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ELEMENTARY NOTES ON
STRUCTURAL BOTANY

By

A. H. CHURCH, M.A.

HUMPHREY MILFORD
OXFORD UNIVERSITY PRESS
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BOTANY, the study of Plant-life, as the autotrophic organisms of the world. Autotrophic as implying life which works solely in terms of physical energy and chemical material in the form of gases, water, and inorganic salts; hence distinguished from heterotrophic life (mainly animal); the latter being dependent on carbohydrate and proteid material previously synthesized by plant-life. The plant normally utilizes the simplest materials, as H_2O , CO_2 , and a few salts dissolved in water, working in terms of direct solar energy. Heterotrophic plants as Bacteria, Fungi, and a few parasites among higher plants, are equally secondary in origin and mechanism.

A vast subject dealing with the structure, mode of life, methods of reproduction and improvement of the race, as also its progressive evolution in past time; ranging from minute forms as Bacteria (1μ) to the vegetation of the sea and fresh-water, forms of prairie and forest-land, as also cultivated plants including organisms exploited by the human race, as plants grown for food (cereals and fruit-trees), decorative effect (florists' flowers), timber, textile, and other economic products.

Botany in the original sense means fodder or herbage, and the science is historically based on Herbs, as used in magic and medicine (**Herbalism**), cf. Herbalists from Dioscorides (A. D. 77) to Fuchsius (1542); scientific botany as the scheduling and identification of Herbs, evolved by necessity from Herbalism to Bauhin (1623) and Morison of Oxford (1680); from the latter passing on to **Systematy**, or classification by academic 'systems', culminating in Linnaeus (1735-53) and the *Genera Plantarum* of Hooker and Bentham (1862-83).

Other aspects as anatomy and physiology, the former dealing with minute structure, the latter with the mechanism of living processes, metabolism as including anabolism and katabolism, the mechanism of irritability, as response to stimulus of changing environment, reproduction, asexual and sexual, heredity, variations, and the relations of the individual to the race.

Anatomy, dependent on the development of the microscope, dates to Nehemiah Grew (1670-80), cf. his large volume with the first plant-sections and drawings of tissues. All conceptions of plant-structure necessarily based on Land-Plants, in more immediate association, taking common objects first; e. g. a piece of stick, seed, as a bean, fruit, as an apple; all show phenomena of cellular organization. 'Cell' from Robert Hooke (1667), from resemblance of a section of cork (cf. bottle-cork, cut dry, low power, reflected light, tangential section) to honey-comb. Hence Cell Theory of nineteenth century; all higher organisms being constructed in terms of cell-units, as living protoplasts building the tissues; many die and give derivative tissues of secondary significance, e. g. skeletal and mechanical in the aggregated soma.

Cell-Mechanism: In the history of the word 'cell' was restricted to the conspicuous wall or chamber, characteristic of plant-tissues, rather than animal: only later were the contents recognized as essentially living, as by Von Mohl (1846), and termed **Protoplasm**: a colloidal albuminous fluid state (sol), coagulated to gel-state on death, containing over 90 % water (more than milk), the actually living substance of all plants and animals; apparently evolved originally in sea-water, and auto-synthetic, from ions of H^+ , O^{--} , N^{+++} , Cl^- , P^+ , S^{vi} , together with other elements found associated, as Ca^{++} , Mg^{++} , K^+ , Na^+ , Cl^- , Fe^{+++} . Mainly of proteid-organization, as investigated dead, giving compounds involving $CHOH$ and $CHNH_2$ groups, &c., in indefinitely complex series. 'Killed' by heat-coagulation at about $50^\circ C.$, and by strong chemical solutions ('fixing reagents'): essentially a non-molecular complex of indefinite chemical action and reaction.

A central tract of individualized nature, suspended in the general cytoplasm (in both plant and animal), for metabolism and reproductive processes of more complex organization, distinguished as the **Nucleus**; identified by Robert Brown (1833), and discussed in detail in cytology.

Plant Tissues, so named by Grew from the similarity of sections to lace-work, are based on typical cells of average dimensions and details, about 50μ diam., (commonly ranging from $10-100\mu$ or more): spherical under action of surface-tension when left to grow freely; but usually aggregated in close contact, with or without intercellular spaces; hence appearing in sections as circles (when free),

or more or less hexagonal if 'packed'. A general term for such ordinary units of construction is retained in 'parenchyma', given by Grew from the fancied resemblance to air-sacs of lung-tissue.

A Parenchymatous Cell, taken as a starting point, is a fairly isodiametric living unit, with cytoplasm and one nucleus as the central control. All plant-tissues are based on such a structure, or have been formed from them, however much they may be modified for special functions: the parenchymatous cell is thus generalized in metabolism and function, and aggregated units constitute a tissue as parenchyma. In addition to the nucleus, the cytoplasm may present vacuoles with cell-sap, often greatly distended until the plasma is left as a peripheral film, and the nucleus is lateral: it is bounded by a wall of waste debris of metabolism, mainly polysaccharide **cellulose**, so called from plant-origin, as a carbohydrate with suggested complex construction $(6 \text{ CHO} \cdot \text{H} - \text{H}_2\text{O}) = \text{C}_6\text{H}_{10}\text{O}_5$ of the type:—

$\text{CHO} \cdot \text{CHO} \cdot \text{CO} \cdot \text{CHO} \cdot \text{CHO} \cdot \text{CH}_2$ (ring-formula, Cross and Bevan, 1918). The wall is deposited on the confines of the cytoplasm, in thinner or thicker series of lamellae; i. e. when thick, stratification may be noticed, while thin areas (pits) are left for conduction of soluble substances between adjacent units, as also perforations (more minute) for protoplasmic continuity.

Living protoplasm in such cells may show movements of circulation in slender strands (bridles), or a foam-like arrangement; the peripheral tract (plasmatic film) is concerned more particularly with the regulation of **osmotic mechanism**. The outer surface of the film may constitute a semi-permeable membrane, to which the freely permeable cellulose-wall may act as a mechanical support: such a cell in water, in virtue of solutes in the cell-sap, presents phenomena of differential diffusion-pressure; water can enter the cell, but the solutes do not pass out: an osmotic pressure of 5–10 atmospheres, or more, is commonly established in ordinary plant-cells, maintaining the protoplast in a state of turgidity. The mechanism is utilized for the absorption of water, distension of the cell-wall, and growth; such turgidity being so far essential for plant-cells growing in air. On placing similar cells in a solution of higher osmotic value, the action reverses, water leaves the cell-cavity, and the protoplast retracted from the wall is said to be plasmolyzed.

Note, all cell-mechanism was originally evolved in the sea for metabolism in a circumambient food-solution of $3\frac{1}{2}\%$ total salts, and later transferred to air with only atmospheric gases and aqueous vapour outside. Hence complications and readaptations.

Other cell-contents include plastids, as tracts of cytoplasm for special functions, with a certain individuality of their own: the most general case that of the **Chloroplast**, coloured green with chlorophyll, and of essential significance in photosynthesis: also vacuoles with oil drops, crystals as calcium oxalate, tannin, pigments, &c., as the commonest products of metabolism.

As good example of cell-detail, cf. blue hairs on stamens of the flowers of **Tradescantia** (available till first frosts): threads (4 mm.) of 20 cells, or so, as oval units, in single series, up to 300μ long, to globular at 75μ diam. distally: optimum 200μ , with thin cellulose walls, and violet-blue cell-sap; the cytoplasm colourless, as a granular parietal layer, with slender bridles across the cell-cavity; the coloured cell-sap filling vacuoles; nucleus (20μ) central or parietal. Healthy cells show circulation of protoplasm in the bridles and around the wall, as active streaming movements; large granules at 3μ per sec., smaller at $6-7 \mu$ per sec. Plasmolysis, by 5% salt-solution, causes the plasma to retract from cell-wall in places; ultimately to a wholly free spheroidal mass, with sap-concentration to deep violet colour. Washing with water will restore full turgidity, and the circulation of living plasma will be seen to be unaffected. Addition of spirit kills the cell instantaneously; the plasma being coagulated irregularly, and the nucleus taking up the pigment that was in the cell-sap after death.

Less satisfactory phenomena of circulation may be noted in the epidermis skinned from the inner scales of Onion-bulb; but special interest centres in the fact that these cells are units of a definite parenchymatous tissue-system.

Elodea: In elongated cells of leaf-midrib, cytoplasm streaming along the walls takes chloroplasts with it at 10μ per sec.

A typical **Land Plant**, as derived from submarine vegetation, is a more complex organism in that the first problem is how to obtain sufficient Nitrates, Phosphates, and other compounds as 'food-salts' to carry out proteid-synthesis, when these are only present in the soil. This involves the necessary differentiation of an absorbing *root* in the ground, with subaerial *shoot*; the function of the latter being to produce and display as much body-surface as possible to air and sunlight. Since the absorbing cells are in a solution of soil-water (often little better than tap-water), a current has to be maintained from the roots to the leaves (Transpiration-current), and enormous quantities of water require to be evaporated at the surface of the leaves (Transpiration).

Hence the Primary distinction in land-plants of *Leaves*, *Stem*, and *Root*: the first being the essential photosynthetic and proteid-synthetic regions of the organism. The Leaf is the Laboratory of the Plant; with conductive system leading to it, as also away from it, in the form of definite strands of vascular tissue known as **Vascular Bundles** (V.B.) of Xylem and Phloem.

The main axis normally grows erect, at right angles to the surface of the ground, to give optimum space-distribution; bearing leaves as laminate extensions of the soma, and branches repeating similar organization; thus giving a 'tree habit' of diffused growth spread over considerable space, as opposed to the concentrated and condensed body of a locomotile animal. The Plant-axis also exhibits continuous growth, by definite 'growing-points', which may go on producing new leaves and new axes so long as nutrition is satisfactory; i.e. the plant continues to grow at the ends.

Growing Point: essentially a mass of undifferentiated growing and dividing cells (meristem); exhibiting phases of (1) centric growth, i.e. around a point; (2) unilateral distribution, i.e. on one side only; maintaining the growing apex at the end of a longitudinal axis; (3) retarded, since the stem attains a definite 'adult' size. Increase is effected by the growth and sub-division of each individual cell in irregular sequence: any cell may be dividing, but the general effect and dome-shaped outline are retained; i.e. the mass grows as a whole, and all the protoplasts are in living communication, as typical parenchymatous cells, or in this case, embryonic tissue, practically immortal, and including generalized germ-plasm.

Mechanism of Cell-Division: The nucleus divides first, presenting phenomena of *Mitosis*: In higher plants and animals the nucleus presents complex organization of plasmic ground-substance, with fluid in vacuolations, and framework of linin, with chromatin distributed in a reticulum of *chromosomes*. The latter are of constant number for a given species, and display a certain degree of individuality, being capable of independent division by longitudinal fission. The mass of the nucleus is fluid, and is held in spherical form among the cell-cytoplasm by surface-tension, and is covered by a plasmatic film (nuclear membrane), as its 'resting-stage' in the metabolizing cell. In Mitosis the membrane disappears; the linin arranges a 'spindle-mechanism', with 'spindle-fibres' from two 'poles', and the chromosomes separate (prophase), arrange in the 'equatorial plate', and each divides: spindle-fibres attach to the halves, and the 'daughter-chromosomes travel to the poles (anaphase), there uniting to build the new reticulum of the 'daughter nuclei' (telophase). In the equatorial plane, across the central spindle-fibres, a zone of demarcation of the fields of the two new centres is marked by a deposit of polysaccharide waste, as the first indication of the dividing wall: this extends to the older walls, and constitutes the primary septum. Later deposits of cellulose on this wall commonly present cleavage-effects, with the production of intercellular spaces at the angles (more or less); the original septum is distinguished as the 'intermediate lamella', and the intercellular spaces are required for the aeration of the tissues.

Apical Differentiation. As cell-division proceeds behind the growing point, organization is shown in the layering of the tissues, following periclinal construction-lines, and indications of tissue-systems appear:

- (1) A peripheral layer controlling relations with the outer air, as *epidermis*.
 - (2) A generalized intermediate region (*cortex*).
 - (3) A central conducting and skeletal region, conveniently included as the *Stele*.
- The early distinction of these regions close to the growing-point led to the

enunciation of three 'embryonic layers', as *dermatogen*, *periblem*, and *plerome*, reflecting academic abstractions on the general lines of the germinal layers of the higher animal (middle xix century). Such layering is often quite definite, but is to be referred to a precocious differentiation of functional regions of the adult, and is not causal. The terms survive as useful conventions and topographical designations.

Behind the growing-point, zones of differentiation may be distinguished as (1) The apical zone of growth and division in all directions; (2) A zone of elongation, in which longitudinal extension is most active, giving a capacity for intercalary growth and rapid increase in length; (3) A zone of differentiation, in which the tissues assume their adult histological character and special physiological activities.

HELIANTHUS, $\frac{1}{8}$ in. stem: In a small herbaceous stem cells and tissues are readily distinguished in transverse section, and may be tested by ordinary reagents: e.g. examine a transv. sect. mounted in Iodine solution. The general circular outline of the section is filled with more or less circular areas indicating the cell-walls, grading from $10\ \mu$ to $100\ \mu$ diam., with intercellular spaces between. Differentiation of more specialized tracts is conspicuously marked at 12-15 spots, very uniformly distributed about $300\ \mu$ from the periphery, as sections of the Vascular Bundles (V.B.). A little distance external to these a distinct line of cells with black dots (starch-grains stained by Iodine sol.) indicates the Endodermis. The whole section is bounded by a single layer of cells as Epidermis, and special tracts may be defined as:—

The tissue beneath the epidermis, as far as and including the endodermis = Cortex: The tissue internal to the vascular bundles = Medulla (pith): tracts between the V.B. are termed Primary (Medullary) Rays; and a region between the V.B. and the endodermis as pericycle.

In further detail note:—

(1) The **Epidermis** of oval cells, $30\ \mu$ diam., with scanty granular contents, thicker outer wall covered by a distinct cuticle; and giving rise to outgrowths occasionally as hairs of single series, or on multicellular bases.

(2) **Cortex** of outer 3-4 layers of Collenchyma, the walls markedly thickened at the angles (mechanically increasing cohesion of periphery).

(3) **Cortical Parenchyma** of larger units, $40-100\ \mu$ diam., with occasional ducts.

(4) **Endodermis** of a single line of cells, $50\ \mu$ wide, with starch-grains ($5\ \mu$); in this stem curiously the only layer with starch.

(5) The central **Medulla**, the bulk of the section, of rounded units, up to $120\ \mu$ diam., with scanty contents and soon dying off.

(6) The **Vascular Bundles**, differentiated by Phloroglucin -25 % H_2SO_4 , into a **Xylem-region** (χ) of lignified tracheides, in 3-5 radial rows, to $40\ \mu$ diam., surrounded by smaller non-lig. cells of $15\ \mu$.: **Phloem** (ϕ) of small cells ($15-20\ \mu$) with more definite contents: between χ and ϕ the suggestion of a **cambium-zone** of smallest cells ($10-15\ \mu$).

(7) External to the phloem the beginning of a group of fibres, as a rule not yet lignified, belonging to the pericycle, $30\ \mu$ diam. In older axes these have thick lignified walls giving the Phloroglucin-reaction.

Approximate details of measurement, freely interpolated, are not necessarily intended to be checked, although it is a useful habit always to use a micrometer eyepiece; so much as to afford a basis for accuracy in drawings, and keeping the figures in their proper proportions. The most useful standardized drawings are those constructed on the 'mu-millimetre' scale (High Power), = $\times 1000$, or in some simple relation.

Powerful reagents used for differentiating celluloses require great care. Alkalis (KOH, NaClO) spoil lenses, strong acids metal-work and clothes. Fuming acids (HCl) should be avoided; weak H_2SO_4 with phloroglucin takes longer time, but does not affect the intensity of the reaction. Preparations involving strong acid, or Chlor. Zn. Iod. should be put in a glass of water as soon as finished with, and not left lying about. Small quantities only should be employed.

A well-grown leaf of **CHERRY LAUREL** (*Prunus Lauro-cerasus*) from a sunny position, consists, of a broad lamina, 8 in. by 3, on a short stout petiole ($\frac{1}{2}$ in.). *Note* conventional usage of borrowed terms as *midrib*, more conspicuous on lower surface; *apex* attenuated as a drip-tip; *veins* (nerves) as paths of conduction; *teeth* of margin, and especially *dorsiventrality* as implying bilateral construction with two sides unlike, the distinction of D.V. surfaces being purely arbitrary.

Orientation on plant in spiral phyllotaxis, with lamina presented to maximum illumination, the upper surface at right angles to direction of incident light; by secondary twisting of petiole giving 2 rows; more or less wanting in shaded shoots.

Venation seen particularly well on lower side, pinnate, in alternating sequence; with expressions of 'triple-arch' system towards margin, as mechanical adaptation against shearing action of wind. Obscure glands (hydathodes) paired at base of lowest lateral veins.

Transverse section of sample of midrib and lamina of fresh leaf (half-way up), cut in pith, mounted in water: *note* shape of midrib, central vascular strand and little green tissue; lamina of uniform thickness ($\frac{1}{2}$ mm.) chiefly of green tissue (mesophyll) with a few obliquely cut portions of small V.B. as 'veins'. Taking the tissues in order from upper surface to lower:—

(1) **Upper Epidermis** of cells fairly isodiametric ($30-60\ \mu$ broad and 30 high), with stout cellulose walls, simple pits, no chloroplasts, slight aqueous contents; with distinct cuticle on outer surface, $3\ \mu$ thick; differentiated by Chlor. Zn. Iod. as blue cellulose, yellow cuticle, and brown intermediate cuticularized layers.

(2) **Palisade Mesophyll** as 2 tiers of columnar cells set at right angles to surface, averaging $50\ \mu$ deep each, and $18\ \mu$ wide; occasional attempts at 3 tiers; shade-leaves have broader more rounded units. Walls thin, of cellulose; contents include discoid chloroplasts ($3-6\ \mu$) with small starch-grains (tested by Iodine sol.). *Note* the manner in which the units of the basal tier are fitted on the subjacent parenchyma.

(3) **Spongy Mesophyll**, a lower zone, $200\ \mu$ deep, of loose isodiametric parenchymatous cells, with chloroplasts and starch in smaller quantity; up to $75\ \mu$ diam., with greatly exaggerated intercellular spaces, but often irregularly pulled out giving stellate effects. Chloroplasts with included starch-granules, being fewer, are seen to be more distinctly restricted to a parietal layer in each cell. *Note* the netted effect of the sponge-like type of spacing for effective aeration. Both palisade and spongy mesophyll may contain large crystal-aggregates of calcium oxalate (sol. in dil. HCl); crystal-sacs contain one stellate cluster ($35\ \mu$), more general in palisade of older leaves, or large single rhombs ($45\ \mu$), especially in spongy mesophyll.

(4) **Vascular Bundles**, in smaller veins, cut more or less obliquely, with a distinct sheath of parenchyma (endodermis), and poorly differentiated *spiral tracheides* (giving phloroglucin - H_2SO_4 reaction), constantly on the upper side of the strand.

(5) **Lower Epidermis**, similar to upper, but cells smaller and more rounded; similar aqueous contents and cuticle, with the additions of—

(6) **Stomata**, as slits communicating with the exterior, bounded by 2 *guard-cells*. These are not well shown in Cherry Laurel, being obliquely cut; more distinct on sloping side of midrib. Guard-cells with comparatively thick inner and outer walls, outer pore-chamber, and cuticle following the contour of the guard-cell its whole course. Irregularities in the epidermis, due to stomata being cut obliquely are more evident in Chlor. Zn. Iod. preparations. Stomata are readily seen in surface-view by skinning off a small piece of lower epidermis and mounting in Iodine sol. There may be 200 per sq. mm., each $40\ \mu$ by 35 across the guard-cells when widely open.

Note the mosaic effect of lower epidermal cells with simple pit-communications (giving beaded effect to walls). The guard-cells contain small chloroplasts, small included starch-grains, and a central nucleus.

(7) **Midrib**, appearing as a broad area of generalized structure, bilateral and eccentric; central vascular strand as conspicuous band of Xylem of pitted tracheides and vessels (to $30\ \mu$ diam.), with radiating bands of parenchyma as 'medullary rays', differentiated by Chlor. Zn. Iod.; tracheides give red reaction with phloroglucin - H_2SO_4 . On the lower side of the Xylem is a narrow band of phloem, with cellulose walls, and

small cavities, through which the ray lines are continued. The rest of the area is mainly parenchymatous, grading to collenchymatous tracts at upper and lower surfaces, as cells with few chloroplasts and few starch-grains. Stomata are rare: the green mesophyll is continued over the upper surface, below the collenchyma, but without the palisade-effect. The lower parenchymatous tract of thin-walled large cells, up to $90\ \mu$ diam., is marked with radiating bands of thick-walled, but non-lignified, fibres, up to $30\ \mu$ diam.: there is no special cambium; but a good effect of radial rows at the junction of χ and ϕ , the smallest cells $10\ \mu$ by 5 . A zone of large rounded cells (especially in sp. mat., in which they go brown as a tannin-effect) may be partially isolated as an *endodermis* on the flanks of the strand.

Shaded leaves differ in smaller size, less differentiated palisade, and little or no starch-content.

Other leaves may be compared, taking more particularly stout forms of evergreen habit, as available fresh at any time of the year, as:—

Privet (*Ligustrum*) with good differentiation of palisade, and abundant stomata on lower surface; but the spongy mesophyll is less marked and the intercellular spaces are scanty.

Box (*Buxus*) with a very dense palisade-region and almost colourless lower half; thick cuticle, prominent V.B. and good stomata.

Ivy (*Hedera*) less differentiated mesophyll, palisade very poor in shade-leaves, abundant stomata.

Aucuba (yellow-spotted variety), ill-differentiated mesophyll and midrib; chlorophyll, as also starch, conspicuously wanting in the yellow areas: variegation implies malnutrition.

Holly (*Ilex*) presents more marked differentiation, but along similar lines: palisade in 3 tiers, covered by aqueous *hypoderm*, as well as aqueous epidermis. Arcs of fibres over the phloem of V.B. Elaborate spongy mesophyll, and good stomata on lower surface. Cuticularized layer of upper epidermis $10\ \mu$ thick.

Stomata in surface-view are readily examined by skinning the epidermis of leaves, as:—

Lilium candidum, large stomata $65\ \mu$ long and 50 broad, all orientated along the long axis of the leaf, on lower surface only: guard-cells with conspicuously abundant chloroplasts: slit to $20\ \mu$ wide, as measured by air-bubble in water-preparation.

Arum italicum, fresh leaves afford admirable example of mosaic epidermis; stomata numerous, 100 per sq. mm.; guard-cells $50\ \mu$ long, with *subsidiary cells* on either flank. Slit opens to $15\ \mu$; closed stomata show guard-cells straightened out and closely approximated. Iodine sol. gives purple-red or violet colour to amyloid material soluble in cell-sap of ordinary epidermal cells only; the cytoplasm and well-defined nuclei ($15\ \mu$) colour yellow. The guard-cells have no amyloid, but small chloroplasts and starch-grains.

Iris, stomata about 120 per sq. mm., on both sides of leaf, all orientated in longitudinal direction with elongated epidermal cells: guard-cells $50\ \mu$ long, slit opens $10\ \mu$. Other leaves as available, cf. *Tulipa*, *Hyacinthus*, *Sempervivum*.

Leaf-arrangement: Leaves arise at the growing-points of the stem only, in strict acropetal order, as outgrowths of the meristem, with definite arrangement, more or less a constant for different plants; in rhythmic sequence, so working out a definite pattern (phyllotaxis); normally spiral, or whorled. Points of insertion termed *nodes*; spaces elongated between as *internodes*. Whorled systems give 2–3 or more leaves spaced at same level, and alternating at successive nodes; e.g. (2+2) system = decussate, a common case; cf. Privet, Box, Ash, Sycamore, Aucuba, Fuchsia, &c.

In spiral constructions, successive members are spaced around the growing-point at about $137\frac{1}{2}^\circ$ (Fibonacci angle), which gives optimum balanced effect, as also maximum exposure to light. A pattern is worked out in which contact-lines may be traced (2:3:5:8:13:21, &c.) according to the size of the members produced, as seen in transverse sect. of the young bud. Low ratio (2:3) in Ivy, Holly, Cherry Laurel, &c.: for better examples, cf. Pine-cone (5:8), or Sunflower-head (34:55), and even (89:144).

ANABOLISM expresses the building of living plasma; initial stages only are open to experimental observation, as:—

Photosynthesis, more usually restricted to the elaboration of carbohydrate from CO_2 and H_2O in the presence of solar radiation: experimental observations show that on exposure to sunlight under suitable conditions *starch-grains*, which can be tested by Iodine solution, appear in the chloroplasts: e.g. in two hours in *Funaria* leaf, and 5 minutes in cells of *Spirogyra*. Such general facts first noticed by Sachs (1862): The presence of chlorophyll is apparently as essential as that of light; 6 factors in all:—

(a) General factors for healthy metabolism of the plasma:

(1) Water-supply for aqueous plasma.

(2) Temperature with max. and min. range; opt. about 80°F .

(3) Oxygen-supply, generally conceded from conceptions of katabolism.

(b) Special factors of the chlorophyll-mechanism:

(1) Chlorophyll in special plastids (chlorophyll-corpuscles, chloroplasts).

(2) CO_2 supply as free gas of the atmosphere; 3 parts in ten thousand.

(3) Light of the Sun, of optimum diluted intensity (white-cloud illumination).

Chlorophyll, a green pigment, soluble in oil on surface of chloroplast; general constitution fairly known (Willstätter, 1910), containing Mg, but no Iron; extracted by solvents as spirit, with other substances, as a more or less complex mixture, giving a similar green solution, fluorescing blood-red, and presenting a characteristic absorption-spectrum, with several bands (7); the chief one in the red ($\text{B}\frac{1}{2}\text{C}$); a faint band, $\text{C}\frac{1}{2}\text{D}$; one in the green (beyond D); a faint one before E, and all beyond F (violet end): i.e. certain light is absorbed (mainly red), much is reflected as green. Hence infer red light is the optimum for photosynthesis: but all rays may be used, as under trees, a soft green light being residual.

Bacterium-method of Engelmann (1882) gives a means of checking the evolution of Oxygen as part of the work done. Depends on the fact that certain Bacteria are motile only in presence of free O_2 : on placing a green algal filament in the field of a micro-spectrum, bacteria congregate in the region of maximum evolution, and a curve may be drawn. This again gives most active decomposition in the red ($\text{B}\frac{1}{2}\text{C}$, wave length $660\text{--}680\ \mu\mu$), with less action in the rest of the spectrum. Hence conclusion accepted that primarily energy of red light is converted into chemical work, with evolution of O_2 and production of Carbohydrate from CO_2 and H_2O . Experimental gas-analysis shows that there is no change of volume involved; i.e. for an equal vol. of CO_2 absorbed, equal vol. of O_2 is set free;

The Theoretical Result may be provisionally expressed in the form:—

$\text{O}:\text{C}:\text{O} + \text{H}\cdot\text{O}\cdot\text{H} = \text{O}_2 + \overset{\text{OH}}{\underset{\text{H}}{\text{C}}}\cdot\text{H}$ the suggestion being that O_2 comes jointly from CO_2 and H_2O ; the Carbon atom comes into association with the ions of water, with the possibility of attaching indefinitely similar (CHOH)" groups in chain-formation. A suggestive formula involving 6 such groups, stabilized in molecular form, is given for glucose, as the simplest monosaccharide found free in the plant:—

One such group would stabilize as $\text{H}\cdot\text{COH}$ (Formaldehyde), invariably associated with the chlorophyll-mechanism. Monosaccharide groups condense with separation of H_2O to form polysaccharides of $(\text{C}_6\text{H}_{10}\text{O}_5)_n$ class, to which starch is ascribed.

Hence the appearance of starch-granules in a chloroplast implies the end of a long sequence of actions in which starch, itself insoluble, is off the main line of synthesis, and so far a by-product, expressing *excess* of carbohydrate production, rather than the actual amount formed. Sugars as monosaccharides are probably nearer the main line of proteid-synthesis: disaccharides (as cane-sugar) are similarly to be regarded as by-products. These have diminished osmotic value, and starch has none at all, hence the meaning of their production may be the avoidance of injurious osmotic action in the cell-sap of the working units. All further production of starch, celluloses, ligno-celluloses, benzene-derivatives, and terpenes, may be regarded as roughly following a sequence of progressive depletion and substitution of OH groups in an anhydro-aggregate of such primary monosaccharides.

Proteid-Synthesis involves further stages of formation of groups as (CHNH_2^+) from CHOH groups and Nitrates, with subsequent introduction of S and Phosphoric Acid, as also traces of Iron, to build more complex proteids, as in nuclei, before plasma can be attained: little is known of such stages; substances found in plants being molecular ends and débris of processes, rather than steps in actual metabolic reactions. The elementary consideration of photosynthesis stops at carbohydrate synthesis, though free energy of light is probably utilized all through; but proteid-synthesis can go on in the dark, as in growing roots or germinating seeds, other energy being employed (katabolic). The entire sequence of events is termed *assimilation* from the analogy of the animal, but may be conveniently distinguished as (1) photosynthesis and (2) proteid-synthesis.

Photosynthesis (= ' CO_2 assimilation') thus involves the utilization of CO_2 of the air, with consequent evolution of free O_2 , as a gaseous exchange. Other gaseous exchanges are concurrently effected.

Respiration: including gaseous exchanges as evidence of *katabolism*, the latter involving oxidation-phenomena in the plasma, with evolution of CO_2 , in the normal process of aerobic katabolism as utilized by animals and plants, in absence of light, as the general method of obtaining energy for living processes. Hence in absence of light, and in all parts not containing chlorophyll even in the light, normal respiratory katabolism takes place. In this way living plants may be presenting a gaseous exchange the reverse of that in photosynthesis, under certain conditions, as by night; and both actions may go on concurrently in green and non-green parts: the net result of the exchange being the balance of two distinct processes. Active photosynthesis is however normally several times (20-40) more intense than the respiratory exchange, and may completely mask it by day. Hence respiratory activity is usually studied in the case of seeds or non-green parts, and in the dark. Rarely does such katabolism raise the temperature appreciably. (*Arum*-spadix, 105-112° F.)

The ratio of $\text{CO}_2:\text{O}_2$ of respiratory exchange is normally less than unity, as more oxygen is used in other reactions, and CO_2 is not the only product of such oxidation, though the most highly oxidized form of carbon; e.g. the next most highly oxidized carbon-compound is $\text{COOH} \cdot \text{COOH}$ (Oxalic Acid), soluble in water, and so retained in the plant, and poisonous. Hence this if neutralized by Ca. may explain the common presence of Calc. oxalate crystals in actively metabolizing parts of the plant. In extreme cases (some succulents) oxalate is formed in preference to CO_2 . Katabolic processes taking place in absence of free oxygen, and expressed in terms of other sources of chemical energy, are termed *anaerobic* (cf. Bacteria).

Orientation: Elementary plasmatic organisms respond to changes in environment by form-alterations, originally the expression of modified surface-tension, giving euglenoid and flagellar *contractility*. In more massive cellular organization form-changes are effected by alterations in osmotic mechanism, as effecting turgidity and growth of cell-units. Little movement is possible once the cellulose framework is established. Such movements express 'Irritability' in response to 'Stimulus', i.e. change; or may be autonomous (spontaneous), i.e. without ascertainable cause.

The most fundamental response is to sunlight, **Heliotropism**; plant-shoots are normally 'positively' heliotropic, and tend to lie pointed in the direction of optimum light-effect (orthotropic); leaves are 'plagiotropic', or tend to lie at right angles to incident light. The movement is originally a general growth-response; but may be differentiated, as effected by the petiole to display the lamina, implying a certain amount of conduction of stimulus, and foliage-leaves normally attain a **fixed light-position**.

In special cases movement is determined by a distinct 'pulvinus'-organ at the base of the leaf or leaflet, and daily movements of presentation, or light-regulation, are effected (cf. *Robinia*, *Oxalis*, and 'Sleep-movements'). In extreme cases the mechanism is so delicate that it responds to other stimuli (electrical, or even a touch), cf. *Mimosa*, leaves only displayed by excessive turgidity of pulvini, and hence 'sensitive' plant.

All such mechanism of response, by turgid protoplasts, is subject to general tonic actors, as temperature &c., and is only feebly expressed in these latitudes. For further expression in warmer climate, cf. Sensitive Plant, and 'Praying Palm' (Bose, 1918).

The **Gaseous Exchanges** of the leaf may be expressed as :—

- (1) CO_2 in, and O_2 out, in **Photosynthetic Assimilation** : the oxygen diffusing out passively when in excess.
- (2) O_2 in, and CO_2 out, in **Respiration** ; CO_2 passively diffusing out in absence of anything to stop it.
- (3) H_2O lost to the tissues in evaporation and **Transpiration** : all gases diffuse out if apertures are available, when in excess ; or may pass away from solution in aqueous media : diffusion inwards continues as long as the gas is used chemically, and so creates a reduced internal partial pressure.

Aeration of the Tissues is provided for by intercellular spaces, always of secondary origin, in free communication throughout the plant as an **internal atmosphere** ; e.g. the gas-content of a potato is the same as that of the external air. The paths of exchange are indicated by the stomata as intercellular spaces in the epidermis, formed as a slit between twin guard-cells: cf. Theory of Multiperforate diaphragm.

Stomatal Control : Penetration by gases, or outward diffusion, may be completely checked by an impermeable (gas-proof) surface-layer ; the normal function of the cuticle, if only thick enough : but this does not give *control*. Stomata, with guard-cells, opening and closing the slit, act as doors controlling the exchanges if the mechanism is suitably adjusted. All three exchanges are thus more or less under the control of the living guard-cells: the most important being the exit of water-vapour.

Transpiration expresses the giving off of water-vapour from living plasma, as opposed to the physical evaporation from free fluid or dead material. Since the only available source of food salts (N,P,S, &c.) is from solution in soil-water absorbed by roots, these have to be carried to the photosynthetic cells for further proteid-elaboration, and a constant supply is required, as the **Transpiration Current**. The tissue in which this ascends is the Xylem of the V.B. ; as the plant can only work in terms of very dilute solutions, considerable quantities have to be passed through the tissues in order that a small amount of salts may be retained. Transpiration is thus of primary significance to all land-plants as the means of removing excess water ; but since too rapid desiccation will soon kill aqueous plasma, an effective mechanism of regulation and control is also essential. Closing the stomata altogether would tend to starve the plant.

Stomatal Mechanism. The guard-cells absorb water from the adjacent epidermal cells (or subsidiary cells) through their thin lateral wall, in virtue of their greater osmotic activity. The fact that guard-cells contain chloroplasts when aqueous epidermal cells do not, and still greater quantity if the latter do, suggests that they retain the power of autosynthesis of osmotic material (sugars or organic acids) as required. The guard-cells thus become turgid at the expense of adjacent units ; and the thickening of the wall is so adjusted that they dilate most on the outer lateral wall, and may be practically immovable in other regions. Hence on dilatation they become convex outwards, and pull away from each other in the middle line, opening the slit the wider the more turgid they become. Any stimulus to the plasmatic film, increasing the permeability, tends to reverse the process ; and water escapes back to the adjacent tissues as the guard-cells become flaccid ; the pore being thus closed to the original position. Excessive loss of water is an effective stimulus, and the motile guard-cells as the most sensitive units feel it first. Stomata thus close on a wilting plant. The effect may be imitated by plasmolysis of the guard-cells.

Food Conduction : The mesophyll of the leaf gives sugars, starch, and proteid as excess manufactured food-material, which may be conducted away to feed other parts of the plant (so far parasitic on the green tissues). Sugars travel in parenchyma, largely as disaccharides ; Proteids travel in sieve-tubes of Phloems : these substances are less readily checked owing to lack of good test-reagents. Starch-grains stored by day are readily redissolved by night, being hydrolyzed back to sugars by *enzymes* of proteid-constitution, classed as *diastase*. These hydrolyze starch to dextrins, maltose, dextrose in turn ; and a leaf full of starch at the end of a summer day may be quite empty by next morning, and so start afresh. All parts using food-material create a drain on the photosynthetic units, and under such stimulus a food-current once set up may be long-continued.

FIGUS ELASTICA (India-Rubber Plant) a tropical forest-tree with leaf affording a good example of high specialization: the lamina 18 in. by 7, with stout petiole, 3-4 in.; midrib, pinnate venation, entire margin, and connecting marginal vein, much on plan of Cherry Laurel. Section at right-angles to the small lateral veins more satisfactory: lamina .7 mm. thick, and highly differentiated. In sect. of fresh material note:—

(1) **Epidermis**, a remarkable aqueous system of 3 rows of cells (originally 1), outermost about 10μ , next 40μ , inner 100μ ; total 150μ of aqueous tissue as protective screen. Cuticle and cuticularized layers uniformly thick, 7μ ; at intervals oval cells enlarge to 200μ long, and show peculiar concretions (*Cystoliths*) as partly crystalline deposits of CaCO_3 on a cellulose basis; sol. in $\text{H}\bar{\text{A}}$, and test Chlor. Zn. Iod. for blue cellulose rest and peg: stratified and striated organization suggestive of that of wall-deposits, and of starch-grains. Function unknown, except as 'waste'.

(2) **Palisade Mesophyll**, of 2 well-marked tiers, leading to a third, in candlelabrum type; cells $40\text{--}50\mu$ by 12 wide, thin-walled, with abundant discoid chloroplasts, grading into spongy mesophyll of loose tissue aggregated around V.B. of veins.

(3) **Vascular Bundles**, larger ones cut transversely, with χ on upper surface; broad crescentic tract of scl. fibres on lower (ϕ) side; small phloem units between; palisade tissue divergent to make way for them.

(4) **Lower Surface** with attempts at a lower palisade (one row); 3-layered epidermis on reduced scale; occasional cystoliths, and conspicuously fine sunk stomata.

(5) **Stomata**, guard-cells sunk midway in aqueous epidermis, 40μ below level of surface, with thick outer and inner walls, mere slit-lumen, with chlorophyll and starch; slit hour-glass shaped. Cuticle follows entire contour, and ledges define outer and inner pore-chambers. Large outer vestibule, 30μ deep and wide. Stomata are cut in all directions in the same section, as many as 4-5 in the field of high power at same time. Well-differentiated in Chlor. Zn. Iod.

(6) **Midrib** of generalized organization; parenchyma and V.B. may show abundant calc. oxalate rhombs.

NYMPHAEA, the leaves of the Water-Lily present a quite different type, as associated with flotation on the surface of water. The lamina is soft, 10 in. by 8, with petiole of several feet in length adjusted to the depth of the water, and is over 1 mm. thick. In sect. note:—

The upper epidermis consists of a single layer of small aqueous cells with thin cuticle. Stomata occur only on the upper surface; the guard-cells being well supplied with starch-granules, and flush with the outer surface.

The palisade is very pronounced, 200μ deep, of short slender, thin-walled cells, in vertical rows, with large discoid chloroplasts, 5μ .

The spongy mesophyll is arranged to form rectangular lacunae, bounded with plates of simple cells, in single series, with chloroplasts and nuclei (10μ) in a peripheral layer. V.B. rudimentary with spiral tracheides. Remarkable *sclerites*, as branched sclerenchymatous fibres, pushing irregularly between other cells in all directions (instead of in one line only), are left more or less suspended in the walls of the lacunae on final distension of the lamina: these are lignified, picked out very prettily by the phloroglucin-reaction. The lower surface shows tannin-sacs in the place of more usual stomata.

Lavandula (Lavender) affords a good example of hair-derivatives of the epidermis; as (1) branched hairs, of shrubby growth of dead air-containing units, forming a protective screen over surface, and covering (2) glandular hairs, with 2-4 celled head on short pedicel. The head-cells secrete ethereal oil underneath the impervious cuticle, which may become enormously distended before rupture (60μ).

Pelargonium tomentosum, intense odour, softly hairy; (1) simple dead hairs, 1 mm. long, as velvety pile; (2) glandular hairs on long pedicels, globular head-cell 60μ diam.; secretion distended 80μ .

Hedera (Ivy) affords pretty stellate hairs, protective on young shoots; esp. larger forms with rusty tomentum: limiting case in peltate closely-set scales of *Eleagnus*, as glistening skin over transpiring surface.

The function of the **stem** is to support, space out, and display the photosynthetic leaf-members, to supply them with food-salts, and act as the general path of conduction from the absorbing root. Hence its tissues are differentiated in connexion with—(1) Conduction of water and solutes to the lamina; (2) conduction of elaborated food-material to other growing but non-photosynthetic regions; (3) mechanical support and ramification over a considerable space-dimension; (4) in lesser degree for storage of reserves.

The tissues concerned with these functions are respectively:—(1) Xylem, (2) Phloem, (3) Mechanical tissues (Stereome), more particularly as sclerenchymatous fibres, to a lesser extent Collenchyma in young axes, (4) all living parenchymatous units.

Ramification of the shoot is normally provided for by the initiation of new growing-points in the axils of the leaf-members, hence termed axillary-buds; the limiting case of one such bud being normal for all foliage-leaves.

A good example is afforded by the stem of the great Sunflower:—

HELIANTHUS ANNUUS, which may grow 12 ft. high, and 2-3 in. diam., in the course of a few months. Small stems, $\frac{1}{2}$ in. diam., from an actively growing plant are most convenient. Hard stems and soft ends may be rejected. In transv. sect. the bundles are visible to the eye, as an enlargement of the $\frac{1}{8}$ in. stem: about 20-30 are evenly distributed around the periphery, about 2 mm. from the margin, and the centre includes a large pith, 9 mm. diam. Section need not include more than 3 bundles. Iodine sol. gives immediate differentiation of the V.B. masses, endodermis with starch grains as before, tracts of scl. fibres (yellow) in the pericycle external to the V.B., as if associated with them: a definite cambium-zone passes from bundle to bundle. The cortex shows an outer collenchymatous region and a few ducts. The bundles vary in size, some very small. Select a medium well-differentiated one for more detailed examination. Tissues from the periphery inwards include:—

- (1) **Epidermis**, of oval cells, 30 μ wide, with aqueous contents, slight pitted areas, thicker outer wall, and distinct cuticle.
- (2) **Collenchyma**, of a dozen rows or more; cells 15-20 μ , oval, with cellulose thickening at angles and on tangential walls; scanty contents with a few chloroplasts; grading into:—
- (3) **Cortical Parenchyma**, of thin-walled cells, oval, up to 100 μ wide, with scanty contents; many in active division by radial walls. Occasional *resin-ducts* show a cavity, 20 μ diam., surrounded by a series of a dozen or more small, 20 μ secreting cells, grading into ordinary parenchyma.
- (4) **Endodermis**, as a wavy line of cells, in single series, pressed outwards opposite the V.B., and dipping between them; cells to 50 μ , more or less with starch-grains. Radial walls in close contact.
- (5) **Pericyclic Fibres**; opposite each primary V.B. an oval tract of very distinct tissue, as closely packed units (up to 500 or so) with minute intercellular spaces only; walls thickened, with slit-pits, and deeply lignified (giving phloroglucin react.). Average diam. 25 μ , but many smaller attenuated ends cut as the effect of sliding growth. Little living contents left at this stage.
- (6) **Pericyclic Parenchyma** fills the regions between the fibrous tracts, cells of which may be also dividing by radial walls to keep pace with the growth of the stem.
- (7) **The Phloem**, immediately within the fibrous tract, consists of units with cellulose walls and protoplasmic contents, differentiated into:—
 - (a) **Sieve-Tubes**, 20-25 μ diam., with contents as dense coagulated proteid masses (or falling out in sect. of sp. mat.).
 - (b) **Companion-Cells**, as small units (6-8 μ) with dense granular contents, associated with the sieve-tubes, as at their angles.
 - (c) **Phloem-parenchyma**, as all cells not distinctly referable to the preceding.
 - (d) **Protophloem**, suggestions of small cells at the external limit of the tract.
- (8) **The Cambium** as radial rows of small cells, 15 μ wide, actively dividing by tangential walls to build new tissues in both directions radially, with occasional

radial divisions to add new rows. The term covers the *initial cell* of each row, as also, more loosely, all units still small and not obviously differentiated.

- (9) **The Xylem-region** internal to the cambium shows at first thin-walled units in process of elaboration; vessels dilating at the expense of adjacent units before acquiring the special wall-thickening, and retaining p. contents and nucleus. The fully differentiated region, picked out by the phloroglucin-reaction, is lignified, and consists of:—

I. Metaxylem of—

- (a) **Pitted Vessels**, appearing as large oval or rounded empty spaces, to 100 μ or more diam., wall thick, with beaded effect due to closely set small bordered pits (5 μ), deeply lignified; between these—
(b) **Xylem Fibres**, as units similar to the fibres of the Pericycle, lignified, with thick walls and slit-pits, closely packed by mutual pressure.
(c) **Xylem Parenchyma**, lignified, with conspicuous pits on end walls.

II. Protoxylem of rounded tracheides, in more or less radial series, diminishing inwards, often in finger-like series, including—

- (a) **Spiral Tracheides**, to 70 μ diam., showing cut end of a spiral thread-thickening: 3-4 in series, to smaller ones of 40 μ .
(b) **Annular Tracheides**, the smallest, innermost, lignified units, with no cut thread (i. e. ring-thickening). Surrounding these—
(c) **Xylem Parenchyma**, as small-celled undifferentiated tissue, ultimately sclerosed.
(10) **Medulla** of larger parenchymatous cells, as also in Primary Medullary Rays, 20-60 μ diam. In the centre of the pith, which soon dies, and contains air only, cells distend to 300 μ diam.

Note.—The connexion of Interfascicular Cambium across the rays by the inner pericycle; differentiation of Metaxylem takes place centrifugally, that of Phloem centripetally. New vascular strands have no 'proto'-regions. The Protoxylems differentiate centrifugally ('endarch'): the vascular tissues will ultimately complete the circle as a 'vascular cylinder'. On the flanks of the bundles pitted-tracheides occur, intermediate to vessels, as at the periphery of the protoxylem reticulate tracheides are intermediate to simpler spiral units.

Longitudinal section, cut radially through one V.B., shows general extension of all the tissues more or less: isodiametric cortical parenchyma may be twice as long as wide; endodermal cells 3-4 times. The fibres are apparently indefinitely long, with attenuated ends, and the slit-pits show on the face-walls. Sieve-Tubes, 200 μ long, with sieve-plates obscurely perforated and 20 μ diam.; the coagulated proteid contents (and slight starch) staining deeply with Iodine-sol. Cambium units as delicate longitudinally extended cells (200 μ), with thin walls, granular contents and elongated nuclei. Pitted Vessels, formed of segments 300 μ long, or more, with close-set oval, eye-like, bordered pits (6 μ). Xylem fibres as slender units with pointed ends, small slit-pits, both ends not seen; mingled irregularly in metaxylem. On the flanks of the bundle, pitted tracheides come next to pitted parenchyma of the M. rays, rectangular cells, 100 μ or more long, with pitted walls.

Protoxylem of tracheides, variously thickened; as *reticulate*, with broad meshes, grading to pitted forms, 300-400 μ long; *spiral* tracheides with spiral thread (1 or 2), running distinct, anastomosing, or branching, pulled out more or less according to age; the thread alone lignified. *Annular* tracheides as the innermost, with perfect ring-thickening alone lignified, and pulled out to 100 μ apart. Transitions to spiral also occur.

Iodine-solution is the best differentiating reagent for cell-contents; Phloroglucin-25 % H_2SO_4 for differentiation of lignified walls; Chlor. Zn. Iod. is often feeble for spirit-material, though admirable for fresh: In extreme cases Iodine sol. and 66 % H_2SO_4 gives a deep blue with celluloses, but is apt to decompose delicate tissues.

Drawings of such an indefinite complex, no two sections being alike, are preferably built up by taking one unit of each kind (or two), in succession, as a composite figure including all cell-details, rather than a fancy sketch of the field of view: In the case of pitted tissues of different order, note the detail on either side of the party-wall, as seen by focussing the cut edges.

Differentiation of form of cells, texture of walls, and character of contents imply differentiation of function. Names given to tissues are of value only in so far as they express a specialization of parts in a complex mechanism. Details of microscopic observation are the chief method of deducing the meaning of the organization; e.g.—What each unit does, how it is done, and on what evidence, are the essential problems.

The **Epidermis** secretes the cuticle as a more or less impermeable film restricting loss of water from the entire external surface; **Collenchyma** affords mechanical cohesion under wind-strain; the ducts secrete terpene-derivatives, but are of little significance in this type (cf. *Pinus*).

The general **Cortex** is photosynthetic as far as light can penetrate, and acts as a ground-tissue of units apparently not required for any more special function: the endodermis controls lateral access to and from the stele. Pericyclic strands of fibres afford mechanical cohesion, strength, and elasticity, to the axis in response to wind-action. The **Phloem** includes tissues distributing synthesized 'food' to non-photosynthetic regions, as soluble carbohydrate sugars and colloidal proteid; the latter requiring perforated sieve-apertures. The sieve-tubes, being destitute of a nucleus in the functional condition, can have only a partial activity: the companion-cells, with distinct nuclei, as sister-cells of sieve-tubes, apparently play a more active part, as in storage and regulation. The **Cambium** is the meristem continually adding new tissues, and implying that the older units become effete. **Xylem** includes tissues devoted to the conduction of the transpiration-current. Pitted-vessels, with continuous tube-cavity, formed by the obliteration of the original transverse septa, represent the most highly efficient water-pipes; the bordered pits acting as countless valves permitting the passage of water but not of air (cf. mechanism of pit-chamber, pit-membrane, and torus). Spiral tracheides, universal in all vascular land-plants, as the first-formed conducting units, merely present a spiral supporting internal thread of lignified material on a cellulose wall, originally close-set. Annular tracheides, as variants, are open to compression between the rings. Living parenchymatous cells, with osmotic pressure of several atmospheres, are stronger than any dead wall unless thickened solid. Medullary-ray parenchyma and pith are of the nature of ground-tissue, storing starch, or dilating instead of dividing, and soon dying off in reduced supply of light, water, and free oxygen.

CUCURBITA (Vegetable Marrow) an interesting example of herbaceous stem; also annual in duration; with more exact number of large V.B. in a 5-6 ridged shoot, bearing enormous leaves (18 in. across), and huge fruits: the plant is a tendril-climber, and the mechanical tissues are ill-differentiated; but the conducting tissues (χ and ϕ) are as fine as may be found, and far more elaborate than those of *Helianthus*, in correlation with the great photosynthetic and transpiring area, as also the amount of food to be conducted to the massive fruits within a few summer months. But the cambium-ring is never completed, the bundles remain isolated, and the medulla breaks down leaving a cavity.

Transv. sect. of the ridged stem shows V.B. in double series, corresponding to the ridges and spaces alternating: the pitted-vessels of the metaxylem, .5 mm. diam., can be seen with the naked eye. From the periphery inwards, note:—Epidermis little differentiated, with thin cuticle; beneath it tracts of collenchyma, partial only, a dozen cells deep (20 μ), with conspicuous cellulose thickening at the angles, giving star-effects. Parenchymatous cortex of half a dozen rows: endodermis without starch, and no special character; but recognizable by being immediately outside a continuous zone of pericyclic fibres, little thickened, 4-6 rows, and lignified. Within this zone pericyclic parenchyma as a tract 1 mm. broad, of cells similar to med. rays, and in older stems storing starch in cluster-groups. The Phloem contains large sieve-tubes, to 70-90 μ diam., with associated conspicuous companion-cells: transverse sieve-plates are seen in face-view, with netted pores (5 μ) and conspicuous proteid-contents, irregularly coagulated, and staining brown with Iodine sol. Cambial cells are 30 μ wide, giving very regular radial rows; the latter much disturbed in the young metaxylem by dilatation of young vessels. The Metaxylem of Pitted Vessels and Pitted Tracheides shows no mechanical fibres, and but little parenchyma. The

protoxylem of ill-differentiated spiral tracheides extends to a broad tract of small celled ($20\ \mu$) parenchyma. Internal to the latter, a semicircular arc of Medullary Phloem repeats the organization of the outer phloem, but is not capable of extension by a cambium.

In **Longitudinal sect.** note,—the large sieve-tubes of the primary (outer) phloem, $600\text{--}750\ \mu$ long, and $50\text{--}75\ \mu$ wide, with sieve-plates as transverse septa, $5\text{--}6\ \mu$ thick, and clearly perforated. In sp. mat. the coagulum of proteid may be squeezed through the pores, and take the impression of the sieve. Pitted areas on the side-walls communicate with the companion-cells, as lateral 'sieves'. In older parts these are all blocked with callus, as carbohydrate waste of proteid-conduction, $30\ \mu$ thick on the main sieve, and as thick masses on the laterals. Later sieve-tubes from the cambium are shorter, $200\ \mu$; companion-cells correspond in length to their sister sieve-tube: young sieve-tubes show nuclei $30\ \mu$ diam., but these disappear later. Cambium cells are $150\text{--}200\ \mu$ long: the Pitted Vessels are built up from segments $100\text{--}200\ \mu$ long, all stages being found; the bordered pits are in the meshes of a fine reticular thickening.

ZEa (Maize) as a strong Grass, affords a convenient example of the Monocot. type of construction: the stem is of annual duration, with well-marked nodes and internodes; the latter with considerable capacity for intercalary growth at basal region. Avoiding pieces too hard, with silicified epidermal wall, transv. sect. of a young growing stem ($10\text{--}15\ \text{mm. diam.}$) shows V.B. scattered somewhat irregularly over the section, about 500, of which $\frac{2}{3}$ are more peripheral; each V.B. consists of χ and ϕ , but with no cambium, and no secondary increase. The general scheme of preceding types appears at first sight wholly wanting, but fibres are more numerous in the peripheral region with smaller bundle-ends, and each V.B. presents normal orientation; the best V.B. are those nearer the centre. Individual V.B. are small tracts $200\ \mu$ ($100\text{--}300$) diam., all on the same plan; one may be taken in detail:—

Two large pitted-vessels placed laterally ($60\ \mu$) are most conspicuous; as also 1–2 smaller ones in the radial line, $50\text{--}30\ \mu$, as roughly a V-shaped group, the apex of which is occupied by an intercellular lacuna, and the fork subtends a small oval phloem tract ($100\ \mu$). The innermost tracheide is annular (often only as suspended loose rings), the next is spiral, and between the large p. v. a series of pitted-tracheides, $5\text{--}6$ wide, closes the gap; while small cells of xylem parenchyma fill the space around the spiral tracheide. The Phloem consists of sieve-tubes ($15\ \mu$), as the larger units of the tract, more or less in a chess-board alternation with smaller cells ($6\ \mu$), apparently functioning as companion cells, with marked contents. Crushed relics of Protophloem appear at the limit of the V.B., pressed against an investing sheath of sclerosed fibres (1–2 deep) which more or less surrounds each bundle, being greatly exaggerated in the cortical region of the stem. Ground-tissue of thin-walled parenchyma, to $150\text{--}200\ \mu$, with marked aeration, fills the intermediate regions of the stem.

In Longit. Sect. different units may be checked by their position in transverse scheme. The pitted-vessels are made up of segments $600\ \mu$ long, with close set oval bordered pits, $6\ \mu$; the annular vessels with hoops $50\ \mu$ diam., spaced as much apart or more, are the finest elements of this stem. The sieve-tubes are feebly differentiated, with sieves hardly noticeable. *Note* general absence of starch, tannin, and crystals. Cellulose tissues are differentiated by Iodine and 66 % H_2SO_4 .

The biological organization of the stem is based on strength and flexibility rather than rigidity, and this is secured by a very uniform distribution of fibrous tissues associated with the vascular strands.

HIPPURIS (Mare's Tail); Dicot. aquatic type with greatly deteriorated conduction system. In transv. sect. of internode, $5\text{--}6\ \text{mm. diam.}$, *Note* central stele, circular, 1 mm. diam. or more, and cortex with large lacunae ($\frac{1}{2}$ to 1 mm.) separated by plates of cells, 1 deep, giving great internal atmosphere.

Epidermis of small cells with thin cuticle; Endodermis conspicuous, cells oval ($40\ \mu$), with starch-grains, and 'radial dot'. No differentiation of V.B., no cambium; no M. Rays, no mechanical fibres, no distinct pericycle: a zone of ill-differentiated phloem of small cells, largest (sieve-tubes) $20\ \mu$ diam., surrounding Xylem of reticulate and spiral tracheides ($30\ \mu$), mingled with small-celled parenchyma. Broad central parenchymatous medulla. A trace of cambial division outside xylem in older stems.

The massive **timber-tree** which may commonly attain a height of 100–200 ft., and live for hundreds of years, yet may take 20–30 years to attain reproductive maturity, is in no sense as efficient an organism as the rapidly growing herbaceous annual with quick returns. Indigenous trees are characteristically deciduous, and work in terms of a short season (May–October), enduring the vicissitudes of the winter. The amount of seasonal increment is relatively small; the tissues are densely sclerosed, giving rigidity to the axis, and the cell-units remain typically small and closely compacted.

The **vascular cylinder** from the beginning is preponderant in the stem; the xylem constituting a close cylinder around the pith; individual V. B. are not noticed. Growth continues by a circular cambium-ring, external to which narrow zones of phloem and cortex are popularly but incorrectly considered as 'bark', because they can be peeled off at the cambium.

Special features require detailed notice:—

I. **Cambium cells** have the shape of greatly elongated rectangular prisms, with definite orientation, and may divide by transverse, radial, and tangential walls respectively; i. e. in 3 dimensions.

(a) *Transverse walls*, beyond the zone of primary extension of the axis, merely produce septation into shorter segments in longitudinal series, as in medullary-ray formation, and production of xylem parenchyma.

(β) *Radial walls* increase the number of initial units, giving more radial rows of the same size to fill the circle as the stem increases in circumference.

(γ) *Tangential walls* give new tissue-units, as phloem on the external side (centripetal), and xylem on the inner side (centrifugal). Each division involves mitosis, and the formation of a new cell-wall: in this last case in the position presenting greatest difficulty. Initial cells (i. c.) in each radial row now control the mechanism, with some sort of power of choice as to which segment shall continue as initial.

II. **Annual Rings.** Increase by cambium may continue indefinitely, and one cambium may persist throughout the life of the tree as a permanent meristem of embryonic activity, but restricted to special tissue-production: a cambium does not originate any other part of the plant (as a branch or root). Where annual periods are marked by climatic changes, tree-types respond by seasonal periodicity. The cambium may be dormant, or 'resting', at certain periods of the year, and start again with renewed activity (as in Spring of the N. Temp.). Differences in the tissues formed at different seasons may give the effect of zones in the wood; i. e. a new growth each year as an *annual ring*. Spring wood is commonly indicated by wider vessels; summer wood by smaller vessels and tracheides, abundance of fibres and increase in deposit of polysaccharide. Decreasing size to a minimum in late summer, followed by sudden growth of larger units in the spring, with special function, emphasizes the ring-effect. Such rings vary in width from 1–20 mm., as annual increments, and afford a clue to the age of the tree, giving the 'grain' of timber as more or less concentric circles; though again naturally wanting in trees growing with little change of season.

III. **Medullary Rays:** The spaces between the primary bundles of a young stem are conveniently known as primary rays. These tend to be obliterated by interfascicular extensions. Secondary rays are more important, as formed at and by the cambium for a special purpose. Any initial cell may be set apart to produce a ray. These rays are distributed at fairly constant intervals (varying in different types); and as the circle of cambium increases, new rays are initiated to maintain equal distribution, midway between the older ones. Being initiated in the cambium, the rays differentiate both ways in χ and ϕ for ever after, following radial lines at right-angles to the curve of the cambium 'circle'; and so with the concentric rings constituting an orthogonal geometrical construction, as seen in cross-section, centric or eccentric, according to the growth of the stem.

Typically of living parenchymatous units, radially elongated, more or less sclerosed in the xylem, and storing starch, tannin, or crystals, the primary function is to act as living units controlling the mechanism of radial and transverse conduction to other living cells of the vascular cylinder. Commonly only 1 cell wide, and several

deep; but often very wide and very deep (broad rays of *Quercus*). In wood split down radial planes the rays show as a 'silver-grain' effect.

IV. Cork: The epidermal cells constitute a specialized integumentary system producing the cuticle, but are not capable of indefinite growth and division. Typically in woody stems with rapid secondary growth, the epidermis is replaced by a new formation (Periderm). A special meristem arising from the cells below the epidermis (in the general case *hypodermal*, but often deeper) presents the dividing mechanism of a cambium, so far as 'initial cells' and 'radial rows' may be concerned. This constitutes the *Phellogen*; and the tissues formed from it centripetally are *cork*, those centrifugally *phelloderm*: the latter is rarely well-developed, and merely adds new units to the cortex, only distinguished by being in radial rows.

The cork-cells retain close lateral contact, but soon die; the wall is 'suberized', and becomes very impermeable to water and gases. The cork-formation may be continued indefinitely from the same phellogen (cf. Bottle-cork), or new phellogens may be initiated internal to the first one. All parts external to the last phellogen are cut off from communication with the cortex, and soon die, decay, or may be exfoliated.

V. Bark: The term bark botanically covers all such dead layers cut off by a Phellogen, whatever their origin, as opposed to the popular and commercial conception of the word. Such bark may be cut off in flakes or rings, sheets or 'scales', the last by oblique sectorial phellogens, and may contain 'stone-cells' (*Pinus*) and layers of different texture. Where the phellogens are initiated deep in secondary phloem, the bulk of the bark of an old tree may consist largely of crushed phloem. The products of one phellogen are traced in terms of radial rows to each initial.

VI. Lenticels: As the cork in its special impermeability replaces cuticle in function, so aeration of the tissues must be provided for, and the stomatal control is replaced by lenticel-formation. These appear on corky surfaces as small wart-like growths, often increasing with age to considerable dimensions on the bark, but are of essentially similar origin from the phellogen: certain cells over localized areas are set apart to give new tissue-units centripetally, differing from cork-cells in that the walls readily separate, and the tissue becomes hygroscopic and powdery, as 'lenticel tissue': on decay, this leaves free communication to the phellogen and subjacent phelloderm, which is usually well-developed beneath the lenticel. Such lenticels may persist for several years, and show seasonal periodicity; closing in winter by a production of cork, and opening in spring as the cork-layers are in turn ruptured, and thrown back like the pages of a book, by new loose-tissue formation. Clogging or closing of these pores by dust or smoke, by cutting off the free oxygen-supply from the internal cambium, where there is little photosynthesis in the cortex, may be distinctly injurious.

Elder (*Sambucus*) shoots cut at the end of the first summer show a well-defined production of large cork-cells ($50\ \mu$ wide), in radial rows of half a dozen or so from hypodermal phellogen; the dead epidermis still persisting, and not conformable with the subjacent radial rows. Phelloderm represented by 1-2 cells per radial row; the initial cell of the Phellogen as the last cell out with protoplasmic contents. Underneath the Periderm collenchymatous cortex. The woody ring is extremely hard, and may be avoided; slips of outer cortex, stripped at the cambium, being cut in pith. Lenticels show as lenticular areas, about 2-3 mm. long, and 1 mm. broad; in section, note great extension of dead layers, ruptured peripherally to a broad gap; loose lenticel-tissue, and great development of phelloderm, a dozen cells or more in the radial rows. Larger growths on second year's shoots, to 2-3 mm. diam., show characteristic reflexed tissue-zones.

Bottle Cork (*Quercus Suber*), as a secondary growth of cork, induced after stripping primary mass ('Virgin Cork'), of very uniform texture, with lenticels as conspicuous pore-canals. These pass radially and transversely, giving the orientation of the tissue.

Note annual zones of growth (2 mm. wide); in transv. sect. radial rows of fairly isodiametric rectangular units, about $40\ \mu$ wide; radial sect. similar radial rows; but in tangent. sect. no radial rows are seen; the cell being isodiametric and polygonal.

Tilia (Lime-tree) is a convenient type of woody stem, owing to softness of wood.
(*Separate detailed Schedule omitted from elementary course.*)

The **Primary Root** of a seedling (e. g. Bean) appears as the direct continuation of the primary axis of the shoot, passing down into the soil, as a main Tap-root, with definite growing Apex, and lateral ramification; the laterals spread more horizontally, and again branch to a highly ramified system penetrating the soil in all directions.

Ordinary **Soil** is a very special material, of inorganic particles and colloidal organic debris, with spaces containing air and water, as a complex organization physically and chemically; and also biologically as containing races of micro-organisms (Bacteria and Protozoa). The essential part of soil may be preferably regarded as a living complex of bacteria engaged in breaking down decomposing plant-residues, largely of cellulose origin, as *humus*, to which inorganic particles are largely accessory. One gram of good soil may contain anything from 10-50 millions of Bacteria. For successful penetration by roots the material requires to be loose in texture, well-aerated, with considerable water-content, as facts of general horticultural experience. Land-plants are normally furnished with 'soil-roots': 'water-roots' and 'air-roots' involve subsidiary problems.

The essential function of the root is **Absorption** of solutions in the soil; the mechanism of the process, being complex, involves a stationary habit; fixation of the plant to the ground, as adaptation to resist uprooting effect of wind, &c., is quite secondary. Normally the connexion has become so intimate that adult plants with less power of regenerating new root-systems are with difficulty 'transplanted'. The solutions in the soil vary enormously, but are normally extremely dilute; inorganic solutes being largely ionized. Essential substances are determined by—

Culture Solutions, experimentally. A typical laboratory medium may contain Potas. Nitrate, 1 g., Sod. Chlor., Calc. Sulph., Mg. Sulph., Calc. Phosphate, each $\frac{1}{2}$ g., and a trace of Iron salt; or about 3 g. of salts to a litre (1000 g.) Sea-water, 35 g. per litre, is over ten times as strong; lake- and river-water about $\frac{1}{200}$ the latter. The osmotic value of sea-water is 23 atmospheres, that of rain-water may be nil; soil waters range between. Absorption can only take place at the peripheral layer of cells in direct contact with the medium; and in typical soil-roots the units of this layer are produced into special filamentous growths presenting greatly increased surface, as 'Root-Hairs'; these may attain a length of 1-5 mm., with a diam. of 6-30 μ . The layer producing them is known as the 'Piliferous Layer', as quite distinct from the conception of the epidermis of the aerial shoot-portion.

A typical **Root-Hair** extends as a dilatation from a localized area of the original cell-wall, with protoplasm, aqueous contents, and nucleus controlling its extension; the plastic apex pressed between particles of soil may become irregular in shape, and contains little cellulose. Such units have usually but a short life, and die away as new ones are continually produced at the growing apex; e. g. on pulling up a plant the root-hairs are usually broken off, and remain in the soil (cf. Groundsel, root-hairs 10 μ diam.).

Root Apex: The root increases by a terminal growing-point, essentially similar to that of the stem, and presenting similar differentiation into distinct layers, conventionally distinguished as *calyptragen*, *periblem*, and *plerome*. The calyptragen is many-layered, and constitutes a definite 'Root-cap' region, giving the apex a pointed conical appearance, the older layers of which are gradually worn away by friction in passing through soil. The initial layers are internal, marking a dome-shaped curve as the true growing point. The periblem (or cortical region) in some cases (*Zea*) reduces to a single row of cells at the actual apex, giving very distinct layering; in others (Bean) it is ill-marked. The central region (plerome) gives rise to the conducting stelar tract. The calyptragen is either entirely worn away as root-cap (*Zea*), or leaves one layer only (Dicots.); in the latter case this becomes the piliferous layer; in the former, root-hairs are produced from 'periblem'. Such discrepancies show that apical layering is of no strict morphological value, but may characterize minor groups as interesting variations on a general physiological mechanism.

Zones of Growth are more condensed than is usual in the case of typical stems. The second 'zone of elongation' is but short, giving increased power to the thrust behind the dividing meristem of the apex; and this region is again responsible

for all correcting curvatures. Adult differentiation of primary tissues is rapid; the first expression of tissue-differentiation being seen in the initiation of protoxylem tracheides at usually only a few points. Hence roots are described in terms of protoxylems as 'diarch', triarch, tetrarch, &c., and 'polyarch' when the number is not obvious at a glance. Maximum number in large Monocot. types may be 100 or more. The limiting case of centric symmetry is *diarch*; and this becomes the commonest case for all small roots. Root-structure also shows a characteristic arrangement of the xylem, possibly as retention of an older mode of organization; the xylems alternate with the phloems on *different* radii ('Radial' arrangement, as opposed to 'collateral' in the stem), and the xylem units differentiate centripetally; the first-formed tracheide being external in the stele, abutting on the pericycle, and hence termed *exarch*, as opposed to endarch and centrifugal in the stem.

RANUNCULUS repens (Buttercup): The general scheme of primary tissue organization may be followed in stout roots, 2 mm. diam., in which no secondary complications obtain. More normal roots present secondary thickening by a cambium at an early stage, and ultimately become woody axes, like old stems, in which conduction alone remains; absorption being restricted to the growing tips penetrating new ground. In transv. sect. note:—

Cortex: wholly parenchymatous, of rounded cells (50–100 μ diam.), with intercellular spaces, and storing abundant starch-grains (12 μ); bounded externally by *Piliferous layer*, of simple papillose cells, 25 μ , without root-hairs, and *Exodermis* of thin walls, no special contents, and closely approximated radial walls; internally by *Endodermis* of oval cells (25 μ), radial walls with 'dot'-effect, owing to chemical alteration of walls at point of contact.

In older roots the cortex becomes ragged and lacunar, the endodermal cells lignify at the dot, add a thickening layer, and this in turn is lignified.

Stele, circular, (300 μ diam.) conveniently fills field of high power.

Type *tetrarch* (varying 3–5), with 4 protoxylems symmetrically spaced, alternating with 4 phloem tracts. The former continue differentiation to meet in the centre, thus leaving no medulla. In young roots only the first spiral tracheides are in evidence, and the others as thin-walled dilatations; in older roots fully differentiated pitted-vessels extend to the centre, and sclerosis may extend to conjunctive tissue on the flanks of the xylem.

The **Pericycle** (as the region between the protoxylem and the endodermis) is reduced to the limit of one row of small units (12–25 μ).

The **Protoxylem** units as spiral tracheides are small (12 μ), and a large pitted vessel (75 μ) may occupy the centre of the stele: the entire xylem-tract is limited to about half a dozen tracheides.

The **Phloem** tracts are vaguely oval regions between the xylems, of a few small parenchymatous units (12 μ), with few (1–2) sieve-tubes (20 μ) with companion cells. A zone of small-celled *conjunctive parenchyma* separates the ϕ from the χ , and follows round internally.

In older roots definite indications of tangential division in some of the cells of the innermost phloem express the initiation of *cambial* mechanism, but get no further.

Deposits of starch in the cortex express the utilization of these roots for storage of food-reserves over the winter; these are conveniently cleared by the use of potash; the tissues are well differentiated by Phloroglucin- H_2SO_4 , or wholly cleared in Eau de Javelle.

Special Cases: The roots of water-plants, attached in mud, show extremely deteriorated organization; root-hairs are wanting, and vascular tissues are reduced to a minimum. Many epiphytic orchids, of tropical rain-forests, and in greenhouse-cultivation, send out aerial-roots, in which a peripheral tissue, delimited by an *exodermis*, and of varying thickness, is specialized as dead units with tracheidal thickenings, which store rain-water, as a spongy system, **Velamen**: conduction is effected by living 'passage-cells' distributed in the exodermis, and storage-tracheides occur in the cortex. The stele is of the polyarch Monocot. type.

Primary structure is also well shown in the primary roots of seedlings of *Phaseolus* (Kidney Bean), about 2 in. from the tip. The tissues are soft, but the radial dot of the endodermis is particularly well-defined.

Secondary Thickening is adjusted to the primary construction; no residual meristem (procambium) being left in the stele as first outlined. Division by tangential walls is first observed in the conjunctive parenchyma immediately internal to the primary phloems; and this continues to give each a definite cambium tract, from which normal differentiation ensues, as xylem products on the inside (centrifugal), and phloem units on the outside: such extension naturally pushes the protophloems farther out, and these are soon crushed out of existence. Similar tangential divisions follow in the pericycle units external to the protoxylems; and the preceding partial cambium arcs are linked up in a continuous system, more or less wavy at first, but soon adjusting to a definitely circular cambial zone, similar to that of the stem, but leaving the protoxylems on the inside more or less unaffected. Quite old roots may be thus distinguished from stems in section by tracing the original protoxylems. The new tissue opposite the protoxylems commonly remains parenchymatous as 'primary ray', rendering the pattern more conspicuous. With a normal cambium in working order, growth follows on as in the stem, and annual rings are produced in successive years; but the first ring is complete in the first year. The cortical region may fail to keep up with the new growth, and is (in a tree-type) commonly exfoliated, including the endodermis.

Phellogen giving a cork-formation, as in stems, normally follows from the outer layer of the pericycle, which thus in old roots looks very much like a cortex. Secondary tissues with vessels, secondary medullary rays, sieve-tubes, fibres, &c., agree with the details of the corresponding stem for different types.

Lateral Roots: Ramification of the stem follows the lines of pre-existing organization, and the laterals are thus associated with the very definite plan of leaf-arrangement as repeating an ancestral mechanism of construction: ramification of the root, in absence of leaves, follows pre-existing organization as that of the protoxylem centres. Owing again to the special mechanism of the absorbing peripheral layers, laterals are *endogenous*; they are initiated in the pericycle, opposite the protoxylems, and are hence put in immediate communication with the water-conducting tissues.

Tangential divisions are initiated in a few cells of the pericycle, thus delimited in transv. sect., but irregularly spaced in the longitudinal dimension, as a *rhizogenic plate*. Two sets of such divisions suggest the 3 tiers of apical meristem (as calyptragen, periblem, and plerome), and the new apex is fully constituted; the young root extending radially to reach the surface and free medium across the cortex. The endodermis normally takes part; its cells divide radially to keep pace with the new growth, forming a pocket over the young root; the cells of this region become glandular, secreting enzymes which digest the tissues ahead, so that penetration is not merely mechanical. On reaching the exterior this digestive pocket is worn away; though in water-plants it may persist as a conspicuous glove-finger over the apex (*Lemna*). The xylem of the young root is linked by tracheides with that of the old, at the point of origin; the phloems are connected laterally, and the gap in the endodermis is made good at a '3-dot' cell, as seen in transv. sect. Tissues of unlike origin have to be fitted together or the machine would not work, and a considerable range of variation may be noted.

Adventitious Roots arising on stem, or even leaf-structures, are similarly endogenous and are initiated in the pericycle. From very embryonic tissues with undifferentiated epidermis, 'bud-roots' may take off exogenously (Water-cress). The rooting of 'cuttings' is effected by the initiation of root-centres in the meristem of 'wound-callus'. In many trees the factors required to initiate a stem-apex are substituted for those of a root, and stem-buds may thus break out endogenously from the pericycle, to come to the surface as 'suckers' (Elm, Poplar). Adventitious roots, emitted from a stem under stimulus of contact with a damp surface, may be utilized for climbing, Ivy (*Hedera*) and Poison Ivy (*Rhus toxicodendron*); in the event of efficient water-supply these may attain a considerable size.

The origin of lateral roots may be traced in Bean seedlings, from the first visible protrusion of the young laterals to near the apex; but owing to the vague apical differentiation of the Bean root, seedlings of *Zea* give more detailed results.

The development of secondary tissues may be followed on the Bean, but more conveniently in the roots of:—

Vitis pterophora, a greenhouse climber, which drops adventitious air-roots for several feet, in lengths with clean surface and very uniform structure.

(1) Softer young roots, 2 mm. diam., show well-marked protoxylems, 4 or more (7), and conspicuous phloem-tracts of small cells, with distinct medulla and broad cortex. The endodermis is thin-walled, and only distinguished by being the first row of cells without intercellular spaces. Conjunctive parenchyma on the flanks of the xylems may become sclerosed; but is distinguished by the different tint with Phloroglucin-25% H_2SO_4 . Root-hairs are wanting; the 2 layers subjacent to the peripheral layer are distinct, and contain tannin. Protoxylem units grade up to 75 μ diam., the first formed small and soon crushed.

(2) A slightly older (firmer) stage shows cambial divisions freely produced along the inner margin of the phloem tracts, giving distinct radial rows: large metaxylem units are soon differentiated on the inner side of the cambium (90 μ); the phloem may show tannin sacs; a few cells of the pericycle become fibres, outside the phloems. An active phellogen on the outside of the cortex gives cork-cells cutting off the peripheral layers. Tangential divisions extend to the pericycle external to the protoxylems, and the cambium is linked up, though distinctly 4-angled in outline in tetrarch roots.

(3) Roots $2\frac{1}{2}$ mm. diam. show a well-marked vascular cylinder with masses of metaxylem alternating with the protoxylems, and large pitted vessels (100 μ); but the xylem is mainly parenchymatous: the tissue external to the protoxylem remains a broad primary ray, and a secondary ray (often even broader) is initiated in the new metaxylem tracts. The cambium zone is fully established, with particularly good radial rows. Pericyclic fibres are followed up by fibres in the phloems; tannin-sacs, raphides, and cluster-crystals of calc. oxalate, add details of interest; all parenchymatous units store abundant starch. Thyloses are frequent.

(4) In older roots, 4 mm. diam., with further increase, the large xylem vessels (150 μ) have fibres grouped around them: the protoxylems remain clearly defined, and the tissues are clearly differentiated by Iodine, Potash, or Phloroglucin- H_2SO_4 .

Quercus (Oak) affords a good example with annual rings, in roots 3-15 mm. diam.; the protoxylems (6 or so) persist as a stellate group in the centre, and the primary rays (broad rays) are clearly seen by the naked eye. The details of the tissues follow those of the stem.

Monocotyledonous type of root-construction typically differs in the complete absence of secondary changes, and in polyarch organization. Succulent roots, 4 mm. diam., of *Asparagus* present a wide cortex of rounded parenchymatous units (50-90 μ diam.) with intercellular spaces. Stele, 1 mm. diam., the endodermis with U-thickening, of small cells (12 μ). Pericycle reduced to one row (15 μ). Protoxylems about 20, of very small tracheides (6 μ) peripherally, but extending as a complete ring of vascular tissue, with large p.v. up to 80 μ diam. Central medulla of 50 μ parenchyma. Phloem tracts small, between the protoxylems, each with 2-3 sieve-tubes, and well-marked cambiform units, apparently functional as companion-cells. The section contains no starch, and clears admirably in Potash, or Phloroglucin- H_2SO_4 . The peripheral layer may have conspicuous root-hairs, but the subjacent tissue (6 rows or so) is thickened and suberized.

Orientation of the Root is normally effected in terms of *positive* Geotropism and *positive* Hydrotropism; i.e. roots tend to grow downwards into the soil and to 'seek water', as part of their essential biological equipment. In lateral roots hydrotropism is more pronounced; the strongly-marked positive geotropism of a primary sinking root is an adaptation to the same end of water-supply. Rarely, in water-logged soils, roots may grow upwards to obtain free oxygen. Sensitivity is more concentrated in the apical meristem (Zone I), and the mechanism of response, by initiating a growth-curvature, is restricted to the zone of elongation, usually only a few millimetres behind the apex. The very general occurrence of starch-grains in the cells of the root-cap (not in the growing layers of the apex) has given support (since 1900) to hypotheses of *statocyte*-mechanism, interpreted in terms of 'Falling starch', still largely speculative.

Experimental observations are followed on the *Clinostat*, in which rotation on a horizontal axis neutralizes gravity by giving equal presentation to the stimulus on all sides. The effect of a continually acting force as 'g' may be imitated, or replaced in intensified degree, by the utilization of 'centrifugal force'.

Absorption of Water by the root-hair is regarded as mainly a matter of osmotic activity, dependent on the solutes of the cell-sap and the control of the semipermeable plasmatic film; the osmotic pressure of the cell being normally much greater than that of the external dilute solution. Capacity for absorption implies a similar capacity for getting rid of excess fluid; and this when passed to subjacent parenchyma implies **Conduction**. The physical mechanism of plasmatic conduction is wholly obscure; speculations in terms of osmotic mechanism remain unsatisfactory, as implying that each cell is an isolated mechanism. Colloidal plasma is undoubtedly freely permeable for water as the original medium of its existence, and continuity of the medium through colloidal membranes implies molecular continuity of the water all the way. The fact of absorption by the root-hair implies turgidity of the entire range of living cells; i.e. living units freely conduct until all are turgid; cells losing water draw freely on the others; younger units drain older ones; as in the familiar process of putting flagging cut-flowers in water, by stalks or tops.

A new departure takes place at the first dead tracheide: here a mechanism of discharge or active **secretion** must be postulated. Plasma of land-plants necessarily secretes water as a necessity of existence; there being no other way of obtaining food-salts in quantity from a dilute solution (cf. Myxomycete plasmodia secrete drops of fluid, Dry Rot Fungus, *Merulius lachrymans*, Water-glands of leaves, and water-pitchers of *Nepenthes*). In connexion with such secretion of water into a dead 'conducting' tracheide, it may be noted (1) the tracheide was full to begin with, and (2) there is no evidence that it was dead or empty when it began to conduct. Such secretion into the tracheidal system marks the beginning of the—

Transpiration Current, and further rise of water in the dead xylem is mainly physical; the system is full to begin with, and remains filled; fluid being drawn off above by the transpiring cells, much as the root-hairs below draw on the soil-solution; as loss is made good, water moves in the stem in the dead tracheides. Such a tracheidal system, more perfectly expressed in terms of *vessels*, is in full communication throughout the plant or even a tall tree. In a tree 300 ft. high, the water-column with a pressure of 10 atmospheres would only just neutralize the osmotic pressure of the turgid cells at the base of the system with 10 atmospheres capacity. The height to which water can rise is thus probably connected with the osmotic possibilities of the parenchymatous conducting cells; while owing to the wet colloidal walls there is practically no waste of energy in friction. Lignified walls cannot be imitated by glass tubes.

Root Pressure: A special case of intensely active absorption, conduction, and secretion is seen in the rise of fluid in the tracheal system of many trees, more particularly in the spring; this being noticed before the new leaves appear as a 'rise of sap' (cf. Sugar-Maple, Birch), and is measured as a *positive* pressure by water-column, mercury manometer, or pressure gauge (e.g. Vine 1,000 mm. Hg; Birch $2\frac{1}{2}$ atmospheres): when the leaves are expanded, a *negative* pressure is generally noticed. Such activity is not confined to the root; and 'bleeding' may be induced in other parts with active parenchyma; cf. *Arenga* (Toddy Palm) 'bleeding' induced by blows, long-continued, and the fluid contains sugars.

Absorption of Salts is independent of osmosis, the latter being solely a phenomenon of water-pressure. In a dilute solution the inorganic solutes are practically completely ionized; diffusion is assisted by the colloidal plasma adsorbing ions and complex molecules with little selective capacity; e.g. poisonous substances are taken freely, as ions of CuSO_4 , and dyes as Methylene Blue.

Selective Absorption follows in the long run, as only the substances removed from the solution in metabolism create a drain for more of the same kind, to give an absorption equilibrium. Hence from the same solution different plants give a net absorption differently for the same salts. There is no excretion of osmotic material from an undamaged root-hair; but an acid effect (as seen by corrosion of marble slabs) may be the effect of (1) contents of dead hairs, (2) excretion of CO_2 in respiration, (3) excessive removal of basic ions (Ca'' , Mg'' , K' , Na') in metabolism.

Culture Solutions: by the omission of one or more constituents at a time, it is possible to trace the possible functions of different materials: e.g., omission of Iron renders green plants *chlorotic*, owing to failure of chlorophyll-production, although chlorophyll contains no iron. Lack of Potassium stops the photosynthetic mechanism,

and implies starvation. Addition of Nitrates stimulates proteid-synthesis, and so reduces polysaccharide deposits, giving rank but often mechanically weak growth. Phosphorus stimulates nuclear activities. A certain relation between Ca, K, Mg suggests that these may be individually toxic, but that they neutralize each other, as possibly inherited from sea-water.

Water Problems are obviously insistent for all subaerial vegetation, but the water-problem is but a part of the wider problem of the source of food-salts and combined nitrogen. Special cases attract attention, as evaporation becomes more acute. Although all land-plants require to transpire excessively to obtain food-salts, regulation is required. Plants in danger of losing water faster than they can replace it are termed **Xerophytes**; and commonly present striking *Xeromorphic adaptations* in form, anatomy, and general habit.

The leaves as the essential transpiring organs are the first to be affected; followed by the entire shoot-system. As available examples, cf.:—(1) Leaves reduced in area (Box, Heath); (2) Reduction of intercellular spaces (Conifers); (3) Diminution in number of stomata (*Aloe*, 10–20 per sq. mm.); (4) Thick cuticle (Holly, *Yucca*); (5) Deposits of wax ('bloom' of Cabbage); (6) Clothing of hairs (*Verbascum*); (7) Rosette-habit, with overlapping leaves (*Sempervivum*); (8) Leaves edge to light (*Eucalyptus*), or vertically orientated (*Iris*); (9) Extreme succulence by osmotic effect (*Sedum*); (10) Sclerosis of covering-sheets of lignified tissue (*Pinus*); (11) Entire loss of leaves (*Cereus*); (12) Replacement of leaves by flattened cladodes (*Opuntia*), phylloides (*Acacia* sp.), or phylloclades (*Ruscus*, *Asparagus*); etc.

Also any combination of such factors, producing characteristic xerophytic vegetation, where such conditions are predominant throughout the year. But a plant may be xerophytic (1) at one period of its life and not another; (2) at some time of the day; or (3) at some particular season: examples as (1) Seedlings with feeble root-system; (2) Herbaceous plants wilting in hot afternoon; (3) The evergreen tree (Holly) with feeble root-absorption in winter, and the deciduous tree, as the common example of the N. Temp. region, shedding leaves when the transpiration-system fails.

Special cases of **Aquatics** and **Hygrophytes** present variants on the water-problem, due to insufficiency in the supply. Aquatics, with all subaqueous parts rooted in mud, impoverished for free oxygen-supply (cf. *Hippuris*), utilize a voluminous internal atmosphere in lacunar spaces, with free communication to subaerial portions of the body.

Transpiration is wholly eliminated in plants growing in a saturated atmosphere, or entirely submerged: in such case (cf. *Zostera* under the sea), salts can be obtained with difficulty by direct adsorption; or by active secretion of excess water, as in *Nepenthes* of tropical rain-forest.

Orientation of the main stem is effected largely in terms of positive Heliotropism; but also in terms of response to stimulus of gravity, as negative Geotropism. The plasma of stationary land-vegetation becomes sensitive to the direction of the fall of its own material particles; and the response to this sense of direction may be positive, negative, or transverse (plagiotropic); or even vary from time to time in the same organ. Interpretations of geotropism in terms of 'falling starch', popular since 1900, as hypotheses of 'statocyte' nature, remain purely speculative. The cells of a growing apex, with maximum sensitivity, have neither extensive vacuoles nor starch-grains. The mechanism of *response*, by a growth-curvature, can be only effective in regions in which the cells present a capacity for dilatation and extension.

Note, that changes in environment can never be postulated as Causal: the individual plant is not an isolated mechanism, but the result of ages of inherited response to similar stimuli, fixed by natural selection as part of the present equipment of the race. Just as it is quite unjustifiable to read into the plant ideas of thought, prevision, and design, based on our own more elaborated perceptions and actions; so it is equally wrong to regard the plant as a mere physical mechanism, and the passive victim of environment. The object of physiology is to hold the balance between these two standpoints, with a view to understanding what is the nature of living response. An inherited capacity for adaptability, within a certain range, with every change of condition, may be termed the **Vitality** of the organism, ultimately translated as self-determination. The mechanism of such inheritance, and racial progression, is included under the heading of **Reproduction**.

Special adaptations to enable organisms to exist in a more or less dormant condition over periods of unfavourable environment are included as phenomena of **Perennation**; since such vicissitudes are most commonly presented in terms of seasonal periodicity. Conspicuous examples are (1) the case of the Cold Northern Winter, (2) that of the hot and dry Southern Summer. Both trace back to problems of water-supply, rather than temperature which only affects the rate of metabolism; e. g. in cold soil, mechanism of root-absorption fails, and plants perish for want of water in cold wind, even if rooted in water. In hot deserts lack of water is more insistent than extreme insolation as leading to xerophytic habit. In cold winter of British Isles trees perennate from mid-Oct.-Nov. to April-May, vegetating in short summer season of 6 months; and leaf-fall becomes a conspicuous feature of the zone of deciduous trees (Central and N. Europe), as opposed to highly specialized xerophytic foliage of evergreens of the Mediterranean region.

Mechanism of Leaf-fall, a special case of the general method of cutting off all useless parts by the formation of an *absciss-layer*; a tract of cells whose walls readily exaggerate intercellular spaces, to loosen entirely along a line of cleavage; all parts intentionally separated follow this method, whether leaf, flower, fruit, or seed. Autumnal leaf-fall may be more elaborate, as commonly preceded by a formation of phellogen across the leaf-base (except through V.B.), giving a cork-layer in connexion with the cork of the stem, and thus 'healing the wound' before it is made. The cork-layer becomes uniformly continuous, except across the axillary bud.

Populus (Poplar), leafy twigs cut in early October show the cork-zone with phellogen on inner side, in usual radial rows; V.B. pass through it: all tissues on the leaf side are dead, and full of cluster-crystals; but a trace of starch at the extreme base. On the stem side all living units are gorged with starch (as also calc. ox., and patches of stone-cells, as conspicuous details). The absciss-layer is formed externally to the first-formed cork (often giving phloroglucin-reaction); when formed, the leaf loosens, hence it is not seen fully developed in sp. mat. Mechanical action of wind or frost separates the dead leaf, rupturing the vessels and fibres of the V.B. The V.B. are subsequently plugged by outgrowth of bundle-parenchyma, as a wart-like scar on each end. The surface of the entire plant is then sealed with a uniform zone of cork.

The Winter Bud: Such deciduous trees protect the shoot-apex and young growth by special formation of *bud-scales* (leaf-base, or stipules); and in order to start rapid growth in spring, the leaves of the succeeding season are commonly all laid down in the previous summer, remaining in a resting-stage enclosed within the 'bud', with its investment of scales (hibernaculum). The finest winter bud is that of—

Aesculus (Horse-chestnut), not indigenous; buds cut in October show Bark with Lenticels, Leaf-scars with smaller scars of V.B., 5-7 in an arc; large T-bud, and smaller axillary laterals following the decussate arrangement of the leaves. The series of bud-scales similarly decussate imbricately in 4 rows, longer distally to the pointed apex, and sticky with resinous exudation (sol. in spirit) from special glands (colleters) on the scales.

In longit. med. sect. note the length of successive scales; the enclosed foliage-members with cottony packing-hairs; and in finer shoots the central terminal inflorescence of young buds. Section of bud-scales shows colleters as small wart-like sessile glands, with secretion poured into chinks between the scales. The latter develop cork on outer surface from hypodermal phellogen.

Similar buds in April show rapid extension of shoot-internodes, divergence of the bud-scales; and often interesting transitions in form from protective leaf-base scale to distal palmately lobed lamina.

Winter-buds are wholly wanting in trees of warm climates; just as leaves remain on more than one season as 'evergreen' habit. But leaf-fall may be again induced by hot dry season (desert vegetation), resting buds similarly perennating over heat-period.

Herbaceous Perennials commonly vegetate over winter by a 'root-stock' portion, at the soil-level or below, of stem parts with reduced internodal extension; but sending up rapidly elongating axes each season, as foliage and flowering-shoots; cf. *Polygonum*, *Hop*.

Special cases may be distinguished, as:—

Rhizome of many forms, as in *Iris*; the main axis remains prostrate at soil level, or even below, out of the way of desiccation, sending up erect foliage-leaves and inflorescences under optimum Spring conditions: essentially an adaptation to hot desert with sandy soil. *Note* short seasonal growths, leaf-scars, advt. roots, and utilization of stem-tissues for storage of reserves, as starch. Perennation over summer heat may be continued over winter cold as well. By further concentration of shoot-system and deeper soil-penetration the case of the 'bulbous' *Iris*, with starch-storage in leaf-members.

The Tuber (cf. Potato, Artichoke) as a special case of subterranean shoot-formation, 1 or more internodes of a rhizome-system being swollen, filled with food-reserves in parenchymatous tissues, and readily separated from parent plant. More or less rounded form; succulence due to water-storage; with corky covering; enduring desiccation, and also utilized for dispersal.

Potato (*Solanum tuberosum*), a plant of Central America adapted for perennation over hot dry season in sand, to germinate in wet season; tubers originally small (1 in.) and round. Utilized in this country for perennation over cold winter (under cover), and often grown in clay soil: cf. stem-structure, stalk-end and apical crown with T-system of leaf-scales and buds ('eyes'), or scars of subtending leaves; section near stalk shows V.B. distributed; delimiting cortex and broad central medulla. Spiral vessels in V.B. (test phloroglucin- H_2SO_4), and large starch-grains (to 90 μ) with conspicuous stratification and eccentric hilum.

The Corm: cf. *Crocus* as a more extreme case; the entire plant dried off and reduced to a solid short main axis, with dense starch-storage; enclosed in dead scale-leaves, with lateral buds (1 or more); these break out as flowering leafy shoots in spring: cf. Yellow *Crocus* with white scale-leaves, green foliage-leaves, and 1-3 flowers in each such shoot. Plants dug up in March show new corm forming at the base of each new shoot. Cf. *Montbretia*, similar enlargements of successive seasons remain attached in linear series.

The Bulb (*Lilium*, *Narcissus*, *Hyacinthus*), a limiting case in which the entire plant is reduced to one perennating bud-construction: cf. *Narcissus*; reduced axis at base of bulb giving off adventitious roots; bulk of structure as a mass of leaves, functional in successive seasons as (1) dead scales remaining as protective wrapping; (2) storage-leaves, with starch and mucilage; (3) young leaves of next season, pale green, with no storage; (4) in section of apex only, rudiments of a few primordia of another season. (Differentiate by Iodine sol.)

In fine bulbs note central flower (*Narcissus*), or inflorescence with many buds (*Hyacinthus*). In *Narcissus* the flower is lateral, and the apex, at its base, follows on: in *Lilium* and *Hyacinthus* the flower spike is terminal, and a lower axillary bud takes on the new growth. The adaptation for summer rest in sandy soil is, in this country, continued over the cold winter, and such plants vegetate in spring only, on a short season (April-June), fruiting and seeding before midsummer; though exceptional species of *Narcissus* and *Crocus* may send up flower-shoots in Autumn months (cf. Saffron *Crocus*).

Cf. also *Onion* bulb, with reserves as glucose and mucilage, no flower. Tulip (bulb), *Anemone* (Rhizome), *Polygonatum* (Rhizome) all storing starch.

Perennation structures of root-origin as **Tuberous Roots**: cf. *Ficaria*, swollen segments, $\frac{1}{2}$ in. long, storing starch, as extension of Buttercup root: *Dahlia*, large 'tuber'-growths, 6 in., store inulin. *Orchis* sp. swollen roots; but greenhouse Orchids commonly perennate as 'Pseudo-bulbs', of swollen stem-internodes with remains of foliage-leaves or scales.

The limiting case of perennation is that in which all somatic structures die and vanish at the approach of winter, leaving the race only in the form of *seeds*, as the **Annual** plant; such perennation may be made effective in these latitudes as the result of frost (*Reseda*, *Phaseolus*); or may be part of the specialized organization of the plant, as a consequence of exhaustion in seed-production (*Helianthus*, *Zea*).

Special interest attaches to the case of the **Biennial** herbaceous plant which takes a second season to attain reproductive maturity, storing reserves in the first season, in foliage-leaves (Cabbage), bulb-scales (Onion), root (Beet, Carrot, Parsnip), or hypocotyl (Turnip), to be exploited as food-crops for animal organism.

Concluding Note. The preceding pages are arranged to cover a course of 12 lectures with associated practical work, as an **Introduction to the Somatic Organization of higher Herbaceous Land-plants**; the general anatomical and microscopical observations being strung together by elementary ideas on physiology sufficient to give cohesion to the story.

The notes have been written as schedules to accompany, and not to replace lectures; it being assumed that the lecturer can add explanatory emendations and enlargements on special points within the time as required. Their defects and omissions are sufficiently obvious to the botanical teacher; but so long as botanical courses are designed largely by non-botanists, on the law of the minimum, it is interesting to see how much can be done within such limitations; and though much ground may be covered in theoretical lectures, the time (24 hours) allotted for obtaining a practical acquaintance with the material is quite inadequate.

One of the results of a mediaeval **University System**, originally based on conditions of agriculture, as a phase of Plant-life, in the North Temperate Region, is that the introduction to such elementary knowledge of vegetation, as the response of autotrophic life to the sunshine and temperature of the Northern Summer, has to be taught, in this part of the world, during the darker winter months, when all active vegetation is perennating; and so the University term begins with the 'Fall of the Leaf'. Only in the Long Vacation can plant-life be studied at its optimum; hence outdoor observation, and experimental work under normal conditions, are necessarily curtailed; while laboratory investigation of the dead plant, or its pickled parts, takes the place of direct contact with living organism of the type of *Helianthus*, *Zea*, and *Cucurbita*, then non-existent. So long as the present educational system prevails this sort of botanical work appears as the unavoidable method of introducing the subject; Botany being naturally the only science affected in this manner, and it being so far nobody's business to change the system.

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