Entry for the Dobbie Smith Prize in Botany.
by
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The Sycamore.

An Account of its Structure, Development, and Life History.

The Sycamore, or Plane, as it is generally called in Scotland, is a tree which thrives in most parts of Britain, and is found at its best in the hilly districts of Northern England and Scotland. It is not, however, a native tree, but has apparently been introduced at an early date. The actual date of introduction is unknown, but there are records showing that in 1690 it was planted in cemetries and around the houses of the nobility. By that date it was obviously fairly common. It was not long before it was well distributed over the whole country, as it is a tree suited for rapid reproduction. Being absolutely unharmed by severe frosts, and susceptible to few diseases and insect pests, it brings forth seed abundantly almost every year, and spreads everywhere with the greatest ease.

The sycamore is immersed in an element of falsehood and misunderstanding. Its scientific name "acer pseudoplatanus" means the "false plane", and in Scotland it is often known as the plane owing to the similarity between the leaves of the two trees. Even the latter is a misnomer our tree being quite different from the "sycamore" of St. Luke 19.4. Our tree was well known to the Romans and it was probably introduced by them, though there is no definite proof of this.

It is difficult to determine the exact geographical limits of the sycamore as it has been transplanted for centuries from its original home, which is probably the great central chain of the Pyrennes, Alps, and Carpathians. It is also found on the hilly ground radiating out from these ranges in all directions. Its western limit lies in the Iberian peninsula among the Cantabrian Mountains and its eastern limit near Astrabad, south-east of the Caspian. It occurs in the hilly districts of France except in the extreme north-west, in the Alps, Carpathians, Apennines, Sicily, Dalmatia, Jugo-slavia, Thessaly, and Epirus: in south-west Russia, Asia Minor, Armenia, and the Caucasus. Thus the tree is not found native in the more northerly parts of Europe, but it has been extensively planted in many countries of the north, and, as a planted tree, reaches its furthest north in Norway and Sweden about Lat. 64°.

In the wild state it occurs as an isolated tree or in a small group, and apparently the only natural forests, and those of small extent are in the Thuringian forests. When full grow~~th~~n at fifty or sixty years of age it reaches a height of sometimes eighty feet, though this height is rather exceptional than common. There is an extremely fine tree at Dunkeld. The soil to promote most rapid growth must be rich, not too moist, and porous, that is to say, unclogged by too great an admixture of clay: yet it is so hardy and bold a grower that it will thrive in almost any soil and will often be seen growing in all kinds of unexpected places.

Everyone is familiar with the scimitar shaped "keys", or samaras, that spin down from the sycamore in countless numbers during the end of autumn. They are beautifully formed for ensuring widespread distribution: in quite a gentle breeze they may be carried up to fifty yards in their fall alone, and in addition are often blown a considerable distance along the ground. By a high wind they are blown immense distances: they can be found in places from which no sycamore can be seen for a very considerable distance roundabout.

Viewed externally ~~it~~ the fruit consists of two distinct portions, the wing and the fruit proper. Its colour when ripe is reddish brown, but it turns to a dark brown soon after falling. The wing is about 1½ ins long and the widest part is near the tip. (fig I). The fruit is between ½ and ¾ inches in diameter. The hard outer coat is a tough leathery skin; marked externally with fine lines running in all directions: it forms the outer portion of the true covering of the fruit, called the pericarp. On removing it, a thin papery shrivelled membrane is found inside adhering to the outer cover. This is the inner part of the pericarp, and is no longer a

Figures I - IV

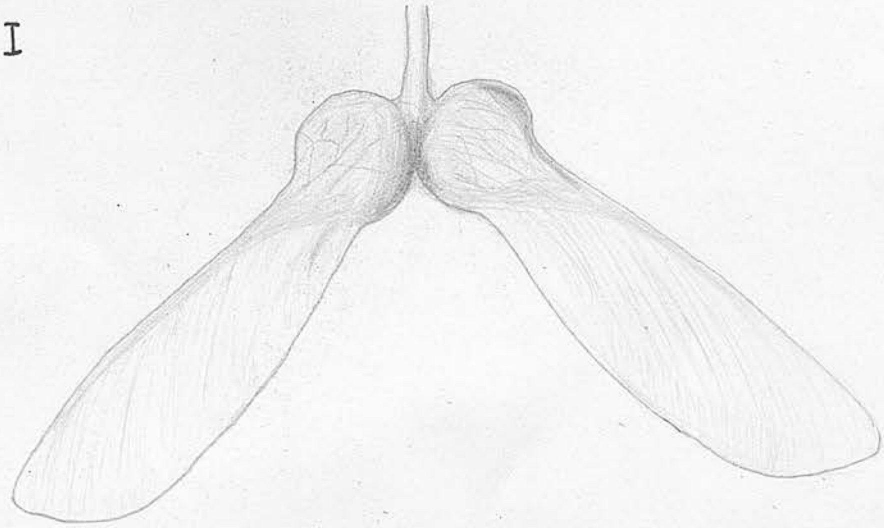
I General view of the "keys". The drawing is actual size shows the fruit the wings and the lines on the fruit.

II Showing the keys just before they fall. The vascular bundles are the last connexion to be severed.

III showing the common method of the arrangement of the cotyledons. The arrangement was studied by cutting a longitudinal section through the embryo

IV The uncommon method of the arrangement of the cotyled
This was found in only two of several seeds examined

I



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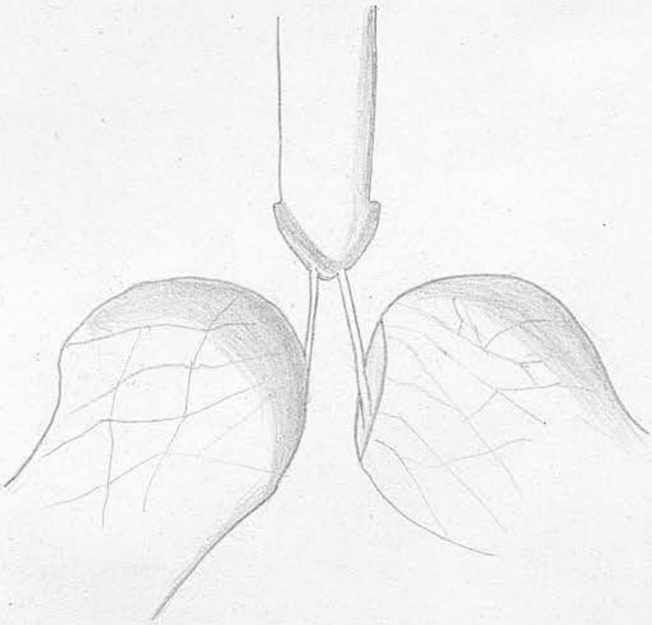

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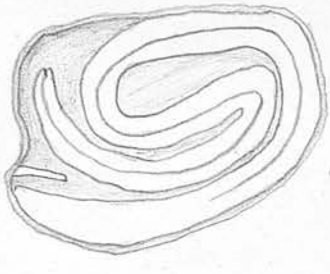
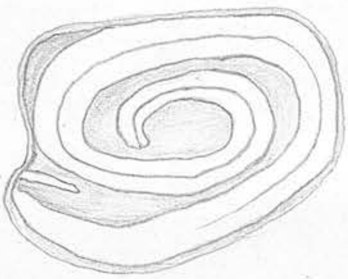


IV



a living structure, but exists simply as a protective covering for the seed inside. The centre is occupied entirely by a hard brown body, the seed, which fits tightly into its case, and so does not rattle about like the seed of an acorn. It is however attached in no way to its case in the ripe fruit, though it was previously attached definitely at the ~~posterior~~ proximal end. The shrivelling up of the tiny connecting cords caused the separation of the seed from the pericarp, and the former may be regarded as a distinct body. It is usually closely covered with a thin brown papery membrane which forms its coat - the testa. In early stages the testa is closely adherent to both the seed and the inner coat of the pericarp and both together to the harder outer coat. As the organism becomes more mature the parts dry up, and so become separated to a greater degree. Nevertheless the testa always adheres fairly closely to the seed.

Envelped in its testa and in the pericarp then, is found the seed proper which appears at first sight to consist mainly of two leaves folded closely together. This is not entirely the case however as may be seen by cutting across the mass and examining it with a lens. The greater part is built up of two sheets of light green tissue which are carefully wrapped round eachother in a characteristic manner. There are two different methods in which the cotyledons are folded, but one is much commoner than the other (fig. III). According to Sir John Lubbock the exact arrangement of the cotyledons depends on the direction of growth. If in development they ~~so~~ strike against the process which encloses the radicle, then their general direction naturally carries them outwards so that they become plicate: if on the contrary the tips of the cotyledons pass just within the micropylar process and touch the radicle, then they are compelled to grow in the opposite direction and thus become spirally coiled. In some seeds there are three
cimen II or even four cotyledons: specimens of this sort are ~~not~~ abnormal, but on the whole are not uncommon. This power of producing seeds with three or four cotyledons is apparently

inherited. Occasionally types are found in which the two cotyledons are partially divided. There are specimens showing all these varieties.

The two cotyledons are not inseperably fixed to eachother except at the begining, and on opening the fruit they may be separated with comparative ease provided that the specimen has been soaked since the cotyledons are somewhat brittle. At the point where they are not completely independent is found a small peg-shaped body. This structure is rather difficult to see and so is easily overlooked, unless some little care is excercised. These two parts together constitute the embryo of the sycamore. The peg-shaped body presents two ends. The larger is termed the radicle, and is destined to become the root of the young tree. The smaller end, the plumule grows upwards and gives rise to the stem and leaves.

The embryo consists almost entirely of a series of polygonal cells known as the fundamental tissue. Their walls are very thin, and the cells are densely filled with granules. Surrounding the cotyledons externally is a layer of specialized cells of a tubular elongated shape which form a covering for the embryo. Running throughout the whole of the cotyledons is a series of fine threads of or vascular bundles which connect up all the various parts as regards nutritive supply. Thus the embryo is built up of three specialized types of tissue, namely cell vascular and epidermal. At the tips of the radicle and plumule the structure is rather peculiar, and the tissue there is termed embryonic.

In the polygonal cells there is a quantity of protoplasm and a nucleus. The cells themselves contain numerous granules of starch which act as a nutrient reserve. Proteids tannin and fatty substances are also found in the cells. The cotyledons of the sycamore, when compared to those of the bean or pea, are peculiar in that they contain chlorophyll, which incidentally has developed in the dark. They do not contain such a large amount of nutrient reserve, but act rather as leaves, building up complex organic materials from simple inorganic compounds in the atmosphere. In the case of the bean the seedling for a long period is entirely dependent on the nutrient reserve: in the sycamore the seedling can supply itself with nutrition as soon as the cotyledons have been unfolded. The vascular bundles are in such positions as to be able to supply the radicle and plumule when they commence growing, all of the small ~~bundles~~ branches leading to one large bundle which enters the radicle. The epidermis is simply a covering tissue and plays no part in storing or conducting food substances: it extends as the plant grows, and so of course requires a certain amount of nutritive material.

When the samara falls it usually lies buried among the decaying leaves near the surface of the ground during the winter, and so it remains for some time without any conspicuous change. Some authorities state that a whole season is passed in this resting state, but some of this year's seeds kept under observation certainly developed in the spring. However a period of rest is required before the oxygen of the air and the moisture of the soil are effective in bringing about germination. Probably some complicated chemical change occurs during this time of apparent inactivity. A suggestion is that until certain ferments have been prepared in the mesophyll, the protoplasm is unable to make use of its food store and so no growth can take place. Thus after a certain period has elapsed germination can take place. Having absorbed oxygen and water, and swollen considerably the embryo drives its radicle through the pericarp. The latter plunges downwards into the earth: it is amazing to observe the way in which the radicle always turns downwards away from the light in whatever position the seed may be. It is obviously essentially necessary that the radicle should emerge first, because it both gives the plant a firm foundation to support the upward growing parts, and also provides nutrition for the

ecimen I

higher parts by aborbing water and dissolved mineral subtances through the root hairs which are developed at an early period in the sycamore.

As soon as the young root has established a firm hold in the earth, it straightens up so that the remains of the pericarp and the cotyledons are raised above the surface of the ground. The cotyledons emerge and unravel themselves taking up positions on opposite sides of the hypocotyl, that is the portion of the root above the ground (fig VI). Almost at once by means of their chlorophyll they begin to manufacture food supplies. The plumule does not make its appearance until the root has dug several inches into the ground. During the early stages it is noticeable that the plumule grows more slowly than the root in order to give the root the required stability. At first the shoot does not appear to bear any leaves, but after some time minute scales appear each of which has a tiny bud in its axil. When the shoot is about six inches high the first green foliage appears near the top. This process continues until there are about four to six leaves at the end of its first year. At the same time "secondary" roots are appearing on the radicle as outgrowths of the primary root. Each pair of green leaves arises at right angles to the axis of the pair below it, so that the pairs are alternately arranged. This is known as an opposite and decussate arrangement, and is one of the characteristic points of the sycamore

pecimen I

ecimen I

The structure of this young plant was examined by cutting transverse sections at various points throughout its whole length. Starting with the root by cutting a section a short distance from the tip and examining it under a microscope, the following structures were seen. The centre is occupied by the axis-cylinder of the root seen as a group of greyish green cells. This is surrounded by a wide margin of cells which serve as a protective covering for the central cylinder and are accordingly given the name of the root cortex. The superficial cells of this layer have the special function of producing root hairs:

Figures V - X

V Shows the seed just beginning to germinate with the radicl beginning its journey downward. Compare specimen

VI The same after about three weeks growth in a moderately warm room. The cotyledons have thrust off the brittle seed case and have expanded ready to receive the light. The plumule can just be seen between the two cotyledons

VII A seedling after the development of the first leaves. These newly formed leaves have not yet assumed the true palmatifid shape of the mature leaves.

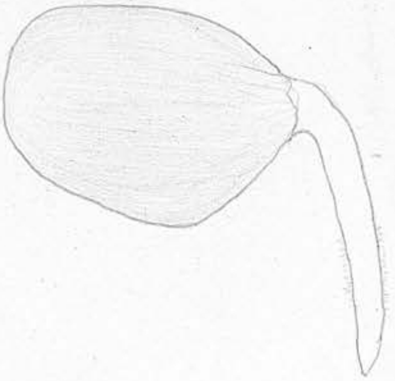
At the same time lateral roots have begun to emerge opposite the primary xylem groups of the main root. Each late root is provided with root hairs and takes part in the absorpti of dilute solutions from the soil

VIII A diagramatic view of a transverse section of a root of a yo seedling showing relative positions of the various parts. In the root the pith is comparatively small and is rapidly replaced by the xylem.

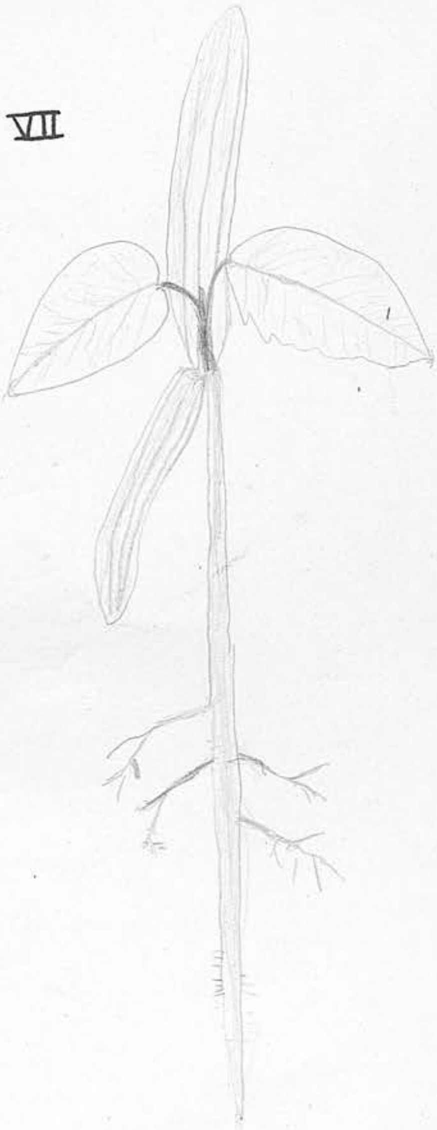
IX A portion of VIII under higher magnification, showing the xylem with the larger and younger vessels nearer the centre. The positions of the pericycle and the endodermis is also shewn. The endodermis was clearly seen by staining with iodine, as it contains much starch. Such a preparation cannot be mounted permanently as the iodine is readily oxidised.

X A diagramatic view of a longitudinal section through the end of a young root, shewing the development of the tissues

V



VII



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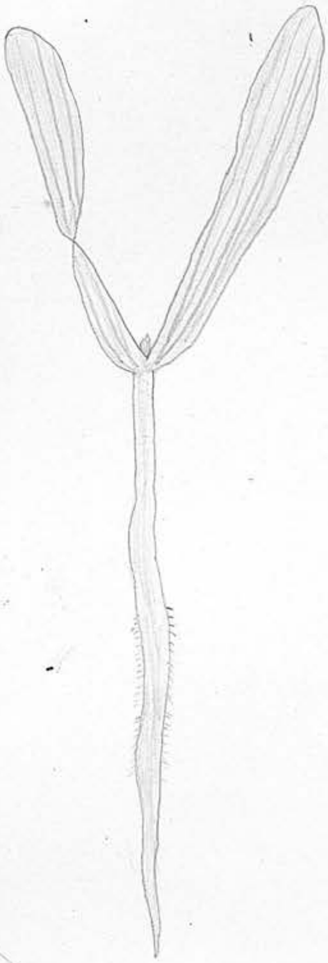
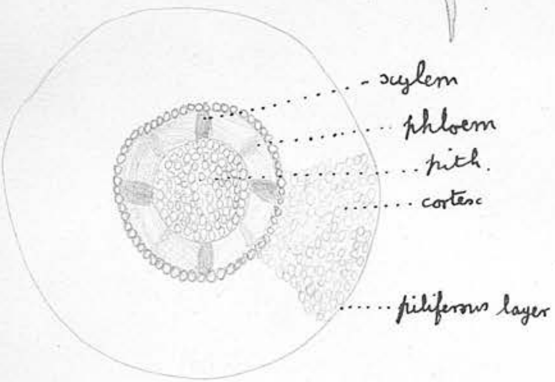
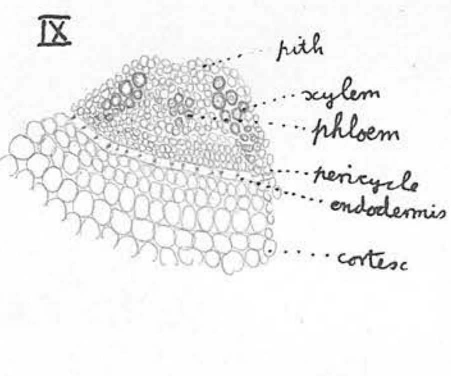


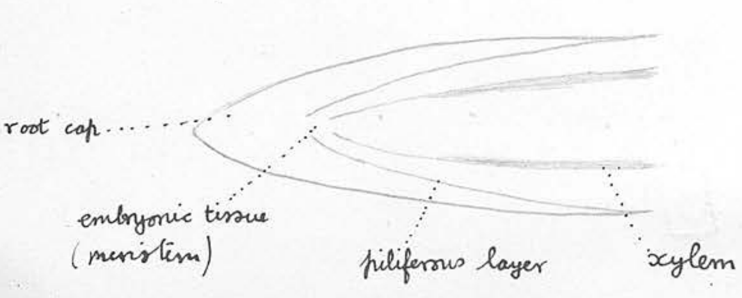
VIII



IX



X



they are known as the piliferous layer. A section nearer the tip shows that ~~lay~~ lower down there is an extra external layer. This is the root cap which covers and protects the tip of the root proper. The outer layers of this cap become gradually converted to mucilage which serves both to diminish the friction and to keep the apex moist. In a section cut further up the root the various parts are seen to be much more sharply distinguished. The central cylinder stands out more clearly as a dark mass of cells in the centre, and the piliferous layer is obvious since its cells give off root-hairs. On closer examination of the central cylinder it is seen that certain structures have been formed within its border. These are the vascular bundles, a mass of fine cords which form the vascular system of the root and can be here traced running up and down. On cutting sections still further up the root it becomes apparent that the higher one goes up the root, the more sharply differentiated are the separate structures. These gradual changes are best seen by taking a longitudinal section passing through the median plane of the root. This shows the thimble-like root cap with its rim fraying away, since the cells of which it is composed die and wear off. Obviously these cells must be replaced in some way. It is seen that the tip of the root fits closely into the cover and is organically connected with it at that point. Here new cells are added to the inner side and those that are worn away are replaced. Also at this true tip of the root it is seen that all the cells are alike and undifferentiated. There is no separation into central cylinder and root cortex: it consists merely of a circular mass of cells with very thin walls and dense protoplasm. This constitutes the embryonic tissue of the root. From here all new growth takes place: consequently the youngest part of a root is that which is nearest its apex, whereas the oldest is that nearest its base.

A short distance behind its apex the root has a broad encircling band of fine hairs. As the root grows by forming new embryonic cells at its apex the root hairs further from the apex get left behind and die off: at the same time new hairs are continually being formed nearer the tip. These hairs live only for a short time for they soon shrivel up and so are found solely on the young and more terminal parts of a root. Taking a section further up the root it is found that all the root hairs have died away and the piliferous layer is a brown cork-like substance impervious to moisture. The cortex in this region is not much changed except that its cells are being compressed or stretched by the growth of the central cylinder.

The cylinder is demarcated from the cortex by a single layer of cells, the endodermis. Inside the endodermis are two or three rows of thin-walled cells - the pericycle, which gives rise to the lateral rootlets by repeated divisions. Inside the pericycle are arranged the vascular bundles. The section shows that there are about eight alternating groups of tissue forming these bundles: of these, four groups are rendered more conspicuous than the rest because they have firm dark contours. These are the xylem vessels: the remaining four constitute the phloem vessels. The chief characteristics of the xylem vessels are that they are composed of long tubes containing air and water, and have fairly strong lignified lateral walls: their chief function is to convey water up the root to the stem. The protoxylem or oldest wood of the root is formed at the outside, and development advances from without inwards. The youngest vessels are larger than those formed early: this form of development is known as centripetal. The phloem vessels are long and tubular, but have thin cellulose walls. They contain protoplasm and other cell contents. They are not so completely tubular as the xylem vessels, the transverse septa of the cells being existent as sieve-like structures. The vascular bundles of the root differ from those of the stem in that the xylem and phloem groups are alternately arranged round the circumference of the cylinder; the xylem vessels develop in centripetal order; the bundles are more concentrated and so the central cylinder is smaller in diameter. A more detailed description of the various parts of the bundles will be given when considering those in the stem.

The chief functions of the roots are to bore down into the soil and to produce root-hairs which attach themselves to particles of soil and supply the plant with water. In the portion of the root above the growing tip lateral rootlets are produced without danger of being broken off from the parent root. These secondary rootlets emit tertiary rootlets and so on - these and rootlets of a higher order growing without any particular reference to the direction of gravitation or light. The symmetry of the root system is soon disturbed as some meet with obstructions such as stones, or are injured or destroyed by enemies. As the need for water becomes greater, the main parts of the root system thicken and act almost entirely as large water channels.

The shoot of the sycamore consists of all the structures which are above the surface of the ground. These were examined by a series of transverse sections which show that the shoot is built up of three separate systems - the epidermis or dermatogen, the cortex or periblem, and the central cylinder or plerome. In the stem, the xylem and phloem of the vascular bundles do not take alternate positions round the section, as in the root, but they are situated on the same radial lines. There is no true pericycle[x], for branches are not developed endogenously. The development of the xylem is in strong contrast with that in the root: it starts towards ~~in~~ the centre of the stem, and proceeds centrifugally. A transverse section close
cimen 4 to the terminal bud shows that the younger axis consists almost entirely of embryonic tissue similar to that at the tip of the root. A transverse section lower
ecimen 3. down shows that the outline tends to become square, though there is of course no definite square outline because the vascular bundles are continually dividing. Patches of a

[x] the outermost layer of the central cylinder however is known as the pericycl

greyish green tissue may be seen at the corners of the square. These are the vascular bundles, four in number in the hypocotyl (i.e. that portion of the stem below the cotyledons). Above the cotyledons the vascular bundles are six in number, though in sections usually more are seen due to the branches coming in from the leaves. Two bundles enter each cotyledon.

The course of the vascular bundles was examined by a close study of the leaf scars and transverse sections at various points along the stem and petiole. The group of vascular bundles which passes into the stem from the leaf is known collectively as the leaf-trace. This leaf trace consists of three bundles. Now in the sycamore the pairs of leaves decussate at right angles. Thus six bundles pass down through the internode. Considering the various bundles separately it will be seen (fig XIV) that the median bundles pass through one internode and divide at the next node into two branches which join with the lateral bundles of the pair of leaves at that point. The two lateral bundles of the leaf also pass through one internode, curve in a converging manner at the next node, and insert themselves on the same lateral bundles with which the branches of the median bundle unite. Thus six bundles continue on through the next internode and so on. In the leaf trace the two lateral bundles each divide into two, and the median bundle into three. The course of the bundles in the petiole is very complicated since these main vessels may again divide: also the bundles on entering the petiole are all concentrated near the top, but further up the lateral ones swing round so that some occupy the underneath surface of the petiole.

The detailed structure of the vascular bundle was studied by examining transverse sections under the high power of a microscope and by maceration. Maceration was carried out by dissolving 1 gm. of Potassium chlorate in 50 c.c. of concentrated nitric acid and heating small pieces

Figures XI - XVI

XI A section through a young stem just at before secondary thickeni begins to take place. The cambium has already been formed betwe the bundles and is beginning to divide to form new xylem and phloem. The endodermis forms the innermost layer of the cortex and the pericycle the outermost layer of the central cylinder. The pericycle has nothing to do with the development of lateral branches

XII A diagramatic drawing of a longitudinal radial section. In this case the section is in the plane of the medullary rays which appear as a fine network.

XIII The individual parts of the xylem as seen in specimen 1

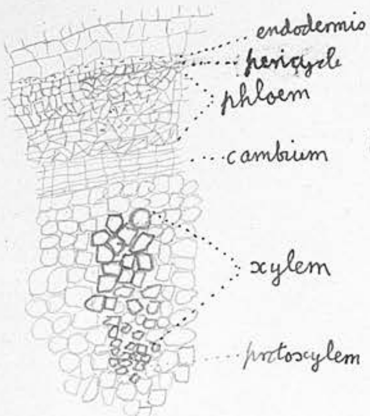
XIV A diagram of the course of the vascular bundles. The central bundle is shown in red and the laterals in black.

XV The leaf scar with a bud in the axil. The vascular bundles may also be seen.

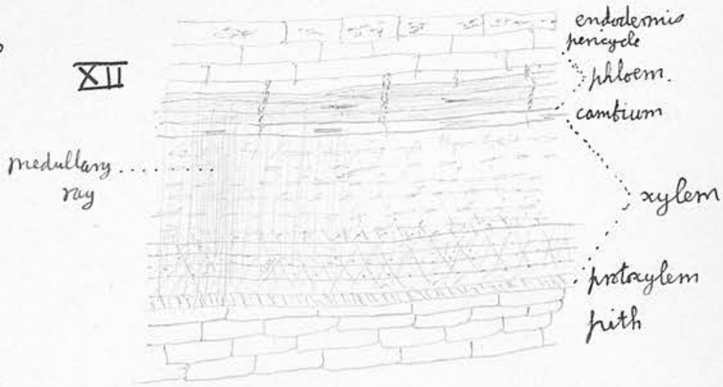
XVI A diagram of the opposite arrangement of the bud scales.

Transverse Section through Vascular Bundle   Longitudinal Section

XI



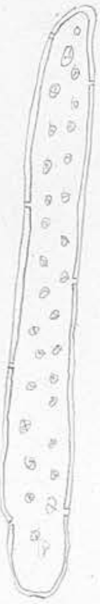
XII



III

fibre

xylem parenchyma

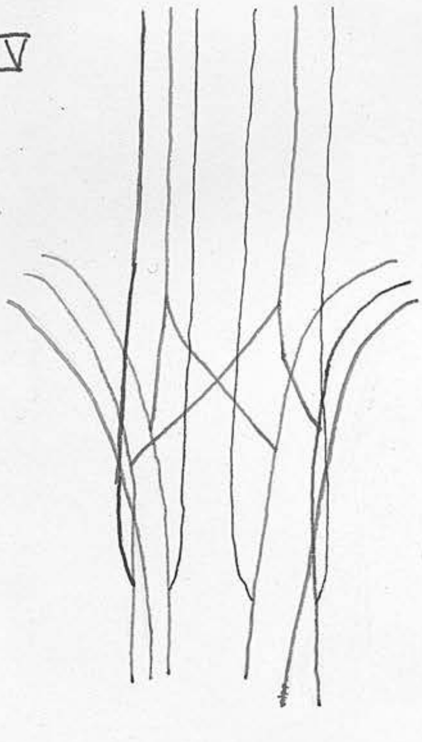


tracheid

spiral vessel

pitted vessel.

XIV



The course of the vascular bundles.

XV

The leaf scar

XVI

The arrangement of the bud scales.

of the stem in this solution. The ~~wood~~ stem is then broken down into its constituent cells. It has already been seen that the vascular bundles consist of a xylem portion on the inner side and a phloem portion on the outerside and that these portions are separated by a cambium layer. The tissue in the centre of the stem surrounded by the ring of vascular bundles is the pith. The tissue between the bundles and the epidermis is called the cortex, and that separating the bundles, the primary medullary rays. New xylem and phloem are formed by the cambium which soon unites round the whole stem forming a complete circle.

The cells of the medullary rays are in several rows: those in contact with the bundles have thick woody walls and in winter are well filled with grains of starch. The cells of the pith are on the whole similar to those of the medullary rays: they are smallest near the rounded edges of the vascular bundle. Imbedded in these cells run long continuous tubes strengthened internally by a spiral thread: their diameter is small. These are the spiral vessels which contain only water and air. The walls between the spiral thread are thin, and the winding is loose, because these vessels are the first to be formed (constituting the protoxylem), and the walls have thickened before the lengthwise growth is completed. Sometimes instead of a continuous spiral thread, isolated rings are found: the vessels are then said to be annular. Further outwards, the vessels are still spirally thickened, but the windings are closer together, as these vessels are of more recent formation. In the outer part of the xylem are found vessels which have several thin spaces in their walls. These are known as pitted vessels. The thin parts serve for the passage of liquids from one vessel to another. These ~~p~~ vessels were formed from a continuous row of cells placed end to end. The transverse cell walls were dissolved and the protoplasm was used in stiffening the walls. The tubes are marked by rings which show the original position of the transverse cell walls. In macerations these pitted vessels usually break up into the original cells, but occasionally a portion of a tube may be found complete. The tubes themselves are dead structures containing no living matter. A ~~certain~~ large number of fibrous cells also are found: these are living organisms which store up starch and give rigidity to the whole structure. They are long with pointed ends and their thick walls almost obliterate the lumen. The xylem-parenchyma consists of vertical groups of short cells which have thick walls with small pits. Cells of this type are always found in contact with the vessels. Lignified cell~~s~~ walls are much harder and stiffer than those of pure cellulose. It is especially the thick parts of the cell walls which are lignified. The secondary medullary rays exist as single radial rows of cells agreeing in structure with those of the primary medullary rays. The tracheids are long cells with gradually tapering ends. The walls are thick but they do not obscure the lumen. Numerous pits, usually elongate oblique or horizontal are found in the walls. (fig XIII)

The cambium cells, owing to their regular tangential divisions, are found in regular layers. They constitute actively dividing layers which give rise to new xylem and phloem. Thus the bundles in the sycamore are known as open because there is no definite limit to their growth in thickness.

The phloem is built up of three main parts – the sieve-tubes, the companion cells, and the phloem parenchyma. The sieve tubes are composed of long cells placed end to end. As in the root their end walls are perforated, and thus the cells are in open communication with oneanother. They retain their protoplasm, and also contain a slimy substance rich in nitrogenous compounds: occasionally starch grains are found. The sieve tubes have no nuclei when mature, since they disappear in the course of development. The sieve tubes are also perforated laterally when they are in contact: thus the contents of all the sieve-tubes are continuous. These lateral connexions are much larger than those normally existent in all protoplasm: they were thus discovered by Von Mohl long before they were even suspected to exist in ordinary protoplasm. These tubes are accompanied by narrow longish cells which are filled with protoplasm and contain large nuclei retained throughout life. The companion cells, as they are termed, and the sieve tubes have developed from the same mother cell and so the former are always found in close contact with the sieve tubes.

The rest of the phloem is composed of a series of large cells which contain protoplasm and a nucleus and form the phloem parenchyma. The oldest cells of the phloem lie at the outer edge, and as they were the first to develop they are known as the protophloem. The function of the phloem is to conduct nitrogenous food substances from the leaves to the actively growing parts. Thus it will be seen that the central cylinder consists of parenchyma and vascular bundles: the former holds the latter together and accordingly is known as the conjunctive tissue. Growth in thickness is brought about by the repeated divisions of the cells in the cambial layer. Those cells of the conjunctive tissue which border on the bundles are usually rich in grape sugar and it is through these cells that the carbohydrates pass on their journey from the leaves to the other parts.

External to the bundles is the pericycle, a layer of thin walled cells forming the outer limit of the central cylinder. The endodermis is a ring of cells immediately external to the pericycle: the cells have thick walls with numerous starch granules in their contents, and they form the inner limit of the cortex. The latter is composed of ordinary parenchyma similar to that of the pith. The outer cells however have thickened walls which are not lignified but consist of pure cellulose and contain also chlorophyll-granules. Parenchymatous cells are not packed closely together, but have small spaces between them called intracellular spaces which contain air and water vapour

After the examination of the structure at two points one in the root and the other in the stem, it is interesting to trace the transition from root to stem. Down in the root there are four bundles of xylem and four of phloem arranged alternately. Higher up the xylem moves inwards and takes up its position internal to the phloem. There are now four large bundles situated at the corners of a square. These bundles divide so that there are finally still the four main bundles together with six smaller ones running up the stem. The four large bundles finally run into the cotyledons while the other six continue up the stem to ~~form~~ follow the normal course of the vascular bundles already described. On entering the cotyledon the pair of trace bundles divide rapidly. It is interesting to note that only two bundles originally enter each cotyledon, but that three enter each leaf. (Fig XVII)

The buds of the Sycamore are usually fully formed in early April. They are of course arranged in the opposite decussate manner, since a bud is simply the young state of a shoot. The bud itself is covered by a series of tough green scales, known as the bud scales. These scales are actually modified leaf bases. The outer scales are much harder and tougher than those further in and nearer the young leaves. As is natural, considering that they are modified leaf structures, they are also arranged in opposite and decussate order, so that a section through the bud presents a more or less quadrilateral figure. Before the bud begins to "burst" about eight scales are visible externally. In the Sycamore the scales, as well as the young leaves invested by them, are provided with

Figures XVII - XX

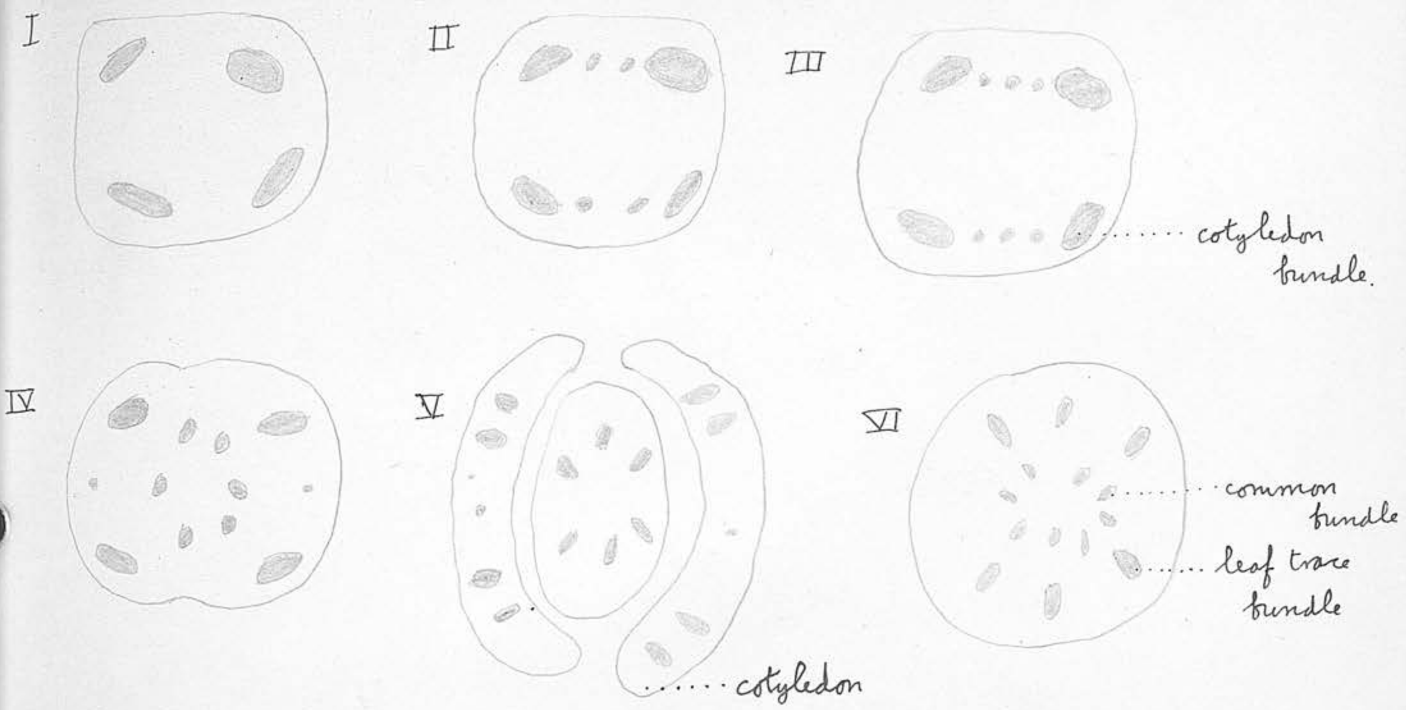
XVII This series of drawings merely illustrates the principle o the course of the bundles. In a normal section generally fa more bundles are seen, but this additional number is caused by the bundles dividing.

XVIII A section through a leaf Specimen 17

XIX The Sycamore leaf. It is described as palmatifid as it i not entirely cut into separate lobes, but is divided only to a certai extent.

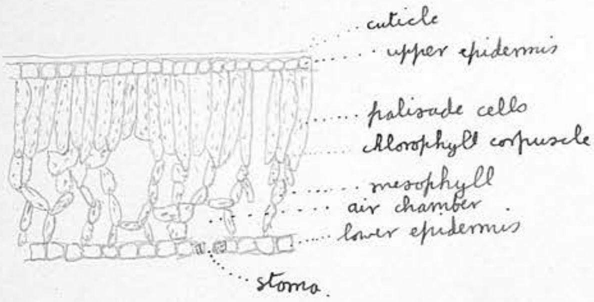
XX Transverse section through root Specimen 12.

XVII



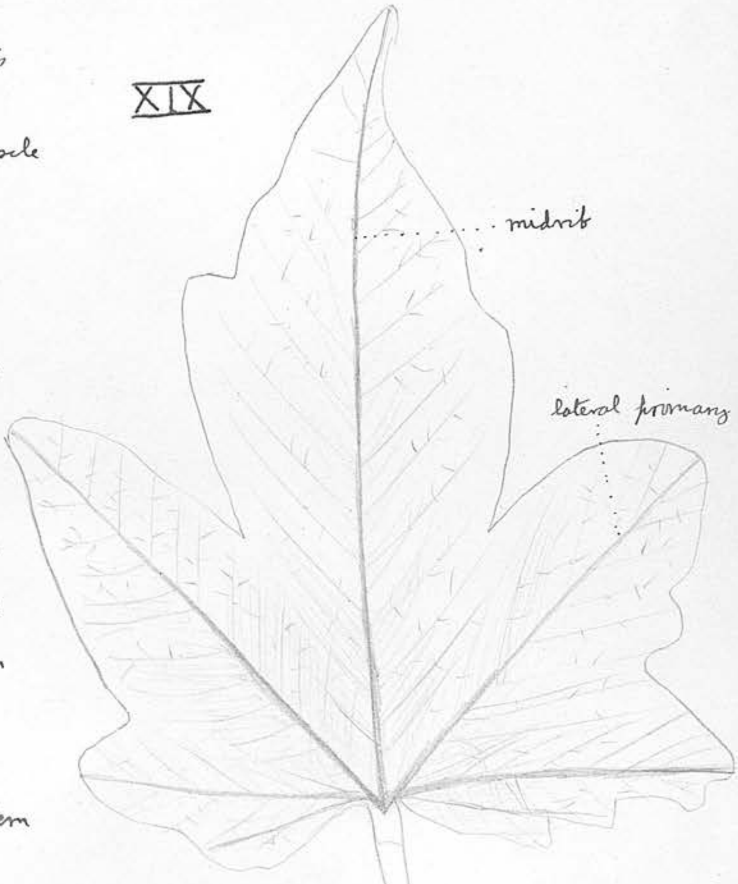
The course of the Vascular Bundles above and below the cotyledons. No I is the lowest down

XVIII



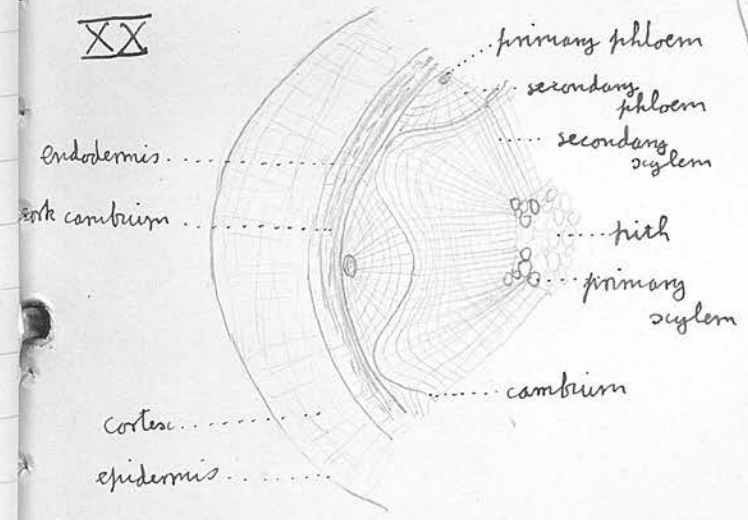
Transverse section through portion of leaf.

XIX



Sycamore Leaf

XX



Transverse section through root

hairs which often mat themselves together. These hairs together with the cork layers and resin are useful in preventing undue loss of water. The removal of the scales causes the young leaves within to dry up and to die finally. The scales however offord no protection against cold during prolonged frost: taking into consideration the fact that naked buds, that is those without scales, can withstand very severe winters it is assumed that resistance to frost is an adaptive character of the enclosed leaves. The growth is continued by a true terminal bud, which is larger and more symmetrical than the others. Occasionally instead of a true terminal bud a twig is found ending in a pair of buds of equal size and with their long axes diverging from that of the twig. They mark the situation of what was a bud in the previous spring, but developed an inflorescence and died off in due course, thus leaving the twig to end blindly. This false dichotomy, as it is termed is found to be common in trees with opposite and decussate buds of which the true terminal bud is liable to develop flowers, or to die at an early stage. This abortion of the bud gives rise to differences in the manner of branching of the twigs which profoundly affect the whole branching system later on. The buds on the lower part of the twig do not usually develop: of those higher up it usually happens that the bud on the upper side, which thus receives more light develops, while that on the lower side dies off.

pecimen VIII

At the foot of each bud may be seen the leaf-scars which mark the position of the attachment of last year's leaves. They are crescentic in shape and the ends of the vascular bundles are clearly distinguishable on them (fig XV)

As the temperature and conditions improve in the spring the cells at the growing point divide rapidly and the stores of nourishment in the pith are consumed. This directs the food supply towards this point, and the numerous newly developed cells begin to absorb water with great rapidity. As a result two changes follow. The leaves which have hitherto been small and lain folded in a fan like manner (plicate) within the bud scales begin to expand. Some of the inner bud scales grow out with them until finally they break through these and the young leaves fully unfold themselves. Once the leaves have emerged the scale leaves wither and die, and finally fall off, leaving a number of small scars in a close spiral which exhibit the point of rupture of the vascular bundles. Occasionally the bud scale grows a small leaf at its tip: this never matures but shows clearly that the bud scales are merely modified leaf bases.

The leaf may be regarded as a flattened green expansion of tissues, which are so arranged that they display a large surface area to the light and air. They are in continuous connexion with those of the stem. The leaves themselves are so arranged that every ray of light is caught on their surfaces, and on looking vertically down on a twig, it is seen that every space is occupied by the surface of a leaf and there are no gaps through which the sunlight may pass. At the same time those leaves near the top do not seriously obstruct the passage of light to those lower down. This is partly brought about by the decussate phyllotaxy, and partly by the fact that those lower down have longer petioles so that they stand further out from the central axis beyond the circumference of the higher leaves. In the case of a horizontal branch as much of each leaf surface as possible is displayed by the twisting of the leaf-stalk so that those leaves, which would lie vertically if they grew straight out in the usual direction, are brought into a horizontal plane.

A foliage leaf may easily be divided into two parts, the lamina and the petiole, which acts as a support for the former. The lamina is marked by certain lines or veins which lie buried in the mesophyll. They offer a certain resistance against tearing, and, being tougher than the mesophyll, generally strengthen the lamina. Running alongside the supporting fibres are the vascular bundles, which serve to carry fluids from the stem to the leaf and vice versa. The pipes which carry fluids to the leaf are however quite separate from those which carry them away. A midrib may be distinguished running up the centre of the lamina. This gives off secondary veins which in turn break up into smaller ramifications and so on. The midrib is accompanied by four nearly equally thick ribs which divaricate from it. Such venation with radiating primaries all springing from one point is termed palmate. These large lateral ribs are regarded as primaries. The lateral ribs also give off secondary branches and vascular bundles, and so every part of the leaf is connected up by this network of curved links and cross connexions and is able to collect and discharge nutritive fluids down the stem.

The leaf is covered externally with an epidermis, and internally are found the vascular tissue and the mesophyll. To form a concise and clear idea of the function of the leaf, it is necessary to examine each of these structures in detail. In the case of the vascular system it has already been seen that the veins divide up into smaller and smaller vessels and finally end blindly: it is in these blind ends that the exchange of fluids between the mesophyll and the vascular system takes place. The pipes from the root bring up water with mineral products in solution, while those running from the lamina take away sugars and other nutritive substances ~~in~~ ~~[illegible]~~ to the other parts of the stem where they are required to build up new tissues. It will be seen that the afferent vessels bring up inorganic compounds, and the efferent vessels take away organic substances containing carbon. The source of the carbon is the carbon dioxide of the air. The carbon is utilised and built up into various compounds by the chlorophyll corpuscles of the mesophyll.

The mesophyll is a soft tissue lying between

the vascular bundles and the epidermis: its bright green colour is due to the numerous chlorophyll corpuscles contained in the cells. The latter are not packed closely together, but have relatively large intracellular spaces between them, which ~~have~~ are filled with gases and vapour and give the leaf its characteristic spongy feeling. The structure of the mesophyll was examined by cutting a
ecimens 16 and 17. vertical section and also by examining the ~~epidermis~~ leaf mounted flat.

In the upper half of the section the mesophyll consists of cylinder-like cells arranged vertically and in close contact with one-another leaving hardly any intracellular spaces. Their shape and arrangement at once suggests the name of palisade cells. The lower half of the mesophyll is composed of smaller cells of irregular shape and arrangement. They are very loosely arranged and have extremely large spaces between them. Both the palisade cells and the spongy tissue cells contain numerous chlorophyll corpuscles. The upper epidermis which is composed of tightly fitting cells without spaces between them is entirely devoid of chlorophyll. The lower epidermis, like the upper is composed of tightly fitting cells which contain no chlorophyll corpuscles, except in certain places, where pairs of smaller cells are found containing chlorophyll. Each pair has a minute gap between them which communicates
pecimen 18 with the intracellular air-cavities. If a piece of ~~a leaf~~ the epidermis is examined flat under a microscope it is seen that these small cells form oval openings or stomata, and that they are very numerous over the whole of the lower epidermis. These stomata regulate the amount of water that passes off by evaporation from the mesophyll by opening and closing their apertures. The close fitting cells of the epidermis are otherwise impervious to water vapour.

It is now possible to summarize the general mechanism of the young tree with regard to the part played by the leaves. The root hairs absorb water from the ground and this water which contains minute quantities of inorganic salts in solution is brought up the xylem of the stem to the mesophyll cells partly by capillarity, root, and osmotic pressure, and partly by the action of the medullary rays. In the mesophyll the water evaporates, and leaves the salt, which is absorbed in the cell-sap. The protoplasmic lining of the cell wall contains a number of chlorophyll corpuscles imbedded in it: these are living organisms which require nutrition for the support of their life processes. This they obtain from the cell sap through the agency of the protoplasm in which they reside. It is essential that these chlorophyll corpuscles have light, and this is the reason for the large expansion of thin tissue. A mixture of ~~air~~ oxygen and carbon dioxide, among other gases, passes into the spaces in the mesophyll tissue. By absorbing energy from the sun's rays, the chlorophyll is enabled to build up complex compounds which are rich in energy and matter obtained from the external universe. The great activity of these chlorophyll corpuscles is at once realised when the many tons of organic material in the mature tree are compared with the insignificant amount of matter in its embryo.

As the young plant slowly grows into a tree, the main external changes are the increase in size of the stem and in the number and spread of the branches. The leaves each spring also become more numerous. Thus obviously more water is evaporated from the leaf surfaces and consequently the absorbing powers of the roots have increased and the vessels are enlarged. This increase of size in the tree demands more support to withstand the pressure of the wind and the force of gravity. This is supplied by greater rigidity in the stem and a firmer hold of the soil by the roots. The increased surface of the leaves also provides more nutritive material for the construction of new roots and branches.

Many changes have occurred in the structure of the roots. They have grown larger and consist almost entirely ecimen 11 of wood (cf. deep saffronin staining in sections of older roots) covered by a thick corky layer. When the young rootlets begin to thicken first the piliferous layer is lost and the cortex assumes a brown colour. Finally a layer of cork, impervious to water is developed all round the pericycle. This layer thus entirely cuts off the cortex from the central cylinder: as the cortex is no longer able to receive nutritive fluids owing to the presence of the cork layer, it quickly shrivels up and dies. At the same time a continuous layer of cambium has been formed right round the cylinder: this layer runs inside the primary phloem groups but outside the xylem groups. The cambium possesses the power of dividing very rapidly by tangential walls and the new cells thus formed on the outerside constitute new phloem and those, more numerous, on the inside new xylem. The xylem and phloem developed by the cambium are termed secondary. It is noteworthy that the secondary xylem is situated between the primary xylem groups, but the secondary phloem is radially inside the primary phloem. The youngest vessels are now those nearest the cambium and no spiral vessels are formed. From now onwards the root grows exactly as the stem. The development of the cork is necessarily continued as the root increases in thickness, and this new jacket assumes the protective functions of the piliferous layer and cortex.

The structure and appearance of the root is best seen by examining a transverse section (fig XX). It is at once obvious that in details it is very different from the root of the young plant (figs VIII and IX). The primary xylem may be picked out in the centre of the section. It is surrounded by the comparatively enormous extent of the secondary xylem. The cambium ring appears as a fine line running between the phloem and the xylem. Annular rings may be seen which represent the position of the cambium ring in earlier years: from their distance apart may be determined the rate of growth, that is the activity of the cambium. Fine medullary rays may be seen running radially and also broader ones which correspond to the radii on which the primary xylem groups were formed. As the mode of formation of both the medullary rays and the cork is very similar in the stem, it will be considered with the structure of the latter.

The stem also has undergone considerable alteration since its development from the seedling stage. In the first place the outside covering is no longer a soft green cellular tissue, but a hard rugged bark. Secondly the pith is extremely small compared with the large mass of encircling wood: now the pith is really the same as before, but the cambium layer has migrated outwards, thus leaving all the solid wood in the centre. The epidermis and cortex have been replaced by the cork and bark, and between the cambium and this outer covering may be found the phloem vessels.

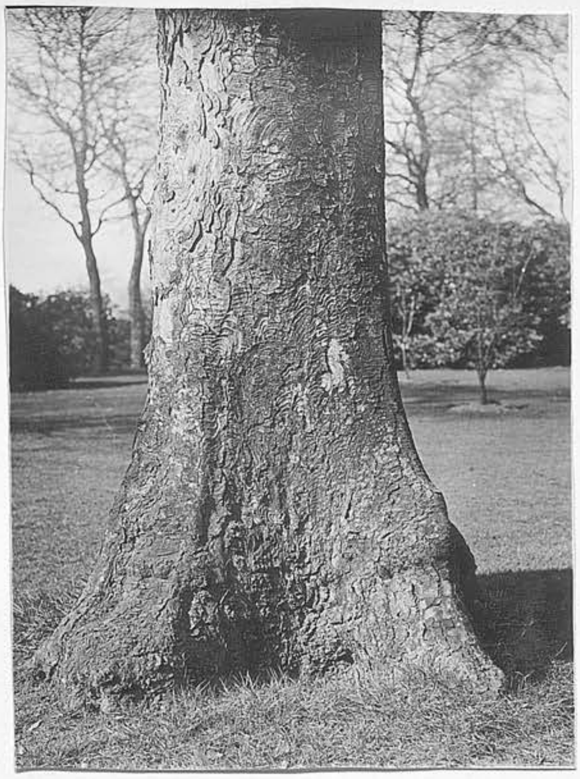
As in the root it is the cambium which is responsible for most of these changes. The cambium in the vascular bundles of the young plant soon becomes continuous across the medullary rays and so forms a complete ring. During the spring and summer the cambium cells continue dividing by tangential walls thus tending to make the ring thicker. The cambium however at the outsides of the ring rapidly changes its nature and is transformed on the inner side into xylem, and on the outer side into phloem, but to a much smaller degree. Thus it will be seen that the thin cylinder of cambium moves outwards as more and more ~~xylem~~ is ~~are~~ formed. Obviously these cambial cells are very important and their structure deserves close examination. Each cell is many times longer than broad or thick, and appears oblong in a transverse section. It contains protoplasm and a nucleus and has a sap cavity which receives nutritive fluids from the roots and leaves. The cell soon enlarges in the radial direction and divides tangentially. As more cells are produced after repeated divisions the older ones are

Photographs.

1. A general view of a Sycamore in winter time
2. A close up view of the bole showing the characteristic appearance of the bark
3. The dormant bud in early March.
4. The bursting bud in April
5. The leaves emerging - late April.

1.

2.



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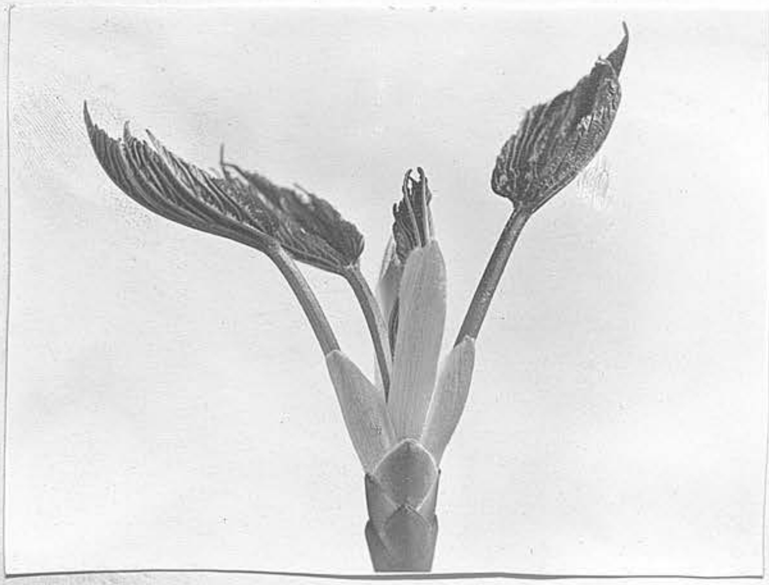


are converted into phloem or xylem. Those cambial cells which lie on the radial continuation of a medullary ray are used to continue the ray. As the cambium ring proceeds outwards, the circumference of the ring becomes greater and as a result new medullary rays are formed between the planes of two older and gradually diverging rays. As the wood increases in thickness more and more of these intermediate rays are formed cutting up the wood into partial sections. At the same time the ~~k~~ cambium keeps on adding to the length of these rays: in a transverse section about six may be counted in one mm. The cambial cells lying between the rays are used to form the elements of the wood proper except of course when a new medullary ray is interpolated. As the tree becomes older these elements that is the tracheids fibres parenchyma etc (fig XIII) increase in size, until they reach their maximum length and diameter.

At the same time the outer cambial cells are passing over into the phloem. Not so much phloem however is formed in comparison with the amount of xylem: the elements do not of course become lignified, but are disturbed in arrangement by the pressure of the rapidly growing xylem and the external covering of bark. Medullary rays are formed and added to just as in the xylem. In the case of the phloem bast parenchyma, sieve tubes together with their companion cells, and bast fibres are formed from the external layers of cambium. The secondary cortex thus formed presents a stratified appearance in transverse section due to the alternate arrangement of hard and soft bast.

imen
+9

When the young stem is a year or so old and is covered with a thin periderm, the surface is seen to be dotted with lenticels. Similar structures are to be found on all the young branches of older trees and also on the root. A lenticel is a gap in the periderm through which gases may pass into the intracellular spaces of the cortex. It is closed in the winter by the formation of a continuous sheet of cork cambium beneath it, but in the spring this sheet is broken by the swelling of the looser cells roundabout the lenticel. These loose packing cells are similar to young cork cells as regards their formation, but they do not become suberised and are thus capable of absorbing water and swelling. The first points of origin are usually beneath the stomata of the stem which supply the outer cells with carbon dioxide just as the stomata in the leaves. The lenticels may be regarded as devices for prolonging the passage of the stomata through the ever thickening periderm. As the branch ages new lenticels are continually being developed with no reference to the stomata, and are mainly used for excretion.

In the examination of a section of a one year old stem such as specimen a ring of cells deeply stained with saffranin is seen just inside the endodermis. These cells are striking, as they are of two different kinds and groups of each kind are arranged alternately. One type has a fairly thick walls but they have a distinct lumen: these are the hard phloem fibres. The other type has a very thick walls with simple pits and the lumina are almost entirely obscured (fig XXIII). As the stem grows older, the number of rows or portions of rows increase: thus in the (specimen 8) longitudinal section in most parts there are two rows of these cells and in some parts there are three rows. In older trees there are many more sets of these fibres.

When the twig is a year or so old the epidermis begins to crack and peel off: at the same time the subepidermal layer of cortex cells acquires the power of active division and are accordingly converted into what is appropiately known as a meristem. This may be regarded as the initial layer of the cork cambium or phellogen. This gives rise to the cork and phelloderm just as the cambium gives rise to phloem and xylem in the vascular bundles. The cells formed on the outer side become cork cells: their cell contents die, and the walls become suberised. The cells on the inner side are transformed

Figures XXI - XXVIII

XXI Portion of lower epidermis of leaf showing stomata Specim

XXII Portion of leaf showing reticulate venation specimen 16

XXIII Transverse section of stem. specimen 9

XXIV A diagram showing the arrangement of the flowers, the position of the male and hermaphrodite flowers, and the comparative age of each ~~plant~~ flower (indicated by the si of the circles).

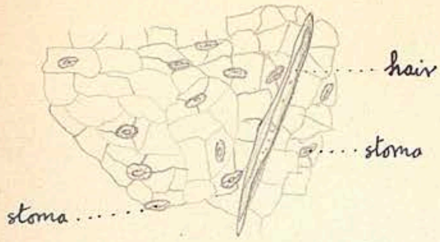
XXV Hermaphrodite flower from above.

XXVI Lateral view of the same with sepals and petals removed

XXVII Male flower from above. The stamens are better develo than in the hermaphrodite flower.

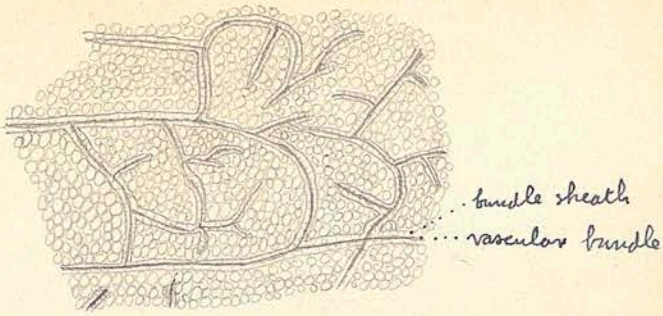
XXVIII Floral diagram. The stamens would be expected in two whorls of five each, and this is often found, but eight stamens are much commoner.

XXI



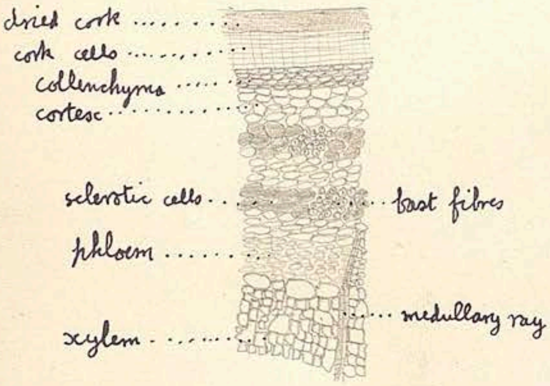
Portion of epidermis from under side of leaf

XXII

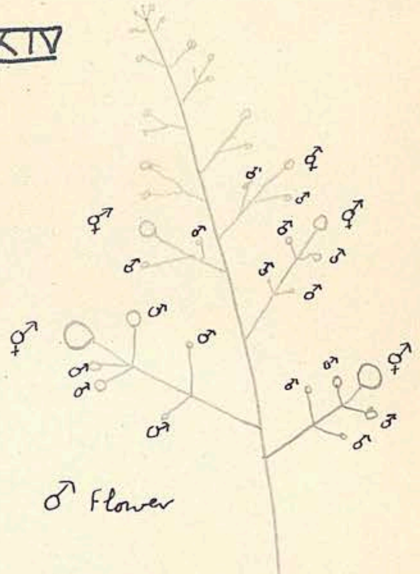


Surface view of leaf

XXIII

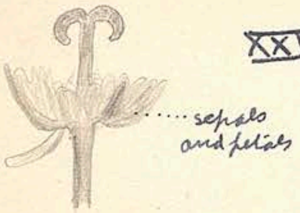


XXIV



⚥ Flower

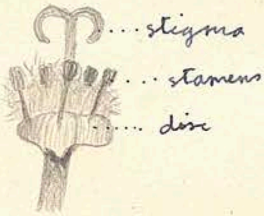
XXV



⚥ Flower

calyx and corolla removed

XXVI



♂ Flower

XXVII

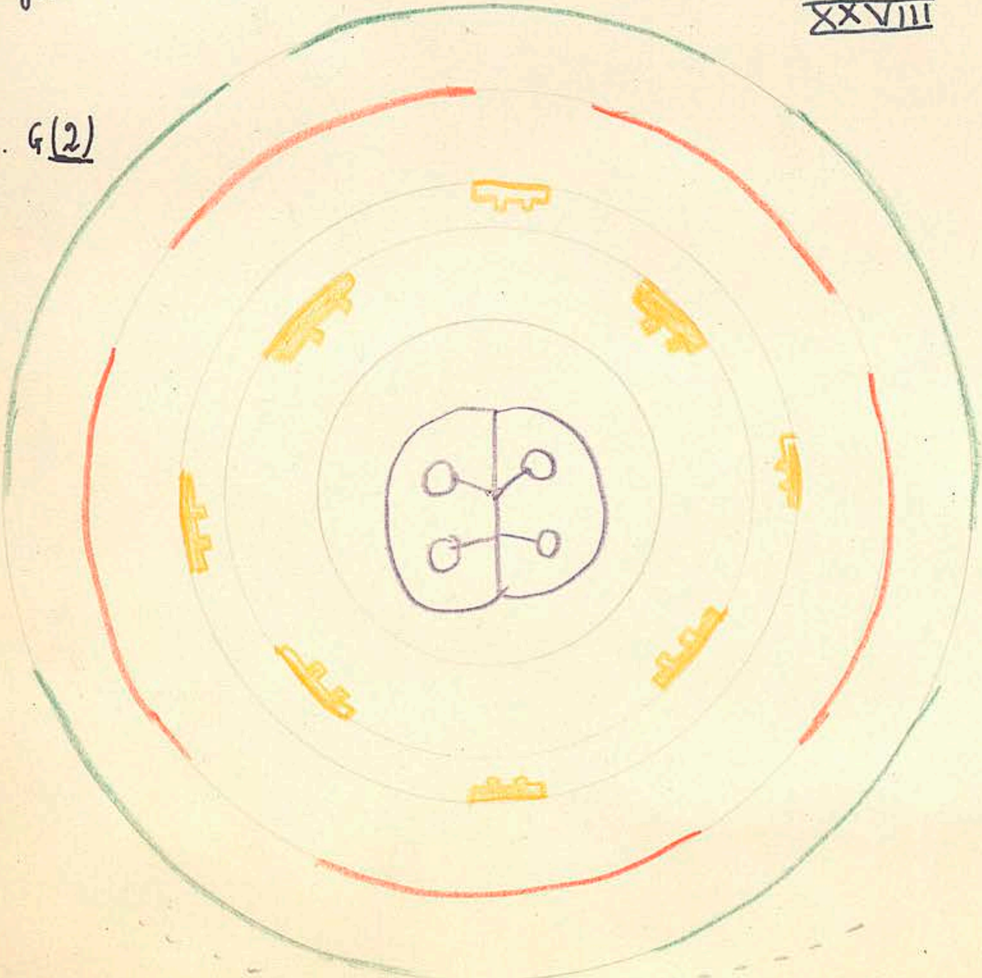
⊕

Floral Diagram

XXVIII

Formula

a5. co5. A 4+4. $G\underline{(2)}$



into phelloderm. This series of three tissues, cork cells, phellogen, and phelloderm together constitute the periderm. The first cork cells to be formed have thin walls, but as the tree grows older the later formed cells have much thicker walls. As the layers of cork increase in thickness new layers of phellogen are formed interior to the newly formed cork cells. Thus parts of the cortex are situated between the new and old layers of cork: thus the bark consists of both dead cortex and of true cork. The phellogen layers are not formed concentrically but often intersect old layers of phellogen, causing very irregular formation of bark scales.

When the Sycamore has been growing for several years and has had time to lay up stores of reserve materials not immediately required for the formation of leaves and wood, it is ready to propagate its own species. The exact age depends to a certain extent on the climate and weather. In dry poor soil in the open the tree may flower when ten years old: a well grown isolated tree will flower when about twenty years old and those that are shut in or crowded may be up to thirty years old before they bear an inflorescence. The inflorescences arise from the axils of the leaves. The flower bud is in appearance very similar to the leaf bud, but it is on the whole probably slightly fatter. Furthermore these buds occupy positions similar to those of the leaf buds. This similarity leads to the conclusion that the flower parts are merely modified leaves. In the case of the Sycamore the sepals and petals are very leaflike in both form and colour. Viewed externally it is more difficult to see in what way the stamens are connected with leaves: they are filamentous organs, each with a club-shaped swelling at the end. Yet each has a vascular bundle running up it suggesting the midrib of the leaf, and its insertion on the axis is similar to that of a leaf. The carpels also are suggestive of leaves in their structure. All the flower parts of the Sycamore have a certain amount of green colouration, and as they have not been modified to a great extent illustrate the leaf like characters of all the parts extremely well.

The sepals form the outer covering of the ~~plant~~ flower and are chiefly protective in function. The petals also are protective and in some plants, though not in the Sycamore, are brightly coloured in order to attract the insect world. The Sycamore makes up for this lock of colour to a certain extent by being extremely rich in honey. The stamens and ~~cay~~ carpels form the reproductive parts of the flower. The structure of all these parts will be considered later in detail.

The flowers are arranged on long "stalked racemes of umbellate cymes of about three each" i.e. as regards the flower stalk the inflorescence is indefinite, because the oldest cymes are those nearest the stem, and the youngest are those developed at the apex. The cyme however is a definite structure, because the terminal flower of each cyme is the oldest flower. Thus on an inflorescence the oldest flower is the terminal flower of the cyme nearest the stem. The description umbellate means that several (in this case two or three) ~~peced~~ pedicels all arise at the same point. The terminal flower of each cyme is usually hermaphrodite, and the lateral male. On the higher branches, however occasionally some of the lateral flowers are hermaphrodite, while lower down all the flowers in a raceme are often only male. The usual number of carpels is two, but three often occur especially in the end flower of a raceme. The other parts also vary considerably in number, the calyx and corolla from 3-6 each and the stamens from 5-11. The usual formula is Ca5 Co5 A 4+4 G$\underline{(2)}$. In the hermaphrodite flowers the stamens are developed first and the gynaecium is superior - both devices to avoid self-pollination. Honey is secreted in large quantities by the disc, a fleshy glandular outgrowth of the torus, and the ~~tree~~ flower is definitely insect pollinated. The hive bee especially gains much of it's honey in early summer from the Sycamore. Methods of fertilization and sex distribution and their causes apparently have not been fully investigated in this species.

The sepals and petals are very similar, but the latter are slightly narrower. Chlorophyll is present in both and they play a small part in carbon assimilation. Their function in the case of the Sycamore is mainly protective. The stamens of the male flowers are considerably longer than the petals and stand out at a marked angle to the axis of the pedicel. The filaments are hairy and carry at their ends the anthers in which the pollen grains are developed. The latter are oval in shape, and are marked by three longitudinal bands with numerous streaks radiating from them. The grains are carried by ~~grains~~ insects to the stigmas of the ovary, which stand well above the general level of the other flower parts. The grain on reaching the stigma proceeds to develop a pollen tube which carries down three nuclei - the vegetative nucleus and two male gametes. The former is lost when the pollen tube enters the embryo sac.

There are two ovules in each carpel, and they are slightly twisted over on each other, but not so far as to be termed strictly anatropous. Before fertilization the embryo-sac contains the female gamete the central fusion nucleus, two synergidae and the antipodal cells. The two latter, having performed their various functions, disappear: the female gamete and the central fusion nucleus fuse with the male gametes. The embryo sac now consists of the central fusion nucleus and the fertilized egg, both surrounded by protoplasm. On fertilization the sepals, petals, and stamens are lost, since they are now no longer required. The central fusion nucleus divides many times giving rise to the endosperm which is absorbed by the cotyledons, and at the same time the latter develop their chlorophyll.

The resulting fruit is known as a schizocarp; the gynoecium consisted of two carpels fused together, but the fruit

breaks up (σχίζω) into two one-seeded parts. It will be remembered that each carpel contained two ovules, but one of these normally degenerates. The seeds are distributed by the wind as already described, and after a period of rest germination takes place. And so once again the whole life cycle is repeated.
The wall of the ovule forms the pericarp, and the integuments the testa. The endosperm supplies sufficient reserve materials to ensure the germination of the fertilized egg, and all that is required is a period of rest. ~~bef~~ Thus once again a new plant will be formed. Of course only a very small proportion of seedlings ever grow into an adult tree: the great majority never get beyond the first year. Yet there are always some that survive to carry on the life of the Sycamore.

Note on the use of the Sycamore as Timber.

The wood of the Sycamore is of a white colour and moderately hard. Though not of very great commercial value like the oak, it is useful for certain special purposes. when of large size it is of considerable value especially in Lancashire where it is found most suitable for making large rollers. It is usually cut in winter to preserve the purity of colour. Butts over 20 ins quarter girth are worth from 3/6 to 5s per foot. Smaller pieces are used in the manufacture of bobbins and planks. Some is cut into veneers and when it has a wavy grain it is used for decorating interiors and other ornamental purposes. In the furniture trade it is known as "hare wood".

It is interesting to note that the Romans used the Maple, a tree closely related to the Sycamore, for making writing tablets. Ovid mentions it, telling how he dedicated his maple tablets to Venus "..... Veneri fidas sibi Naso ministras dedicat, at nuper vile fuistis acer". Pliny the naturalist probably refers to our sycamore in XVI. 15. 26. and in this passage there is ~~much of interest~~ an interesting description of the various types with which he was acquainted.

Notes on the Specimens.

Microscopic Preparations.

Transverse sections have been cut at various points in the young seedling. They include one in the region of the root hairs and two at various points in the hypocotyl. There are several sections through the young stem leaf etc. as under:-

Section of the young plant 1-3

Sections of the older plant and various other preparations 3-

1. A section of the root of figs VIII and IX

2. Sections of hypocotyl } fig XI

3. Sections of hypocotyl (further up) } fig XI

4 Section through a leaf bud shewing meristematic tissue in the centre and the origin of the xylem and phloem vessels.

5. Section of Stem 1st year showing secondary thickening XXIII

6. Section of Stem 1st year showing especially the schlerenchyma

7. Section of Stem cut in early ~~spring~~ autumn showing the large "spring" vessels and the small "autumn" ones.

8 Longitudinal radial section of stem fig XII

9.+10. Section of stem in 2nd year showing two years growth of xylem. In 9 the extra development of schlerenchyma can be seen as compared with a stem in its first year fig XXIII

11. Section through root showing the large development of the xylem, the water carrying tissues, These older parts of the root serve as little more than large tubes for the supply of water. The remains of the phloem may be seen crushed against the bark

12. Section through root fig XX

13. Products of maceration showing constituent parts of the xylem fig XIII

14. The arrangement and structure of the bud scales showing leaf like characters fig XVI

15. Section of petiole showing vascular bundles and strengthening fibres.

16. Portion of leaf showing reticulate venation. fig XXII

17. Section of Leaf fig XVIII

18. Portion of the epidermis fig XXI

Pressed Specimens.

A series of specimens shows the growth of the Sycomore from its earliest stage as an embryo to a seedling at the end of its first year. The root hairs may be distinguished with the aid of a lens in most of the younger specimens which were grown in a damp atmosphere so that no earth might be caught up in them and thus obscure them. The seed case is not usually cast off until the root is at least an inch long, but if kept inside and carefully protected it is retained much longer. Secondary roots are not usually developed until the plumule has begun to emerge. A collection of specimens shows varieties in the number of cotyledons. These unfortunately are not very clear as the cotyledons being very brittle are difficult to press without breaking. Another series shows the "bursting" of the bud and the emergence of the young leaves. Specimens of the leaves of the normal type of sycamore are shown together with those of a variety, Acer purpureum. This variety in which the under surface of the leaf shows a faint purple hue, originated in a nursery in Jersey in 1828 as the result of cultivation. The only true wild variety is A. villosa, which occurs in Sicily, Calabria, and Dalmatia. Its fruits have very broad wings.

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