation of the level to which the intercotyledonary poles persist upwards is correlated with the rate at which the successive phases of vascular differentiation supersede one another as the hypocotyl is ascended.

The succession of phases which has been conclusively demonstrated by Chauveaud, and receives the support of Compton and of Thomas, accounts also for the discontinuity which sometimes exists between the central protoxylem in the base of the cotyledons and that present at lower levels. In the youngest stages, development of the xylem proceeds centripetally from the first centres of differentiation ('éléments alternes' of Chauveaud). This is followed by development in a tangential or lateral direction on either side of the centre, and this in turn by centrifugal differentiation, both primary and secondary.

As the seedling elongates, successive increments of growth will have their vascular differentiation initiated in continuity with the phase which is active in the preceding increment. In the hypocotyl the earliest differentiation takes place in the region of the collet and of the cotyledonary node. When there is much intercalary elongation between these two regions a succession of phases may be found in ascending from the collet and to a less extent in descending from the node, and thus there will be lack of continuity between, for example, the 'alterne' elements or central protoxylem of the cotyledonary petiole and those of the root pole (e. g. in *Carpinus*).

Although, in general, the massive hypogeal seedlings possess the larger number of root poles, there are very striking instances of the absence of a definite relation between size or habit and the number of root poles present. Thus tetrarchy is equally characteristic of the largest hypogeal seedlings examined (species of *Fuglans*) and of the slender epigeal seedlings of *Casuarina* (as instanced by Thomas¹), *Myrica*, *Alnus cordifolia*, *Carpinus*, &c. The relatively slender epigeal seedling of *Fagus sylvatica*, while resembling in external habit the diarch and tetrarch species of *Calycanthus* described by Chauveaud and by Thomas, nevertheless exhibits diagonal octarchy.

¹ Thomas, E. N. : A Theory of the Double Leaf-trace founded on Seedling Structure. New Phyt., 1907, p. 85.

SUMMARY.

1. Members of the following cohorts have been examined : Verticillatae, Salicales, Myricales, Juglandales, Fagales, and Urticales.

2. Diagonal types of transition are of frequent occurrence, and are correlated with the presence of large numbers of root poles and hypocotyl strands.

3. Diarchy is characteristic of the Urticales and also of the Piperales described by Mr. T. G. Hill, but is otherwise seldom met with.

4. The form of the vascular strands in the hypocotyl is remarkably constant, and is that of the triad defined by Dr. Thomas as the unit of hypocotyl vascular structure.

5. The hypocotyl may contain triad units, in addition to those continuous with the double bundles of the cotyledons, which are related in a similar manner to plumular leaf-traces.

6. Doubleness of plumular leaf-traces occurs very generally.

In conclusion, I wish to thank Dr. Thomas for much helpful criticism and advice, and also for having placed at my disposal for purposes of comparison her own preparations of the seedlings of other groups.

Davey, A. J. 1916. "Seedling anatomy of certain Amentiferae." *Annals of botany* 30, 575–599. <https://doi.org/10.1093/oxfordjournals.aob.a089625>.

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