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Morphological and physiological correlations in the solanaceae

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Morphological and Physiological Correlations in the Solanaceae

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MORPHOLOGICAL AND PHYSIOLOGICAL CORRELATIONS IN THE SOLANACEAE

David Potter

Thesis Submitted for the Degree

of

Master of Science

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INTRODUCTION

Up to 1911 it had been more or less tacitly assumed that the herbaceous stem was more primitive than the woody type. This assumption rested on the fact, which no one denies, that in stelar ontogeny there is a "fusion of a ring of separate fibro-vascular bundles by the extension of the fascicular cambium across the intervening tissue, and by the formation of xylem by this interfascicular cambium."⁹ It will be evident that the inference as to the superior antiquity of the woody type rested upon the application of the biogenetic law to the foregoing facts. In 1911, however, Eames⁹ concluded that "there is clear evidence in the Rosaceae for the origin of herbaceous stems from woody, as a consequence of the formation of large storage rays in relation to the incoming foliar traces." This view of the relationship between herbaceous and woody stems has been upheld by recent investigators and in 1921 we find Jeffrey and Torrey¹⁵ reaching the conclusion that "the herbaceous type is the extreme expression of efficiency and that the correlated reduction

in, or the complete loss of, secondary growth is physiologically advantageous to the plant."

This theory, if correct, should be of considerable agricultural significance since, as has been pointed out by the geologists, the evolution of the Mammalia has been coincident with the evolution of the angiosperms.^{2'} In their larger leaves, reduction in inedible tissue and greater emphasis on fruit and seed formation the herbs stand as the principal plants in the mammalian dietary. Increased knowledge of the herbaceous stem and the factors at work in turning woody plants into herbs may well be of assistance to future geneticists who might wish to produce superior vegetable strains through the elimination of woody tissue and increase in storage parenchyma.

This theory, i. e., that the herbaceous stem is physiologically superior to the woody stem, which was arrived at inductively from anatomical studies, has not as far as known been experimentally tested. Since we find the herbaceous stem playing such an important rôle in our life, it seemed desirable to undertake a detailed study of the applicability of the aforesaid theory. It is the writer's purpose to point out through physiological as well as morphological studies that the herb exhibits (1) a superior physiological efficiency of the histological elements,

(2) a progressive increase in parenchyma which leads to greater storage capacity, and (3) an increase in chlorenchymatous tissue which lends to the plant a superior photosynthetic efficiency.

As a subject for investigation it was deemed advisable to work upon some representative of a family of considerable economic importance, hence the writer has selected the Family Solanaceae which includes both woody and herbaceous types, not too difficult to obtain, and at the same time offers the prominent herbaceous plant Solanum tuberosum L. - the potato. Solanum Pseudo-capsicum L., S. Dulcamara L., S. Melongena L., and S. Lycopersicum L. are the other species which have been chosen for detailed comparison.

History of the Solanaceae

The Solanaceae of Bartling, formerly the Solanaceae of Jussieu and Luridae of Linneus, is a family of the Tubiflorales. This family comprises a vast group of temperate and tropical trees, shrubs and herbs comparatively poorly represented in North America,² there being according to LeMaout et Decaisne¹ only two species attaining high

latitudes, namely, Solanum nigrum L. and Solanum Dulcamara L. Little is known of their fossil history, one representative only having been discovered according to Karl A. Zittel,³⁵ who states "Aus der durch Beeren-und Kapselfruchte charakterisirten Familie der Solanaceen kennen wir nur eine fossile Blüthe aus dem unteren Oligocän von Aix; Solanites Brongniarti Sap. Saporta vergleicht sie mit jenen von Sarracha und Witheringia, ebenso gut lässt sie sich mit einer rädformigen Blüthe von Solanum vergleichen." However, Wettstein³⁶ states "Fossil wurden in den Gypsen von Aix Bl. gefunden, welche als Solanites Saporta beschrieben wurden; doch ist diese Bestimmung nicht vollkommen sicher."

Representatives of the Solanaceae have been known and cultivated for many years far antedating the Christian era. Dunal³⁷ in 1852 recognized 901 species, but today according to Engler-Gilg³⁸ approximately 1700 species are known. Of these Bailey³⁹ says that there are about twenty-five of horticultural importance. It may be of interest to introduce a short account of the more important representatives, more especially those used in the human dietary and those found in the United States Pharmacopoeia (1905). The most important of the latter are:

Atropa Belladonna L., a strong growing perennial, native of Europe. The medicinal property is the alkaloid, atropin, which has a specific action on the muscle fibers and is hence employed to dilate the pupil in diseases of the eyes. It is also called Dwal, and in olden times Dwal water was a favorite with ladies for removing freckles, hence its name Bella donna, meaning Fair Lady.²⁵

Hyoscyamus niger L., the henbane, an annual or biennial. The biennial form is used in place of opium for dilating the pupil of the eye. The poisonous principle is the alkaloid, hyoscyamin.²⁶

Nicotiana Tabacum L., the tobacco, an annual. This was employed by the Caribbeans as a sedative. It was introduced about 1520 into Portugal and Spain by Dr. Hernandez; into Italy by Tournaban and Cardinal de Sainte-Croix; into England by Captain Drake and into France by Andre Thevet. It is a native of

America. Tobacco is sometimes used medicinally; it contains an extremely poisonous alkaloid, nicotine.¹⁸

Solanum Dulcamara L., the bittersweet, is a depurative in cutaneous disorders.¹⁸

Those plants which are used in the human dietary are for the most part included in the genus Solanum, all the species of which contain an emetic and narcotic principle, solanine. This poison is dissipated, however, on treating with an acid or on boiling, thus rendering the plants edible. Among these are:

Solanum nigrum L. and Solanum guinense Lam. are employed like spinach in the tropics under the name of "bredes".²⁸

Solanum Melongena L., the eggplant; Solanum Lycopersicum L., the tomato; Solanum laciniatum L., the Kangaroo Apple of Australia; Solanum quitoense Lam., the Narangitus de Quito (Quito orange); and Solanum tuberosum L., the potato.

In passing it is significant to note that all the above mentioned plants are of the herbaceous type.

Phylogenetic Position of the Solanaceae

Phylogenetically, the Solanaceae stand high among the flowering plants. This is shown by their floral anatomy as well as by their histological elements. From a study of their floral structure it may be shown that the family Solanaceae is closely connected with the family Convolvulaceae, which in its turn shows affinities with the family Apocynaceae. Many of the former recall climbing, suffrutescent apocynaceous forms in habit, general appearance and similar floral formulae, while both manifest plicate aestivation.¹⁸ The advance which the Convolvulaceae has made is in the reduction of ovules to two per carpel and in its stronger tendency toward the herbaceous habit. Thus, the Solanaceae, on the one hand, lie close to the apocynal stock through their relation to the Convolvulaceae whose affinities with the Apocynaceae have already been pointed out. The transition is effected through Nicandra which has a convolvulous-like flower with ovary divided by cross walls into three to five loculi, which matures into a dryish berry. The embryo is sharply curved. On the other hand, the Solanaceae are related to the Scrophulariaceae, the connecting group being the Salpiglossideae. This tribe was included in the Scrophulariaceae by Bentham⁵ and Baillon,³ but Engler¹⁰

considers it as belonging to the Solanaceae. The distinguishing features of the two families just mentioned are weak zygomorphy of the Solanaceae together with the presence of inner phloem, while the Scrophulariaceae exhibit strong zygomorphy, greater oligomery of the androecium and no inner phloem.

Plate I shows a diagrammatic representation of the floral structures of the four families just considered along with their embryos, and in addition, a longitudinal figure of a typical solanaceous flower. To aid in understanding the floral comparisons previously discussed and to make clear why the solanaceous flower is considered to be of an advanced type, it will be well to briefly describe what is generally conceded to be a primitive type of flower. This may be illustrated by the flower of our common marsh marigold, Caltha palustris L., which has an undifferentiated perianth with an indefinite number of sepals, an androecium composed of many free stamens, and a gynoecium made up of an indefinite number of free carpels. All these floral members are borne in spiral phyllotaxy upon a slightly raised torus. In Figures A. B. C. and D. of Plate I a perianth of five sepals and five petals is shown, the corolla being sympetalous. The androecium of A. B. and C. consists of five stamens placed opposite the sepals. This is believed to

indicate the loss of an inner row of stamens which in the more primitive archichlamydeae would stand opposite the petals. The androecium of D. shows further reduction by the additional loss of one of the stamens of this outer row. All four of these flowers possess a bicarpellary gynoecium whose ovary is bilocular and whose placentation is axillary. Thus, from a standpoint of floral anatomy the solanaceous flower when compared with the ranunculaceous flower shows a decided advance. Figures a, b, c and d show the type of embryo found in the seeds of the four families. Figure E. represents a typical solanaceous flower cut longitudinally with perianth differentiated into calyx and corolla. The latter is sympetalous with an oligomeric epipetalous androecium and a bicarpellary gynoecium. If their floral anatomy is any criterion, it is clear from a study of these figures that the four families under consideration are closely linked together and that the solanaceous flower is of an extremely advanced type. A further comparison of the floral organs of these families is given in the following table.

Table 1.

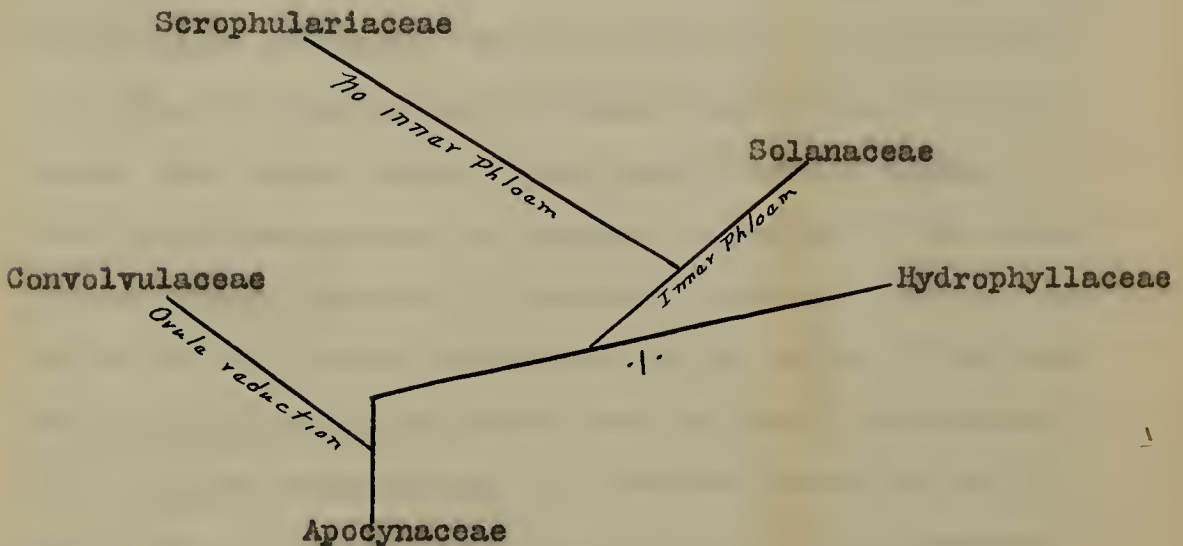
Comparison of the floral organs as found in the families
Apocynaceae, Convolvulaceae, Solanaceae and Scrophulariaceae.

Habit	Trees, shrubs, herbs.	Trees, shrubs, herbs.	Trees, shrubs, herbs.	Shrubs, herbs.
Leaves	Opposite or whorled, rarely alternate; exstipitate; simple.	Alternate, exstipitate.	Alternate, exstipitate.	Alternate, opposite, or whorled; exstipitate.
Flowers	Perfect, regular, terminal or axillary, corymboid cymose, rarely solitary.	Perfect; peduncles axillary or terminal; bracts sometimes enveloping flower, usually bibracteolate.	Perfect, often extra-axillary and with ebracteate pedicels.	Perfect, more or less regular, inflorescence variable.
Calyx	Free, five-fid or partite, rarely four-fid.	Five sepals; persistent.	Monosepalous with 5 (rarely 4-6) segments; persistent.	Four to five free or cohering sepals; persistent.
Corolla	Hypogynous; monopetalous, infundibuliform or hypocrateriform. throat naked or furnished with scales. limb 4-5 fid or partite. aestivation valvate or contorted.	Hypogynous; monopetalous, campanulate or infundibuliform; limb 5-segmented; aestivation usually contorted.	Hypogynous; monopetalous, campanulate, infundibuliform or hypocrateriform; limb 5 (rarely 4-6) segmented; aestivation induplicate or contorted.	Hypogynous; monopetalous, campanulate, rotate or bilabiate; upper lip bilobed, lower lip trilobed; tube sometimes gibbous or spurred at base; aesti-
Stamens	Five, inserted on corolla tube or throat, alternate with its segments; anthers introrse, 2-celled, ovoid, usually acuminate or mucronate; dehiscence longitudinal.	Five, inserted at the base of corolla tube, alternate with its segments; anthers introrse, 2-celled; dehiscence longitudinal.	Five, inserted on corolla, alternate with its segments; anthers introrse , sometimes connivent or even coherent at the top. 2-celled, dehiscence longitudinal or by an apical pore.	Inserted on the corolla tube, normally as many as and alternate with its lobes, often fewer, the posterior being absent or rudimentary the other four didynamous, anthers 2-celled.
Ovary	Carpels two, sometimes distinct, sometimes cohering into a 2-1 celled ovary, sometimes 3-4; style single, stigma generally bifid.	Sometimes girt by a disk, with 2-3-4 1-2 ovuled cells, or 1-celled and 1-ovuled by atrophy of septum; style terminal, simple or 2-partite.	Ovary two-celled, carpels two, placentas thick.	Carpels two, cohering into a 2 (rarely 1) -celled ovary; style terminal, rarely bifid at top; stigma often bilobed.
Ovules	Many, anatropous or semi-anatropous.	Many, anatropous.	Many, campylo-tropous.	Many, anatropous or semi-anatropous.
Embryo	Straight; albumen cartilaginous or fleshy, sometimes scanty or none.	More or less curved; albuminous.	Curved; much albumen.	Straight or slightly curved; albumen fleshy or cartilaginous.
Fruit	Various	Capsule or berry.	Capsule, pyxidium, pulpy or dry berry.	Capsule or berry.
Seed	Usually compressed, often comose.	Erect, testa sometimes very villous.	Compressed	Horizontal, ascending or pendulous.

This table compiled from data obtained from:

La Moout et Decaisne - - General System of Botany
Engler-Prantl - - - - - Natürliche Pflanzenfamilien
Gray - - - - - New Manual of Botany. 7th Ed.

As stated on page 7, the Convolvulaceae show an advance over the Apocynaceae in a reduction in the number of ovules. Before this reduction had gone very far a line of zygomorphy emerged which was to be the main trunk of the Tubiflorales. Far down on this line appeared a side branch with herbaceous habit, with an aggregation of flowers into a scopioid inflorescence and with unilocular ovary. This line terminated in the Hydrophyllaceae. A short distance farther on appeared a second branch which gave rise to the Solanaceae.³² These relationships may be diagrammatically represented as follows:



In the foregoing brief discussion of the floral details of the Solanaceae and allied Tubiflorales it has been pointed out that in sympetaly, staminal epipetaly, and androecial and gynoecial reduction the order affirms its advanced phylogenetic position: so much the older inductions based on floral morphology declare. But we need not rest our conclusions wholly on comparative floral anatomy for within the last two decades another line of research has been vigorously pursued which has its quota to add to phylogenetic conclusions.

In Soler²⁶eders' monumental work, "Anatomie der Dicotyledonen," the histological details of angiosperm anatomy are listed with painful accuracy, but there is practically no attempt to show the phylogenetic sequence of histological elements. This is, however, the very basis of Jeffrey's¹³ "Anatomy of the Woody Plants" and from this source and several papers which have recently appeared from his laboratories, the general evolution of the woody (histological) elements is becoming evident. The work is so new and so little understood that a resume of the main evolutionary principles which reached their consummation in the higher dicotyledons and monocotyledons may not be amiss. The ultimate genesis of all the xlyary elements of

the higher plants (vessels, wood parenchyma, rays, etc.) is to be sought in the tracheid, that element so eminently characteristic of the gymnosperms. Through septation and retention of its primary (ontogenetic) cellulose walls wood parenchyma arose and early became diffuse in many of the Cupressineae. The striking anatomical feature, however, which marks the advent of the angiosperms is the introduction of the vessel. There can be little doubt that its origin was in the vertical fusion of rows of tracheids. Phylogeny and ontogeny are at one in support of this thesis. Through the lateral fusion of rows of bordered pits on the oblique end walls of the antecedent tracheids arose the scalariform vessel perforation best seen today in those angiosperm woods, which, according to the Englerian system, stand low in the phylogenetic scheme - such for example as the Betulaceae and Fagaceae. Through a subsequent breaking down of the bars between the slits of the scalariform perforation the so-called porous perforation comes into being. It may be pointed out in passing that in the Gnetales and in certain families of the angiosperms the porous perforations may arise without the antecedent state of scalariform perforations through a direct and irregular fusion of the bordered pits. This will be better understood by referring to Plate II in which figures a, b, c, and d illustrate the genesis of the Gnetum type of vessel.

Figures e, f, g, h, i and j illustrate the transformation of scalariform perforations into a single large porous perforation. The remaining figures of Plate II are copies of actual photomicrographs of the vessel conditions as found in Gnetum, Alnus, Pelargonium and Potentilla. Figures k and l show the different types of vessels found in Gnetum sp., while m, n, o and p illustrate the transformation of the scalariform type of perforation to the simple porous type. The first two are found in Alnus japonica Sieb. & Zucc., while the last two are exhibited in Potentilla monspeliensis L. Figures r and s illustrate the type of vessel opening found in Pelargonium, the former being the Gnetum type, while the latter is of the porous type.

The evolution of the wood ray, too, has been clearly worked out. Originally simple, there have arisen three main types of wood ray. The first or aggregate ray is a phenomenon associated with the foliar appendage and consists of the intimate association of many uniseriate rays with the intervening tracheids reduced to a few radial files only. The conversion of the aggregate to the compound ray is accomplished by the transformation of the included tracheids into vertical parenchyma. Another and far commoner modification of its constituent parts is into the fan-shaped diffuse ray. In the diffusion each of the moieties of the aggregate become slightly

increased in the tangential diameter and at the same time new rays are intercalated. The four types of wood rays referred to above are diagrammatically shown in Plate III. Figure A. represents the simple ray as found in Picea; B. shows the aggregate ray as exhibited in the stem of Alnus; C., the compound ray found in Quercus, while D. represents the diffuse ray of Solanum.

As a corrective of the mechanical weakness of the wood incidental to the introduction of large vessels the addition of mechanical fibrous elements (wood fibers) to the xylem became necessary. All transitions from tracheids through fiber tracheids to true fibers are known in various woods of primitive type. One of the most interesting of these modifications is that which instituted the so-called substitute fiber (Ersatzfäsern) so very characteristic of herbaceous plants. Without sacrificing living tissue to mechanical uses, the substitute fiber retains its protoplasm and at the same time thickens its wall to subserve the mechanical function.

It remains for us now to try to point out that the progressive phylogenetic histological changes are all concomitants of a progressively more efficient vascular system. There can be little question that the introduction of wood

parenchyma into the tracheidal complex of some of the early Mesozoic conifers was a step forward in physiological efficiency, leading as it did to an increased storage capacity in plants just becoming subjected to the progressive refrigeration of the climate which was to culminate in the Glacial Period. That the vessel lends greater conductive efficiency to the angiosperms is attested by the following quotation from Jost: "

"If we now consider that the water lost through the transpiration of the twigs passes through the vessels in the same manner as through the glass tubes of Askenasy's apparatus, then it becomes evident that the water vessel is better adapted for water conduction than the tracheid. In the first place, they are wider tubes than the tracheids, and a known law in physics states that the volumes of water which pass through two tubes at the same pressure are proportional to the 4th power of the radius. In the second place, the vessels are seldom interrupted by cross-walls; each cross-wall, however, offers resistance to the passage of water." It has also been stated that a birch twig is twenty times as efficient in water conduction as a pine twig of the same diameter.

The evolution of the wood ray is conducive to the same physiological benefits which we have already seen were associated with the addition of wood parenchyma. It is

highly significant that the inception of the aggregate and compound ray was at the node - that region where the entering foliar traces could best discharge their load of synthates. Here was started the chain of events which led eventually to the herbaceous angiosperms whose physiological superiority lends to them the ability to slowly dominate the earth's vegetation and to conquer those more austere regions where their woody relatives of close affinity are unable to grow. It is significant that in the family Solanaceae, with which we are more intimately concerned, the only species which run into high latitudes are Solanum nigrum L. a true herb, and Solanum Dulcamara L. - a half woody vine. It has been often pointed out that the vine and herb are on the same anatomical level.

Little need be said concerning the supreme efficiency which is possessed by the substitute fiber. An element which retains its protoplasm and at the same time lends mechanical rigidity to the slender stem of the herb must necessarily represent the acme of physiological efficiency.

The Histology of the Solanaceae

With this brief introduction to the foundational principles which must guide us in any attempt to apply histological studies to the investigation of the affinities

of vascular plants, we may now turn to a consideration of the anatomy of the Solanaceae.

Plate IV shows a cross (C), radial (A) and tangential (B) section of the xylem of Solanum Pseudo-capsicum L., a woody representative of the Solanaceae and thus a primitive member of the family, together with the individual xylary elements a, b, c and d of the same plant. It will be noted that but three types of xylary elements are present - the substitute fiber (a), the vessel (b) and the wood ray (c). The plant has suffered a complete loss of both wood parenchyma and tracheidal tissue. In place of the tracheid is found the substitute fiber, a phylogenetic derivative of the tracheid. Thus, the plant has introduced a new element which serves a dual purpose, a point which can only mean an advanced evolutionary position as well as high physiological efficiency. In addition, these substitute fibers are much longer than were the antecedent tracheids. The vessel (b) is clearly shown to be a series of cells joined end to end. The horizontal walls in this case have completely broken down to form a porous perforation. Phylogenetically, the vessel arose from the tracheid which increased in size and utilized the tertiary spiral as a means of strengthening its walls. This permits of more conduction area which is an advance over the more

primitive condition, i. e., the condition of many minute conducting (tracheidal) tubes. The walls of the vessel are heavily pitted with the typical bordered pit, thus allowing for the quick transference of water to those surrounding tissues requiring it. The wood ray is of the diffuse type as shown in Fig. D. of Plate III. Its individual cells are elongated vertically and the same condition holds for the whole ray itself. Many simple pits are borne on the walls of the ray cells which indicates the possibility of quick movement of water and synthates wherever needed for metabolic processes as well as rapid transfer to the storage tissues such as the fibers and pith. By referring to Plate V, Fig. A., it will be noted that the major part of the stem is composed of the xylem and that the pith area is reduced to a minimum. The plant, however, has introduced the substitute fiber to compensate for the loss of storage tissue.

In other representatives of the family the xylem has given way to parenchymatous tissue, which, without question increases the storage capacity and hence lends to the plant an increased physiological efficiency.

All these facts; the introduction of the substitute fiber, the presence of many vessels, the increase in storage capacity, supported by the proof derived from

floral anatomy, justify the statement that the Solanaceae stand high among the flowering plants.

A Comparative Morphological and Physiological Study
of Woody and Herbaceous Species of Solanum.

It has been pointed out that the Solanaceae is an advanced family both from a morphological and physiological standpoint. It is now desirable to determine the histological advances which have been made within the family itself. As was stated earlier in this paper, the general consensus of opinion upholds the belief that the woody type of stem is the progenitor of the herbaceous type. "The factors which have been at work to mold woody plants into herba are essentially the following:

(a) Increase in storage parenchyma leading to a progressive reduction of tracheidal tissue.

(b) Gradual restriction of secondary growth till finally cambial activity is completely abolished and only primary tissues remain."^{3/}

The steps in this evolution have been ably pointed out by Jeffrey and Torrey.^{4/} Their conclusions are based upon the following facts which have been brought to light through their studies on stelar anatomy:

(a) Foliar rays are developed in woody herbs as a result of the clustering of ordinary rays of the wood in

relation to the incoming leaf traces. These aggregate rays are often characterized by the elimination of vessels in the bands of longitudinal woody elements separating the constituent members of the foliar aggregation of rays from one another. This condition appears in Figure A. of Plate VI - a stereogram of a section of stem of Alnus japonica Sieb. & Zacc., in which is shown the aggregate ray both from a transverse and tangential aspect.

(b) This is followed by the transformation of the strands of fibers separating the members of the aggregate ray and their ultimate assimilation to the ordinary radial parenchyma. This condition is called the compound ray and is illustrated in Figure B. of Plate VI. This figure is a stereogram of the condition found in the stem of Leea sp. Here is a representation of the compound ray and it is readily seen that the stem is becoming cut up by broad bands of parenchymatous tissue. As the herbaceous condition becomes more and more established, the foliar rays become not only more homogeneous, due to the loss of identity of their originally woody elements, but also more elongated in the vertical direction.

(c) The stem becomes segmented into strands more or less regularly alternating as to size in which certain

members radially extended and woody in structure, while the alternating segments consist of slender bundles subtended outside by massive storage tissue. The storage tissues also occur on the flanks of the slender bundles just referred to which are the foliar traces in their course in the stem. An examination of the stereogram C on Plate VI will reveal the further segmentation of the stem by bands of parenchyma which both subtend and flank the outgoing leaf traces. This condition is found in the stem of Helianthus sp. and in hundreds of other semi-herbaceous plants.

(d) The last phase is the thinning down of the axis. This automatically results in the elimination of the parenchyma of the foliar ray which radially subtends the foliar trace. As a consequence of this condition only the flanking parenchyma of the rays persists. Figure D. of Plate VI is a diagrammatic representation of the condition of the stem of Ranunculus acris L. The stem has now become a mass of parenchymatous tissue in which are embedded many fibro-vascular bundles. Thus, we have for the end product the extreme herb, the latest manifestation of a dynamic plant.

Of the species selected for study, i. e., Solanum Pseudo-capsicum L., Solanum Dulcamara L., Solanum Melongena L., Solanum Lycopersicum L. and Solanum tuberosum L., the first should, theoretically, stand in a more primitive position

phylogenetically than the other species mentioned. Its stem structure should show more archaic features and its physiological efficiency should be inferior. Solanum Dulcamara L. is a half woody vine and with Solanum Melongena L., a half woody herb, should stand as intermediates between the woody type of stem and the herbaceous forms Solanum Lycopersicum L. and Solanum tuberosum L. Solanum Lycopersicum L. is an herb which has retained a thin cylinder of wood and will undoubtedly stand very close to Solanum tuberosum L. from a physiological standpoint. The latter, a true herb, should stand highest among the species selected for study both in its phylogenetic position and in its physiological supremacy. These five species will now be treated separately in order to ascertain their true relationships.

Solanum Pseudo-capsicum L.

This is a woody plant with simple leaves and in northern latitudes attains a height of about two feet. A nodal section presents the following features:

(a) A very small amount of pith where cells are uni-nucleate and are filled with stored starch. The walls are covered with simple pits.

(b) Passing outward the next group of tissue observed is the inner phloem. This constitutes several masses closely approximated forming an almost closed ring around the pith. Each mass is accompanied centripetally by sclerenchymatous

fibers. The phloem is composed of sieve cells with their companion cells and phloem parenchyma. The individual elements of the phloem are very poorly defined in this species. Their lumina seem almost obliterated through excessive wall thickening suggesting, perhaps, a diminution in function. This condition is not characteristic of the more herbaceous types of stem as found in Solanum Lycopersicum L. and Solanum tuberosum L. where the structure of the inner phloem is identical with that of the outer phloem. The question of inner phloem is of special interest and it is well to consider briefly the theories which have been put forth to explain its origin. According to Worsdell,⁴ the inner phloem strands, though vestiges of a medullary fibro-vascular system are, nevertheless, as well developed and as functional as the outer phloem. He also claims that the internal phloem arises at a later period in the course of ontogeny than does the outer phloem and this is in favor of its being a vestigial tissue. This view is opposed by Artschwager,⁵ who states "These innermost phloem groups clearly belong to the stele proper and do not represent the vestigial remains of a second set of vascular bundles." In either case, the inner phloem is highly significant from a physiological standpoint, since it adds more conductive tissue for the removal of synthates from the leaf to meristematic and storage tissues. In the younger plants

there is a fusion of the inner and outer phloem groups as they traverse the stem. In the older stems, containing a cylinder of xylem, this fusion occurs through the leaf and branch gaps.

(c) Outside the phloem is encountered the xylem which comprises the greater portion of the stem. Three elements make up the xylem: the vessel, the substitute fiber and the wood ray. The vessel is composed of cells joined end to end. The horizontal walls, however, have broken down and thus have given rise to the porous perforation in the manner previously described. The vertical wall of the vessel is heavily pitted with the typical multiseriate, alternating bordered pit and overlain with the characteristic tertiary spiral. These vessels are uniformly scattered through the wood except where a foliar segment is encountered, in which case the vessels have entirely disappeared. The substitute fiber is an elongated cell much greater in its vertical dimension than is the tracheid, the element so characteristic of the majority of the lower angiosperms. These fibers are nucleated and starch is found stored in their lumina. Their walls bear but few simple pits. The greater portion of the xylem is given over to the substitute fiber. The ray condition is diffuse. The individual ray cell is much elongated in the

vertical dimension. Its wall is profusely covered with simple pits. Of particular interest is the condition of the foliar segment. Subtending the leaf trace is found an aggregation of rays, the constituent members of which are separated by one to four files of substitute fibers. In other parts of the stem the individual rays are separated from each other in many instances by as many as twelve to fourteen files. Thus, we find a diminution of fibers outside the leaf trace, their place being taken by the more efficient storage tissue of the wood ray. All evidence of vessels has been lost in the foliar segment. It will be noted, too, that the inner phloem moves outward with the trace and enters the petiole where the bundle eventually becomes collateral. A distinct cambium is present composed of two or three files of meristematic cells. The external phloem is cut up into bundles due to the flaring of the outgoing wood rays. Its constituent members are the same as those of the inner phloem. Each mass is subtended by sclerenchymatous protective fibers.

(d) A study of the root of Solanum Pseudo-capsicum L. does not reveal any histological features which would aid in the solution of the present problem. This applies to the root structure of all the species studied and hence no

further discussion of this organ will be introduced.

(e) The cortex may be divided into an inner part composed of storage parenchyma, while the outer portion has developed a corky layer. It is evident, as has already been noted by many writers, that the cork in solanaceous plants is of epidermal origin. The cork is but three or four cells in thickness. On young stems its place is taken by an epidermis one cell thick.

Solanum Dulcamara L.

This species, a half woody vine, presents practically the same histological features as found in Solanum Melongena L. Their differences are so slight that a detailed account of both would be duplication and for this reason Solanum Dulcamara L. will not be considered further.

Solanum Melongena L.

This species offers the transition between the woody type of stem exhibited in Solanum Pseudo-capsicum L. and the true herbaceous type as shown in Solanum tuberosum L. Solanum Melongena L. is a half woody herb. The stem exhibits much the same histological features as found in the first species discussed, the greatest difference being in the amount of areas utilized by its several con-

stituent tissues. An examination of a cross section shows approximately the same area devoted to pith in both. The woody cylinder, however, has been cut down and a reduction has taken place in the number of vessels per unit area. The area of the individual vessel is the same as that of the vessels found in Solanum Pseudo-capsicum L. This reduction may be correlated with the fact that the eggplant is undoubtedly xerophytic. An examination of the plant reveals the fact that the leaves are densely clothed with pubescence which prevents the rapid evaporation of water. Its stomata are sunken below the epidermis of the leaf. For these reasons the plant would not require as much water as Solanum Pseudo-capsicum L. and hence would require fewer vessels for its conduction. The cortical area has increased and there is a band of subepidermal collenchyma inside which is found chlorenchymatous tissue. The addition of supporting tissue in the form of collenchyma is to be expected, for the exiguity of the woody cylinder reduces the mechanical strength of the stem. To compensate for this, the plant has added cortical collenchymatous tissue. From our present standpoint, it is significant to note that there has been an increase in storage tissue at the expense of xylem, a point which will be considered later.

Solanum Lycopersicum L.

This species is an herb which has retained a small woody cylinder. There has been a much greater reduction in xylary tissue than was the case in the two preceding species. The vessels have decreased in number per unit area, but there has been a compensatory increase in the size of the individual vessel. The vessels have now become aggregated into six areas from which arise the leaf traces. The elements making up the stem are in general the same histologically as those found in the three species previously described. On examination of the pith, however, the cells are found to be binucleate.. This condition was not found in the more woody types. In the stem under discussion a large amount of the area is given over to pith and in a rapidly growing stem, it is necessary that the pith cells divide quickly in order to keep in step with the other parts. According to Pranker^d, binuclearity is characteristic of regions of active growth. Beer and Arber^z have reached the conclusion that in case of cortical and medullary tissue, in which each cell contains more than one nucleus, this is a normal intermediate stage in the development from meristematic to mature tissue. The condition of bi- and multinucleated cells has been found by them to occur in the stem organs of fifty species of

Dicotyledons belonging to twenty-seven natural families and of seventeen species of Monocotyledons belonging to four families. These examples are found in plants which range from trees to small herbs. In older tomato plants the pith dies and the stem becomes hollow, but this does not take place until a great part of the photosynthetic activity has ceased. The epidermis is one cell in thickness.

Solanum tuberosum L.

This species is a true herb. An examination of its stem exhibits the true herbaceous condition, i. e., the breaking up of the stele into separate fibro-vascular strands. The individual bundles are connected by an interfascicular cambium, which, later in the ontogeny of the plant gives rise to secondary wood. Thus, in the older stems is found a small ring of xylem. The number of vessels per unit area is somewhat greater than the number found in the stem of the last species considered, but the area of the individual vessel has decreased. The histological elements are much the same as those of the other species discussed. It is interesting to note in passing that Artschwager, in his publication on the anatomy of the potato plant, states "Typical tracheids and wood parenchyma cells are found scattered among the larger vessels." In all the solanaceous plants studied, the writer has been unable to find any trace of

tracheids other than those of the primary wood, which is, of course, strictly endarch. Wood parenchyma is also conspicuous by its absence. These two elements have been entirely replaced by the more efficient substitute fiber which serves the dual purpose of storage and support. There is a small band of subepidermal collenchyma, the rest of the cortex being chlorenchymatous. The epidermis is one cell in thickness. The anatomy of the tuber has been treated by Reed²³ and others and hence will not be discussed in this paper.

From the foregoing discussion of the stem conditions as found in Solanum Pseudo-capsicum L., Solanum Melongena L., Solanum Lycopersicum L. and Solanum tuberosum L., it is evident that a considerable difference occurs between the four species. In the first place, there has been a progressive reduction in the amount of xylary tissue accompanied by a reduction in the number of vessels per unit area, and to compensate for this there has been an increase in the average area of the individual vessel. Correlated with this reduction has been the aggregation of rays in the foliar segment, the loss of vessels in that region and a decrease in the radial files of substitute fibers. This was exhibited in the first two species discussed. The next evolutionary advance that was shown in xylary transformation was the aggregation of the vessels into six areas, the areas

from which the leaf traces would eventually depart. Here the radial depth of the xylem was greater than in the intervening spaces by about one-half. The last step in this particular advance was the final breaking up of the woody cylinder into individual bundles. In the second place, in correlation with the degeneration of the xylem, an ever increasing amount of storage tissue was built up so that we pass from the almost solid stele of Solanum Pseudo-capsicum L. to the true herbaceous condition of Solanum tuberosum L. in which the major part of the stem is given over to parenchymatous storage tissue.

This gradual parenchymatization of tracheidal tissue is brought out in Plate V. The four figures represented are diagrammatic renderings of cross sections of the stems of the four species of plants which we have been considering. Figure A. is based on the stem of Solanum Pseudo-capsicum L., B. on Solanum Melongena L., C. on Solanum Lycopersicum L. and D. on Solanum tuberosum L. The black areas in each figure represent the amount of storage tissue found in each of the four stems exclusive of the substitute fibers and the wood rays. These two elements, however, must be included in the total storage area, since it has been found that they store starch. These sections are all drawn to the same scale and after careful computation it has been found that the total storage area (including substitute fibers and rays) available in Solanum Pseudo-capsicum L. is 79 per cent of the total area; in

Solanum Melongena L. is 81 per cent; in Solanum Lycopersicum L. is 84 per cent and in Solanum tuberosum L. is 87 per cent. The writer realizes that these figures are but approximate and that an exact percentage is well nigh impossible. However, the same errors enter into the computation of the areas of each stem and, therefore, though the percentages may vary two or three points, the differences between the percentages will remain constant. Thus, for all practical purposes, it may be stated that the difference between the amount of storage tissue available in the woody stem of Solanum Pseudo-capsicum L. and that available in the herbaceous stem of Solanum tuberosum L. is approximately 8 per cent. The writer is aware of the fact that in the older stems of Solanum Lycopersicum L. and Solanum tuberosum L., there is a breaking down of the medulla which results in hollow stems, but since this takes place late in the season after the main photosynthetic activity has ceased, we need not consider this point in our present discussion. As was stated above, the interfascicular cambium in the stem of Solanum tuberosum L. gives rise in later stages of its ontogeny to secondary xylem, so in the older stems we do find a partial woody stele. This condition is not found, however, in the younger plants nor at the nodes. For this reason, the writer has shown the woody type of stem in Figure D. Though there is a slight error in the stated

percentages, the fact that the whole stem is not as woody as here represented more than compensates for this error. The areas of the constituent tissues of the cross sections of these four solanaceous representatives together with the percentages of total storage area is shown in Table 2.

Thus, it may be inferred from the above discussion that the woody representative does show more archaic features and from a standpoint of storage capacity, it is physiologically inferior to the herbaceous type of stem. In this particular case, the tuber may also be added to the available storage area which leaves little doubt as to the advance which Solanum tuberosum L. has made over its more primitive relative Solanum Pseudo-capsicum L.

Let us now turn to a consideration of the leaf - that organ which is primarily connected with photosynthetic activity. A comparison of the leaves of the four species of plants with which we are concerned, both from a histological and physiological standpoint should substantiate the inference drawn from the preceding

Table 2.

Comparison of Areas of the Constituent Tissues of the Stems of Four Solanaceous Plants.

Areas in sq. mm.

Plant	Area of Stem	Area of Epidermis	Area of Cortex	Area of External Phloem	Area of Cambium	Area of Xylem	Area of Internal Phloem	Area of Pith	No. of Vessels in Xylem	Average Area Per Vessel	Total Area of Vessels	Area of Substitute Fibers and Wood Rays	Total Storage Area	Percentage of Storage Area
Solanum Pseudo-capsicum L.	7854	311.02	1734.17	653.81	222	4317	61.6	554.4	880	.46	404.8	3912.2	6200.77	79
Solanum Melongena L.	7854	466	3315	440	210	2716	70.7	626.3	580	.46	266.8	2449.2	6390.5	81
Solanum Lycopersicum L.	7854	614	1430	306	92	872	46.58	4493.42	57	2.9	165.3	706.7	6630.12	84
Solanum tuberosum L.	7854	311.02	2762.38	360.8	232.8	1146	8.25	3032.75	72	1.05	75.6	1070.4	6865.53	87

comparative study, i. e., the stem of Solanum tuberosum L. exhibits a physiological superiority over that of Solanum Pseudo-capsicum L.

From a study of Table 3 the following points will be noted:

1. Solanum Pseudo-capsicum L. has the greatest thickness of leaf followed by Solanum tuberosum L., Solanum Lycopersicum L. and Solanum Melongena L. respectively.
2. Solanum Melongena L. has the greatest superficial area of its constituent palisade cells per cubic millimeter and this is followed by Solanum Lycopersicum L., Solanum tuberosum L. and Solanum Pseudo-capsicum L. respectively.
3. Solanum Lycopersicum L. has the greatest number of spongy parenchyma cells per cubic millimeter followed by Solanum Melongena L., Solanum tuberosum L. and Solanum Pseudo-capsicum L. respectively.
4. Solanum tuberosum L. has the greatest superficial area of its constituent spongy parenchyma cells per cubic millimeter followed by Solanum Melongena L., Solanum Lycopersicum L. and Solanum Pseudo-capsicum L. respectively.

5. Solanum Melongena L. has the greatest total surface area of palisade cells and of spongy parenchyma cells per cubic millimeter and is followed by Solanum tuberosum L., Solanum Lycopersicum L. and Solanum Pseudo-capsicum L. respectively.

6. Solanum Pseudo-capsicum L. has the greatest percentage of air space per unit area followed by Solanum Lycopersicum L., Solanum Melongena L. and Solanum tuberosum L. respectively.

7. Solanum Melongena L. has the greatest number of stomata on the upper surface of its leaf per unit area followed by Solanum Lycopersicum L. and Solanum tuberosum L. respectively, while Solanum Pseudo-capsicum L. has none at all. The stomata, however, of Solanum tuberosum L. are much larger in diameter; those of Solanum Melongena L. stand second, while those of Solanum Lycopersicum L. are third. On the lower surface, Solanum Pseudo-capsicum L. has the greatest number per unit area followed by Solanum tuberosum L., Solanum Melongena L. and Solanum Lycopersicum L. respectively, but here again the average diameter of the stomata of Solanum tuberosum L. is much the largest. Those of the other three species are equal in size.

8. The stomata of Solanum Melongena L. are sunken below the epidermis and the leaf is densely clothed with hair. The type of hair is shown in Plate VII.

9. Solanum tuberosum L. has the greatest amount of surface area available for photosynthetic activity, the largest average diameter of the stomata and the greatest number of spongy parenchyma cells per unit area.

From these general observations the following conclusions may be derived:

1. Though Solanum Pseudo-capsicum L. has the greatest thickness of leaf and the greatest amount of air space, these facts are offset by the reduction in the surface area available for photosynthetic activity and by the fewer stomata. These are confined entirely to the lower surface of the leaf and are smaller in size than the general average of those for the other three species.

2. Though Solanum Melongena L. has the greatest amount of surface area available for photosynthetic activity and has the greatest number of stomata per unit area, these facts are offset by a smaller amount of air space than is found in Solanum Pseudo-capsicum L. and Solanum Lycopersicum L. The stomata are small and sunken below the epidermis which inhibits transpiration; the leaves

are densely clothed with hair which further retards water loss. These factors obviously decrease photosynthesis. This decrease in photosynthesis is correlated with the reduction in the number of vessels per unit area found in the stem. This was pointed out in the discussion of stem structure. Thus, Solanum Melongena L. would of necessity fall into a less efficient class from a physiological standpoint.

3. Though Solanum Lycopersicum L. has the greatest superficial area of its constituent spongy parenchyma cells, this fact is offset by the reduction in the surface area of both spongy parenchyma cells and palisade cells available for photosynthesis. Solanum Lycopersicum L. has more stomata per unit area than does Solanum tuberosum L. as well as more available air space. Solanum tuberosum L. overcomes this difficulty by the greatly increased diameters of its stomata, which indicates a more rapid diffusion of gases and its much greater combined surface area available for photosynthesis. Solanum Lycopersicum L. stands higher as to physiological efficiency than Solanum Pseudo-capsicum L. in available surface area and in diameters and distribution of its stomata.

4. Solanum tuberosum L. has the greatest superficial area of chlorenchyma available for photosynthesis and its stomata, though fewer in number than those of Solanum

Melongena L., exceed the former in their long diameter. This means a more rapid diffusion of gases, since Browne and Escombe⁸ have shown that the movement of gases through stomata is proportional to the diameter of the openings. Furthermore, the stomata are not depressed. Also the diameters of the stomata of the potato plant are greater than the diameters of the stomata of the other three species. The available air space is less than that found in the other three species, but there is a compensation in the increased rate of diffusion.

According to Haberlandt¹² "the palisade cells take the first place in respect to chlorophyll content, a circumstance which in itself suffices to characterize these cells as the special photosynthetic elements of the plant." Willstätter,³³ however, has pointed out that chlorophyll content alone is not a sure criterion of the amount of photosynthetic activity.

Theoretically, Solanum tuberosum L., having the greatest amount of superficial area per cubic millimeter available for photosynthesis and having stomata which allow the greatest diffusion of gases, should be more efficient than the other three species under discussion.

From the above conclusions we are justified in placing Solanum tuberosum L. first from a physiological standpoint with Solanum Lycopersicum L. second. It is a

Table 3.

Comparison of the Areas and Volumes of the Constituent Parenchymatous Elements Found in the Leaf of Four Solanaceous Plants Together With the Number and Dimensions of the Stomata per Unit Area.

	<i>Solanum Pseudo-capsicum</i> L.	<i>Solanum Melongena</i> L.	<i>Solanum Lycopersicum</i> L.	<i>Solanum tuberosum</i> L.
Thickness of the leaf in mm.	.2340	.1188	.1440	.1944
Thickness of the upper epidermis in mm.	.0180	.0108	.0180	.0216
Thickness of lower epidermis in mm.	.0180	.0108	.0108	.0144
Depth of palisade cells in mm. one cell deep.	.1260	.0432	.0540	.0756
Depth of spongy parenchyma in mm.	.0720	.0540	.0612	.0828
Average length of palisade cells in mm.	.1260	.0432	.0540	.0756
Average width of palisade cells in mm.	.0180	.0090	.0119	.0180
Average diameter of palisade cells in mm. cell cut parallel to the surface of the leaf.	.0144	.0108	.0180	.0144
Average number of palisade cells per unit area. unit area = .0024 sq. mm.	8.8	18.	9.	10.
Average number of palisade cells per 1 sq. mm. of surface.	3667.4	7504.	3753.	4170.
Average number of sq. mm. of surface of palisade cells in 1 cu. mm.	165.76	254.38	212.04	189.48
Average diameter of spongy parenchyma cells in mm.	.0180	.0194	.0144	.0216
Average volume of spongy parenchyma cells in cu. mm.	.00000305	.00000382	.00000156	.00000517
Average volume of unit area in cu. mm.	.04x.06x.072	.04x.06x.054	.04x.06x.061	.04x.06x.082
Average number of spongy parenchyma cells per unit area. area = .0024 sq. mm.	.0001728	.0001296	.0001464	.0001968
Average volume of spongy parenchyma cells per unit area in cu. mm.	.0000498	.0000565	.0000561	.0001034
Average volume of air space per unit area in cu. mm.	.000124	.0000731	.0000903	.0000934
Number times unit area is contained in 1 cu. mm.	5787.	7792.	6831.	5081.
Average number of spongy parenchyma cells per cu. mm.	92592.	115321.	245916.	101620.
Average volume of spongy parenchyma cells per cu. mm.	.2824	.4405	.3836	.5253
Average volume of air per cu. mm.	.7176	.5595	.6164	.4747
Percentage of air space	71.76	55.95	61.64	47.47
Average area of spongy parenchyma cells in sq. mm.	.001	.0011	.0006	.0014
Average number of sq. mm. of surface of spongy parenchyma cells in 1 cu. mm.	92.592	126.853	107.549	142.268
Average number of stomata per unit area in upper epidermis area = .047 sq. mm.	0.0	22.	21.	9.
Average size of stomata in upper epidermis in mm.	0.0	.0216x.0216	.0144x.0252	.0252x.0396
Average number of stomata per unit area in lower epidermis area = .407 sq. mm.	30.	19.	7.	25.
Average size of stomata in lower epidermis in mm.	.018x.0216	.018x.0216	.018x.0216	.0252x.036
Position of stomata on leaf.	not sunken	sunken	not sunken	not sunken
Average surface area of cells in 2 cu. mm. exposed for photosynthetic activity. 1 cu. mm. of palisade cells plus 1 cu. mm. of spongy parenchyma cells.	258.352	381.233	319.589	331.748

little doubtful which of the other two species should be placed third. In comparing the woody plant Solanum Pseudo-capsicum L. with the herb Solanum tuberosum L. there is no doubt but that the latter is far more efficient from a photosynthetic standpoint. This is shown by the greater number and the greater average diameter of the stomata, their better distribution, and the greater amount of available surface area whereby the plant carries on its food manufacture.

Plate VII presents a comparison of the cross sections of the leaves of these four species together with the types of hairs found on the leaf surfaces.

It will be recalled from the discussion of the stems of these four solanaceous plants that it was definitely shown both from a morphological and physiological standpoint that the stem of the herbaceous plant was superior to that of the woody plant. We have just shown that the comparative study of the leaf from a histological viewpoint bears out the same conclusion.

Experimental Evidence Attesting the Physiological Superiority of Herbaceous Plants

Table 4 presents the results of experiments carried on to determine the amount of starch manufactured by a unit area of the leaf of three species of Solanum. Leaves of

Solanum Melongena L. were not available at the time of these experiments, hence it does not appear in the table.

To obviate the disadvantages of the leaf-half method,²⁴ which is used to determine the amount of starch manufactured, a modification of this method was employed.

The plants were placed in a dark chamber over night. In the morning ten to thirty discs were cut from one side of the midrib of one or more leaves, the discs being immediately dried in the electric oven. The leaves minus the discs were either left on the plant or were removed and placed in distilled water. All were now exposed to the light and after a lapse of approximately five hours they were collected and the same number of discs taken from their opposite untouched halves. These discs were then dried and the dry weights of both were determined.

A number of leaves were left in the dark during the time of the experiment to determine whether or not there was any change in the leaves if not exposed. Discs were taken as explained above but no differences in weight were noted except in one instance. This may be attributed to lack of exact homology in the discs.

The differences in the weights of the unexposed and exposed discs were next averaged and as is shown in

Table 4.

Experimental Data to Determine the Amount of Starch
Manufactured per Unit Area of Leaf.

	No. of discs taken.	Exposed	Time in hours.	Total weight in mg.	Increase or decrease in mg.	Leaves left on plant or taken off.	Light	No. of test.
Solanum tuberosum L.	30			42		on	sunny	A
"	30	#	5	46	+4	on	sunny	A
"	30			40		off	very br.	B
"	30	#	4.5	52	+12	off	very br.	B
"	30			45		on	very br.	C
"	30	#	4.5	44	-1	on	very br.	C
"	10			16		off	dull	D
"	10	#	5	19	+3	off	dull	D
"	10			17		off	dull	E
"	10	#	5	17	0	off	dull	E
"	10			16		off	dull	F
"	10	#	5	22	+6	off	dull	F
"	10			13		on	very br.	G
"	10	#	5.5	18	+5	on	very br.	G
"	10	#	5.5	17	+4	on	very br.	G
"	10			14		on	very br.	H
"	10	#	5.5	18	+4	on	very br.	H
"	10	#	5.5	18	+4	on	very br.	H
"	10			14		off	very br.	I
"	10	#	5.5	17	+3	off	very br.	I
"	10			15		off	very br.	J
"	10	#	5.5	17	+2	off	par.shad.	J
"	10	#	5.5	17	+2	off	par.shad.	J
"	10			12		off	sunny	K
"	10	#	5	14	+2	off	sunny	K
"	10			13		off	sunny	L
"	10	#	5	16	+3	off	sunny	L
"	10			10		off	sunny	M
"	10	#	5	14	+4	off	sunny	M
"	10			13		off	sunny	N
"	10	#	5	13	0	off	sunny	N
"	10			14		off	dull	O
"	10	#	5	17	+3	off	dull	O
"	10			14		off	dull	P
"	10	#	5	17	+3	off	dull	P
"	10			16		off	dull	R
"	10	#	5	17	+1	off	dull	R
Solanum Lycopersicum L.	10			15		off	sunny	A
"	10	#	5	15	0	off	sunny	A
"	10			14		off	very br.	B
"	10	#	5	15	+1	off	very br.	B
"	10			12		off	very br.	G
"	10	#	5.5	15	+3	off	very br.	G
"	10			12		off	very br.	H
"	10	#	5.5	15	+3	off	very br.	H
"	10			13		on	very br.	I
"	10	#	5.5	17	+4	on	very br.	I
"	10			13		off	sunny	K
"	10	#	5	17	+4	off	sunny	K
"	10			13		off	sunny	L
"	10	#	5	15	+2	off	sunny	L
"	10			14		off	dull	O
"	10	#	5	16	+2	off	dull	O
"	10			16		off	dull	P
"	10	#	5	17	+1	off	dull	P
Solanum Pseudo-capsicum L.	30			50		off	sunny	A
"	30	#	5	57	+7	off	sunny	A
"	30			55		off	very br.	B
"	30	#	4.5	60	+5	off	very br.	B
"	10			24		on	dull	D
"	10	#	5	22	-2	on	dull	D
"	10			23		on	very br.	G
"	10	#	5.5	25	+2	on	very br.	G
"	10			25		off	very br.	H
"	10	#	5.5	26	+1	off	very br.	H
"	10			19		off	sunny	K
"	10	#	5	21	+2	off	sunny	K
"	10			19		off	dull	O
"	10	#	5	23	+4	off	dull	O

The following gives the results obtained from leaves
kept in the dark during the time of exposure of
the leaves given in table above.

Solanum tuberosum L.	10			10		off		K
"	10		5	10	0	off		K
"	10			12		off		O
"	10		5	12	0	off		O
"	10			13		off		A
"	10		5	12	-1	off		A
"	10			15		off		D
"	10		5	15	0	off		D
Solanum Lycopersicum L.	10			15		off		K
"	10		5	15	0	off		K
"	10			15		off		O
"	10		5	15	0	off		O
Solanum Pseudo-capsicum L.	10			13		off		K
"	10		5	13	0	off		K
"	10			18		off		O
"	10		5	18	0	off		O

The following gives the average amount of starch
manufactured per ten discs.

Solanum tuberosum L.	2.7 mg.
Solanum Lycopersicum L.	2.2 mg.
Solanum Pseudo-capsicum L.	1.6 mg.

Table 4 Solanum tuberosum L. showed the greatest increase, while Solanum Lycopersicum L. stood second.

Thus, if a unit of area of surface of Solanum tuberosum L. manufactures more starch in a given time than does the same area of Solanum Pseudo-capsicum L., and the former has a greater leaf surface though the number of leaves be less, it stands to reason that the whole plant of Solanum tuberosum L. will be more efficient than the whole plant of Solanum Pseudo-capsicum L.

The Problem of Seed Sterility in the Potato

The main problem of our investigation thus reaches a satisfactory conclusion. There remains, however, a subsidiary question which may be briefly considered, though not with the idea that it can be summarily solved.

It has often been maintained that the prevalent seed sterility of the potato receives its explanation in the fact that this plant is abandoning sexual for asexual methods of reproduction and that reproductive vigor has been transferred from gametes to tubers. Yet this interpretation is open to serious question. It is generally known that gametic sterility obtains widely among the variable races of plants that have been long under cultivation and particularly among such as have been widely hybridized. Let us

consider briefly the facts in regard to the history of Solanum tuberosum L.

History of Solanum tuberosum L.

Solanum tuberosum L. is a native of southern Chile and was cultivated in northern Chile and Peru in the time of the Incas.²⁸ "The earliest mention of the potato, if it be not the sweet potato, is that of Peter Martyr, who, referring to the time of Columbus' voyages, says that the Indians of Darian 'dygge also out of the grounds certayne rootes growing of themselves, which they call betatas, muche lyke unto the navie rootes of Millane, or the great puffes or mushromes of the earth. Howsoever they be dressed, eyther fryed or sodde, they geve place to no suche kynde of meate in pleasent tendernes. The skinne is somewhat tougher than eyther the navies or mushromes, and of earthy colour, but the inner meate therof is very white: These are nourished in gardens They are also eaten rawe and have the taste of rawe chestnuts but are somewhat sweeter.'" According to Bailey,² the potato was probably carried to Spain from Peru in the 16th century. It seems to have been introduced into Europe as early as 1565. Recent investigation gives the credit of introducing it into England to Sir Francis Drake, (1586).

According to Sturtevant,²⁸ it is quite possible that Hawkins carried the potato to North America in 1565. Potatoes are said to have been introduced into New England by a colony of Presbyterian Irish, but cultivation did not become general for many years.

The wild varieties still bear a close resemblance to the cultivated varieties, except for the enlarged vine and abnormal development of the tubers in the latter.

The ancestor of Solanum tuberosum L. is still in question. Much has been done on this point, but the question still remains unsolved. Sutton²⁹ concludes that Solanum etuberosum Lind. is a primitive specific form and it may probably be the parent form of the cultivated potato. Berthault,⁶ after an intensive study on the following species (varieties?) of Solanum, i. e., tuberosum, immite, etuberosum, verrucosum, squamulosum, columbianum, Maglia, stoloniferum, suaveolens, Valenzuelae, Commersonii, collinum, Nava, Caldasii, fraxinifolium, appendiculatum, Oxycarpum, Jamesii, Juglandifolium, boliviense, bulbocastanum, Bridgesii, Mandonis, cardiophyllum, Ohrendii, polyadenium, Cayeuxi and Andreanum, states "J'ai donc recherché comment ils se transmettaient ou se modifiaient dans la reproduction et la multiplication de ces Solanum. J'ai ainsi été amené à voir

s'il était possible de passer d'un de ces types à un autre, et j'ai envisagé la question de savoir si la culture de ces formes sauvages les modifiait, au point qu'on puisse passer de l'une d'elles à la plante cultivée." The same author further concludes "Or l'étude des herbiers montre que differants Solanum, qui ont été récoltés comme sauvages, possèdent ces caractères de tuberosum, et, si ces plantes, comme le Solanum de Heller, sont bien spontanées, la question serait résolue, et l'on trouverait dans cette plante l'ancêtre de la Pomme de terre," and finally "L'ancêtre de la Pomme de terre serait donc un Solanum tuberosum, dont la forme spontanée est maintenant très rare ou a depuis longtemps disparu."

Thus, we reach the same conclusions concerning the potato that we attain in considering the ancestry of scores of other variable culture plants: the ancestry is unknown and extreme heterozygosis characterizes the germ-plasm.

It is beginning to be suspected that hybridism plays a prominent part in the genesis of new "species."

Lotsy¹⁹ has gone so far as to say that hybridism is the initial cause of all new species. Solanum tuberosum L.

is conceivably a hybrid and interspecific crossing has in the past been easily possible.

Jeffrey¹¹ has pointed out that "Where interspecific crossing is possible, there is often clear evidence of its presence in the form of a high degree of variability, accompanying a considerable manifestation of sterility in the gametic cells, particularly the pollen."

On examination of the pollen condition in the potato the writer has found on the average slightly over 96 per cent sterility. Thus, if interspecific crossing is correlated with sterility, the reason for this lack of seed production might be explained without recourse to the theory that tuber production inhibits sexual vigor. The whole question is one of great uncertainty and no positive statements can be made.

Table 5 gives the percentages of sterility as found in the flowers of the potato and tomato plants. For this purpose flowers of the potato were collected from a three-acre field in Amherst, Massachusetts, the variety being Green Mountain, together with flowers from a five-acre field in North Nobleboro, Maine, this variety being the Irish Cobbler. The tomato blossoms were collected in Amherst, Massachusetts.

Table 5.

Percentage of Sterility in the Pollen Grains of
the Flowers of the Potato and Tomato Plants
Together with the Average Number of Pollen
Grains per Flower of the Potato.

	No. of flowers from which pollen grains were taken.	Total number of pollen grains counted.	No. of fertile pollen grains.	Percentage of sterility.	No. of pollen grains per flower	No. of fertile pollen grains per flower.
<u>Solanum tuberosum</u> L. Massachusetts	100	2150	72	96.8	182520	5841
<u>Solanum tuberosum</u> L. Maine	200	5069	158	96.9	182520	5659
<u>Solanum Lycopersicum</u> L. Massachusetts	100	1527	1382	9.4		

The average number of pollen grains per flower of Solanum tuberosum L. has also been estimated and found to be 182,520. Thus, for each flower there would be only 5700 fertile grains which obviously decreases the possibility of the fertilization of the eggs. This gives us undoubtedly the reason for the scanty seed production in the potato, but it does not explain the cause of the gametic sterility.

Summary

It has been assumed that the evolution of the herbaceous type has been accompanied by an increased physiological efficiency which is distinctly correlated with anatomical modifications. Through a study of woody and herbaceous representatives of the Solanaceae, the writer has tried to bring forward proof of the correctness of this theory both through induction from histological studies and from physiological experiment.

1. It is pointed out that the family Solanaceae is remarkably advanced from the histological standpoint and that these advances correlate well with its assumed phylogenetic position as based on comparative floral anatomy.

2. It is shown that the histological features of the stele are such as to lead to high mechanical and conductive

efficiency.

3. Applying Wernham's³² principle of economy (originally referred only to floral organs) to an interpretation of the increasingly herbaceous stems of the Solanaceae, it can be shown that archaic features are more and more given up in the interest of fewer and more efficient elements.

4. The assumption, that the node of plants is the critical area where the changes incidental to a superior mechanism for storage have spread to the internode, is substantiated by comparative studies on woody and herbaceous Solanaceae.

5. Physiological experiments confirm the above inductions.

6. The prevalent view that there is a correlation between tuber formation and gametic sterility is open to question.

Conclusion

From the above summary we are justified in concluding that:

1. The herb exhibits a superior physiological efficiency of its histological elements.

2. There is an increase in parenchyma which leads to greater storage capacity.

3. There is a superior photosynthetic mechanism which rests upon an increase in content and efficiency of chlorenchymatous tissue.

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PLATE I.

- Fig. A. Floral diagram of Periwinkle. (after LeMaout et Decaisne).
Fig. B. Floral diagram of Calystegia. (after LeMaout et Decaisne).
Fig. C. Floral diagram of Hyoscyamus albus L. (after Eichler)
Fig. D. Floral diagram of Scrophularia sp. (after LeMaout et
Decaisne).
Fig. E. A solanaceous flower - longitudinal view.
Fig. a. Seed of Periwinkle, cut vertically. (after LeMaout et
Decaisne).
Fig. b. Seed of Bindweed, cut vertically. (after LeMaout et
Decaisne).
Fig. c. Seed of Nicandra physaloides (L) Gurtn., cut vertically.
Fig. d. Seed of Scrophularia, cut vertically (after LeMaout et
Decaisne).

PLATE I

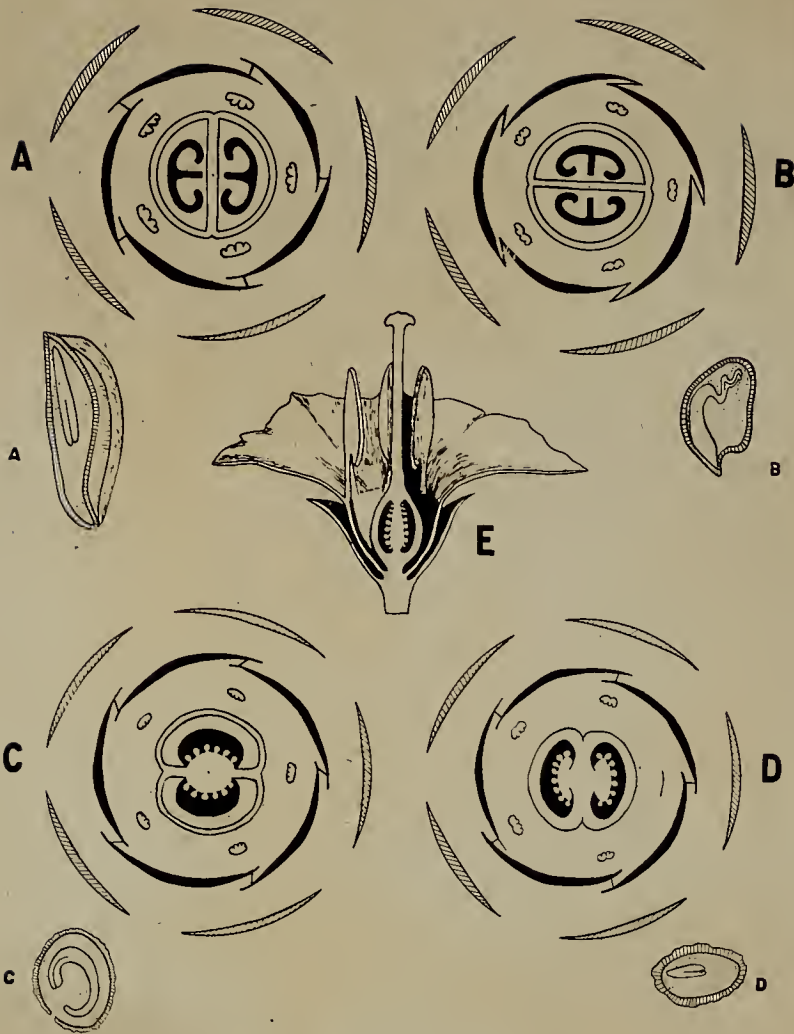


PLATE II.

- Figs. a, b, c, d. Series of vessels from node of Gnetum moluccense, illustrating transitional stages between Ephedra type and Gnetum type of vessel. (after Thompson).
- Figs. e, f, g, h, i, j. Series of vessels from wood of Vaccinium corymbosum L., illustrating transformation of scalariform perforations into a single large perforation. (after Thompson).
- Figs. k, l. Radial sections of wood of Gnetum sp. (after MacDuffie).
- Figs. m, n. Radial sections of wood of Alnus japonica Sieb. & Zacc. (after MacDuffie).
- Figs. o, p. Radial sections of wood of Potentilla monospeiensis L. (after MacDuffie).
- Figs. r, s. Radial sections of wood of Pelargonium sp. (after MacDuffie).

PLATE II

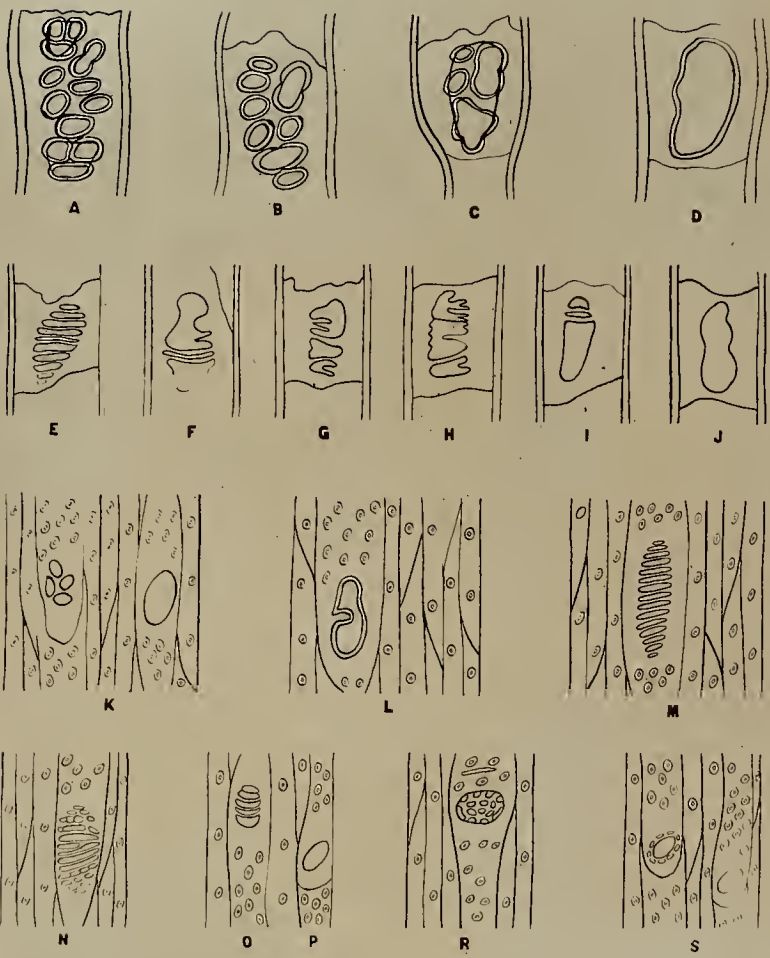


PLATE III.

- Fig. A. Diagram of section of stem of Picea sp.
Fig. B. Diagram of section of stem of Alnus japonica Sieb & Zacc.
Fig. C. Diagram of section of stem of Quercus. sp.
Fig. D. Diagram of section of stem of Solanum Pseudo-capsicum L.

PLATE III

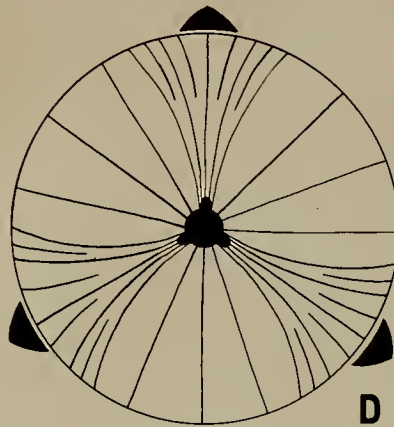
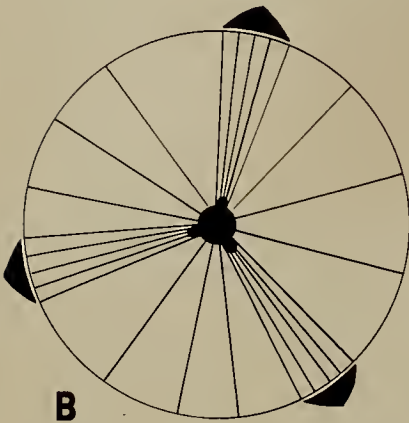
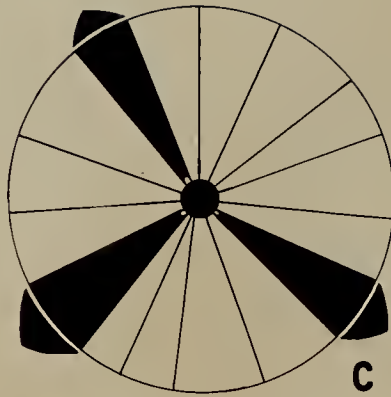
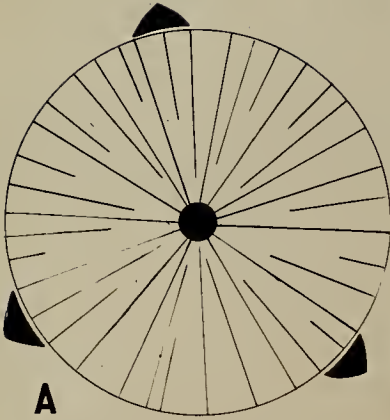


PLATE IV.

- Fig. A. Radial section of xylem of Solanum Pseudo-capsicum L.
Fig. B. Tangential section of xylem of Solanum Pseudo-capsicum L.
Fig. C. Transverse section of xylem of Solanum Pseudo-capsicum L.
- Fig. a. A substitute fiber.
Fib. b. A vessel.
Fig. c. A wood ray cell.

PLATE IV

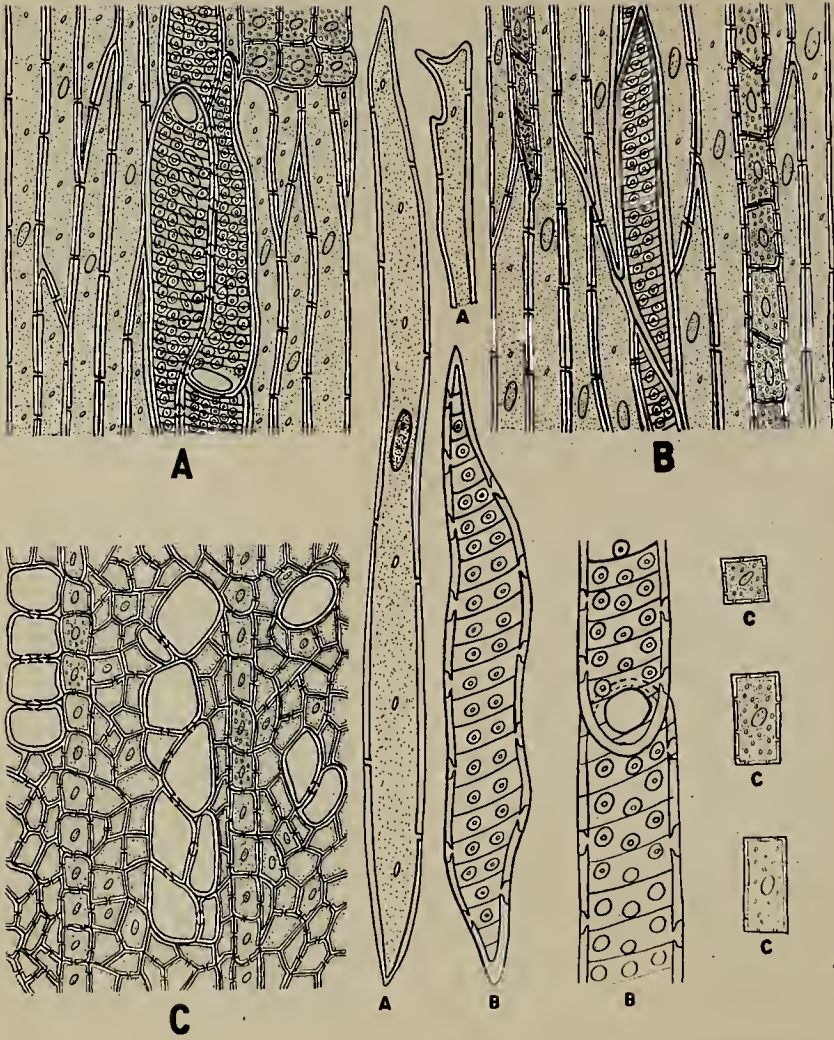
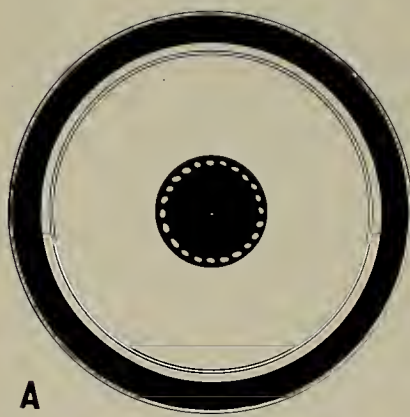


PLATE V.

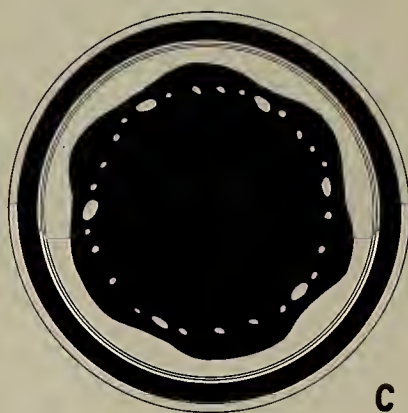
Diagrams showing the approximate areas utilized by the constituent tissues of the stems of

- Fig. A. Solanum Pseudo-capsicum L.
Fig. B. Solanum Melongena L.
Fig. C. Solanum Lycopersicum L.
Fig. C. Solanum tuberosum L.

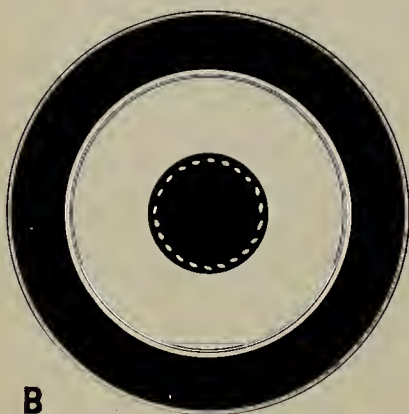
PLATE V



A



C



B



D

PLATE VI.

- Fig. A. Stereogram of a section of stem of Alnus japonica
Sieb. & Zacc.
- Fig. B. Stereogram of a section of stem of Leea sp.
- Fig. C. Stereogram of a section of stem of Helianthus sp.
- Fig. D. Stereogram of a section of stem of Ranunculus acris L.

PLATE VI

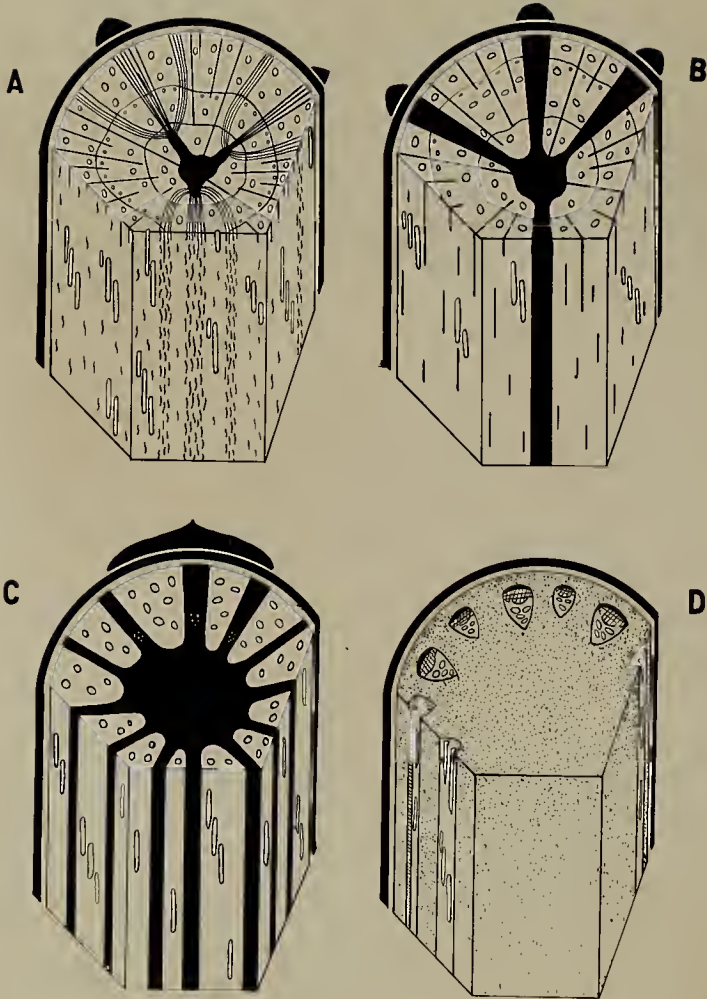


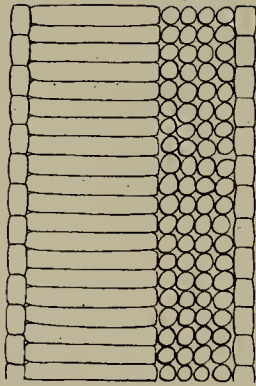
PLATE VII.

Diagrams of Leaf Sections.

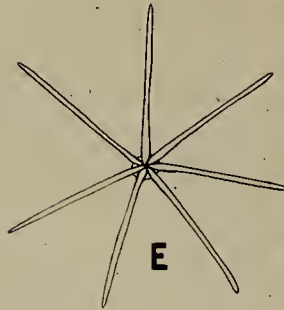
- Fig. A. Solanum Pseudo-capsicum L.
Fig. B. Solanum Melongena L.
Fig. C. Solanum Lycopersicum L.
Fig. D. Solanum tuberosum L.

- Fig. E. A hair from the leaf of Solanum Melongena L.
Fig. F. A hair from the leaf of Solanum Lycopersicum L.
Fig. G. A hair from the leaf of Solanum tuberosum L.

PLATE VII



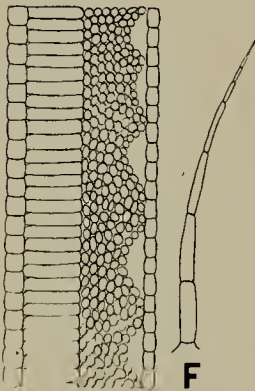
A



E



B

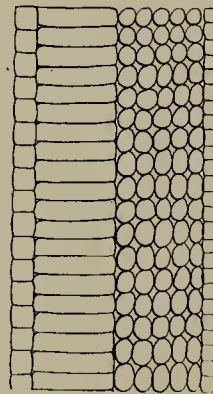


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