ANATOMICAL MATERIAL FOR THE STUDY OF GROWTH DIFFERENTIATION IN HIGHER PLANTS*

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(WITH THIRTEEN FIGURES)

As Fauré-Fremiet¹ says very explicitly in his introduction to "The kinetics of development," the morphological study of ontogenesis of the organs and the order of their developmental succession in the individual during the formative period represents a merely external point of view; it offers merely a point of contact. The author does add, however, that morphological indications are as yet of too great importance to be completely neglected.

Our physiological studies on one hand, and certain anatomical investigations on the other, made during a botanical expedition² in the Brazilian Amazon, have by their coincidence made it possible for us to furnish anatomical material for a study of growth differentiation.

We wish to draw attention to a singularly interesting case which illustrates that morphological considerations are able to bring us to the same point as purely physiological results are doing.

Physiological studies of growth phenomena have permitted us to perceive the relations between growth and age, between growth and the chemical composition of the plant organs and the correlations existing in the development of the different organs. It has proved possible to trace curves expressing mathematical laws. These have the same general trend in plants as in animals. The majority of authors have recorded their observations in successive measurements of weight, of volume and of length during the course of development; for example, the works of Brody³ on the growth of the domestic fowl, Brody and Ragsdale⁴ on the cow, and those of Priestley, Pearsall and Evershed⁵,⁶ on Tradescantia and other plant roots.

* Translated from the original French manuscript by Dr. Mary John, research assistant in zoology, the University of Chicago.


² Belgian botanical expedition in Brazil, 1922–1923, organized by the Belgian Government and the "Fondation Universitaire."


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The observations at our disposal on the morphological variations correlated to these modifications of weight, of length and of volume, though of the greatest importance, are very few in number. In zoology, for example, descriptions of embryonic developmental phases and of metamorphoses have been furnished since a long time. To-day the attempt is being made to find the physico-chemical reasons for the processes of differentiation and a distinction is made between the part due to heredity and the part due to actual causes (causative embryology). Valuable arguments in histology and in cytology have been furnished by CONKLIN's paper on the nucleo-cytoplasmic relation during the course of development. These findings have been amplified by ROBERTSON in his book, "Chemical basis of growth and senescence."

Botanical literature, however, appears to contain little information concerning the different morphological stages through which a plant passes during its developmental period. I do not at all wish to discuss the adaptations or accommodations to actual conditions such as have, for example, been described by MASSART for Polygonum amphibium, but rather to consider the variations in structure during the normal developmental period. The reason for this is that plant embryology can only be considered from a very special point of view, and this point of view differs considerably from the one used in animal embryology.

Thus metazoan embryology ends with the recognition of a young individual whose general organization is, so to speak, established and which will subsequently undergo only modifications of size, of maturation, and senescence. In the plant on the contrary, the stage of embryonic differentiation does not terminate with the formation of the embryo and the ripening of the seed. The meristematic tissues of the stems and the roots of plants continue to function as generative tissues during the entire life of the plant; there is a kind of prolonged embryonic condition which is confined to certain regions, at the extremities of stems and roots, and to the cambium. These meristems appear to be exposed at every moment of the plant's life to the internal conditions of heredity, ontogenetic evolution and to the external conditions of the environment.

These generative tissues, but undifferentiated ones, give rise to primary tissues within which structures become established; and so appear new regions of stems and roots.

We know that every part of a stem, for instance, has its own structure, varying within the limits of the species. Are we able to conclude from these variations that meristem has different potential qualities?

The question proposed in this paper is as follows: Are there any morphological proofs for different potentialities of the meristem during the normal growth phenomena? Is it possible to find structures whose succession, along a stem or a root, is parallel to the physiological variations of growth?

Our intention is not to make a study of the relations between the physico-chemical phenomena of growth in plants and their forms and structures but rather to add new material to the knowledge of these correlations; in other words to give these latter an interesting morphological illustration.

Description of material

Up to the present time, the leaves, stems, branches and inflorescences have been the only parts of higher plants to furnish information on the subject of correlations between growth and structure. As to roots, they generally show no important variations; they have a very uniform anatomical structure in all vascular plants and this structure is identical or constant along the long axis. In the Monocotyledons as well as in the Dicotyledons the root consists of a central cylinder, forming in cross-section a perfect circle, limited at the external periphery of the central cylinder by an endodermis and a pericycle. On this curve is oriented a large number of vascular bundles, and the whole is surrounded by the cortical parenchyma. In the young stages one can scarcely distinguish the root of Monocotyledons from those of Dicotyledons except perhaps by the greater number of vascular bundles in the former. In the adult Dicotyledon a cambium tissue modifies the structure. The Monocotyledons which have no cambium retain their diameter and primitive organization.

We have had occasion to study from a purely anatomical viewpoint a very interesting case of variation, the “stilt” roots of the Amazon Palm, *Iriartea exorrhiza* Mart. We believe it will be interesting to present the facts, freed from the purely anatomical considerations.7

*Iriartea exorrhiza* Mart., a ceroxylian palm, lives in the forests of Varzea8 along the banks of the Amazon in very muddy soil which is inundated during the greater part of the year. The palm, fig. 1, has large, stilt-like aerial prop roots which take their origin from the stem at different nodes and which enter the soil at an oblique angle. This arrangement constitutes an unique case among the palms and is very rare among the Monocotyledons.

We will describe the structure of these roots in young palms of different ages and in the adult; this will show the different peculiarities of root structures from germination.

We find that the roots are inserted higher and higher up on the lower region of the stem, and that the most recently formed aerial roots in the

8 Varzea = alluvial prairies or forests.
adult palm are given off at more than two meters from the soil. The roots are not all of the same diameter. Those inserted nearer the soil have a smaller diameter than do the upper roots.

![Image of Iriartea exorrhiza Mart. (Palm), from the Botanical Garden, Rio de Janeiro, showing the prop or stilt roots which arise at different levels from the base of the stem. The inflorescence is visible beneath the leaf sheaths at the apex of the stem.]

**Fig. 1. Iriartea exorrhiza Mart. (Palm), from the Botanical Garden, Rio de Janeiro, showing the prop or stilt roots which arise at different levels from the base of the stem. The inflorescence is visible beneath the leaf sheaths at the apex of the stem.**

### I. Young plants

The entire series of observations made can be demonstrated from two of the numerous young plants that we collected in the Varzea forests. We
will therefore limit our description to these two, the youngest and the oldest, of the entire lot.

The youngest plantlet (fig. 2) measures 0.4 m. in length and has three leaves, the narrow stem having a diameter of 2.5 mm. at the base and 10 mm. at the apical end. The diameter increases regularly from the base to the tip. The basal part of the stem itself has two little roots, one of which is the principal root. Adventitious, aerial roots have been given off singly at some of the nodes, quite close to the leaves.

These aerial roots appear therefore at different levels; they cause an extensive rupture of the epidermis a little beneath the nodes. These five aerial roots have diameters measuring 2, 3, 3, 4, and 5 mm., respectively. The measurements have a direct relation to the diameter of the stem at the point of their insertion, in other words, the nearer the point of insertion of the aerial root to the apical end of the palm, the larger is its diameter. See table I. This observation is equally true of the plantlet (fig. 3).

The oldest of the lot of young plants (fig. 4) measures one meter in length. The diameter of the stem in the region near the leaves is 20 mm.; the five aerial roots formed in this region measure from below up 6, 7, 8, 9, and 10 mm. in diameter. As one can see, there is a regular gradation in
the thickness of these roots. This observation is confirmed by data from other plants, which will not be presented here, but which are incorporated in the graphic data of fig. 10 and table I.

**TABLE I**

<table>
<thead>
<tr>
<th>Diameter of Roots</th>
<th>Diameter of Stems</th>
<th>Nodes counted from principal root up</th>
</tr>
</thead>
<tbody>
<tr>
<td>mm.</td>
<td>mm.</td>
<td>1st</td>
</tr>
<tr>
<td>2.0</td>
<td>2.5</td>
<td>2-3rd</td>
</tr>
<tr>
<td>3.0</td>
<td>3.0</td>
<td>7th</td>
</tr>
<tr>
<td>4.0</td>
<td>4.0</td>
<td></td>
</tr>
<tr>
<td>4.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.0</td>
<td>5.0</td>
<td>9th</td>
</tr>
<tr>
<td>6.0</td>
<td>6.0</td>
<td>16th</td>
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</tr>
<tr>
<td>10.0</td>
<td>10.0</td>
<td></td>
</tr>
</tbody>
</table>

It is by no means possible to demonstrate sharply this correlation of stem and root diameters on larger parts of stems and on adult plants. On the one hand, there is a greater number of roots appearing at nearly the same point and modifying the true diameter of the stem; on the other hand, roots are lacking on the upper parts of stems.

![Graph](img)  
**Fig. 10.** Correlation of stem and root diameters.
Anatomy of the different roots of the young plants

Cross-sections were made through the roots of these two plants at a distance of 5 cm. from the stem. This level corresponds to the aerial parts. The narrowest root, the primary root, is 2 mm. in diameter and has a true central cylinder, forming a perfect circle and having 12 xylem bundles alternating with 12 phloem bundles. The structure of this root can in no wise be distinguished from that of a normal Monocotyledon (fig. 5).

The root measuring 4 mm. in diameter and inserted at the seventh node, approximately at a distance of 10 cm. from the soil, reveals an extremely interesting condition of the central cylinder. 1. The central cylinder is larger than that of the root just described; it has 31 xylem bundles and 33 phloem bundles. 2. The peripheral outline of the central cylinder is wavy. 3. The central cylinder is ruptured (fig. 6).

The root measuring 6 mm. in diameter (fig. 7) and inserted in the plantlet at the sixteenth node, at a distance of about 20 cm. from the soil is characterized by the same three differences described for the 4 mm. root, but in a more marked degree. 1. There are 62 xylem bundles forming a yet larger central cylinder and 63 phloem bundles. 2. The wavy outline is even more distinct, and the undulations are of different sizes. The most important ones, five in number, take the form of lobes, within whose curves the xylem bundles are oriented. These five lobes are wavy in outline as well. 3. The central cylinder is ruptured in several places so that it appears as if divided into segments. There are five segments corresponding to the five principal lobes, the edges of these segments are more or less separated from each other by parenchyma (fig. 8).

The root measuring 10 mm. in diameter and inserted in a thick node at 50 cm. from the soil shows the following arrangement: 1. There are 229 xylem bundles. 2. The central cylinder is deeply lobed. Each of these lobes is itself bi- or trifurcate, and these secondary lobes are also separated from each other by strands of parenchyma. The lobes themselves are ruptured in several places, giving the appearance of segments of different sizes.

The large roots of the adult plant

The large aerial roots of the adult Iriartea (figs. 11 and 12) are inserted very high up on the stem and their diameter varies from 50–60 mm. This diameter remains approximately constant in the entire aerial region. A cross-section through such a root shows a peculiar design, occupying the entire section, a kind of star with blunt rays. These lobes, of different sizes, are separated from each other by deep sinuses, and are themselves formed by smaller secondary and tertiary lobes. The contour of the lobes is not continuous but broken up into numerous segments of various sizes.
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Fig. 11. Cross-section, × 1.3, of root of adult Iriartea exorrhiza. Diameter, 5 cm. The central cylinder is visible, and shows the star-shaped outline formed by its lobes and segments. Two thorns, sclerified radicles, may be seen.

Fig. 12. Single lobe of the central cylinder, × 3. One can distinguish the elements constituting the lobes and segments.

B = xylem, indicated by black arrows.
L = phloem, indicated by small white circles.
end. = endodermis.
1. = intercellular spaces.
par-e. = external cortical parenchyma.
par-i. = internal cortical parenchyma.
rad. = sclerified radicle, forming a spiny projection.
sel. = sclerenchyma.
seg. = a segment.
v. = an isolated vessel surrounded by sclerenchyma; the vessel is indicated by a black triangle.

The star-shaped design is composed of xylem bundles that are arranged perpendicularly to its outline, each composed of 3–5 tracheae and one or two large vessels. The number of these xylem bundles is quite exceptional, being 1300–1500. The phloem bundles usually, though not always, alternate with the xylem and are present in even greater numbers, 1600–1800. To our knowledge such a complicated structure has been described only in the roots of Iriartea. It is easily explained from transition stages revealed by the study of the young rootlets, although first studies on the adult plant did not lead to an understanding of its root nature.

These different stages are not to be considered as stages in the evolution of the structure of a root in the course of its development. In the roots of the Monocotyledons, the diameter once attained, the structure once established, remains without change. Each of the roots as it is given off from the stem has a structure such as we have described, and retains it during its entire existence.

Discussion

I. In studying the structure of the roots of Iriartea exorrhiza Mart., one finds that the central cylinder shows modifications, lobing and breaking up into segments, the degree of complication being directly related to the width of the diameter. Another very remarkable peculiarity of the structural aspect of the root sections is the number of xylem and phloem bundles. The number of these bundles varies, being greater the larger the root and the more complicated the structure of the central cylinder. See tables I and II. The number of the bundles, the structure of the central cylinder

and the increase in width of the diameter of the root are parallel to each other in their changes from one root to another.

II. When one follows the development of the plant from the beginning of germination, one observes that the first roots formed on the plant are
narrow and simple in structure, and that the roots which appear later during the growth period of the stem are more and more complicated; finally, that the most recently formed roots, which appear on the adult palm, are the largest and have the most highly differentiated structure. We find therefore, from node to node, from the basal to the apical end, all the transition stages between the typical Monocotyledon root to the aberrant root of the adult palm. The succession of these structures depends on growth phenomena.

III. These structures result from the functional activity of the meristematic tissue of the root, passing through a primary stage of tissue development. They appear at the outset with their peculiar structural features at the moment of the formation of the root. They are closely related to the height of insertion in the stem. In proportion to the growth and development of the stem, the meristematic tissues of the roots, which appear at different levels, participate in the stem ontogenetic development.

IV. We know already that a close relation exists between the structures of branches, leaves, and inflorescences, and the stem. A. The leaves arranged along the length of the stem of any annual plant from the base to the tip show the following arrangement: a. Cotyledonary leaves; b. primordial leaves, relatively simple; c. leaves that from node to node show progressive stages of complication until they achieve the typical form of the species considered; d. leaves situated beneath the inflorescences, which are reduced in size, and take the form of bracts.

B. The branches, arising from the development of the axillary buds, have a structure the pattern of which is influenced by that of the stem at the point of their insertion. One knows that the same meristem has formed stems and buds at a given moment; the stem continues to grow while the buds often remain in the resting stage until favorable circumstances arise to release their activity, in the formation of lateral branches. These lateral branches are at the beginning, larger and more complicated in structure when they are inserted on a part of the stem having a higher degree of differentiation and a wider diameter.

C. The inflorescences may be considered from the same point of view. The observations of Gravis\textsuperscript{11} showed already a correlation between the region of the stem at which the inflorescences appear and the type of structure evolved at this level.

D. The stems themselves show modifications of their anatomy. According to the level, the number of fibro-vascular bundles varies, and so does their arrangement and their pathway through the node as well as the internode. The author previously quoted, studied the different types of

structure in the internodes of *Urtica dioica* and *Tradescantia virginica*. At the beginning of the growing period of a stem, the structure becomes successively more complicated, next it becomes uniform and finally undergoes a period of degradation or retrogression.

The meristem at the different nodes of a stem therefore did not function in a uniform manner. It has led to the formation of structures, varying around the specific type, according to the growth periods. These different modifications have for a long time attracted the attention of different workers; they have been attributed to factors of nutrition, to the influence of the surrounding medium. These factors certainly play a part, nevertheless it appears to us that it would be a mistake not to consider the evolution of the growth itself. It is generally said, that the meristem, for example that of a stem, is the youngest and the most active tissue of this stem. Since it is the generative tissue, it is as a matter of course the most active. But, borne at the tip of the stem, during growth, it functions since germination, and in the adult plant, at the extremity of the stem which it forms, it is the oldest tissue present. And this tissue will become still older, the more the stem will elongate over a long period. Therefore, even though it is a generative tissue, the meristem ages. A part of the organographic and anatomical modifications of plants appear to be attributable to this evolution of growth. The vigor of the meristem and the complication of the structures formed are on a par; they augment in proportion as the plant grows up to a maximum, after which there is a slowing down to winter rest or death. This illustrates the bell-shaped curve of the majority of the phenomena of development.

**Conclusion**

Our observations on the “stilt” roots of the palm, *Iriartea exorrhiza* Mart. make it possible to add a new element to these connections between the morphology and the physiology of development. They establish between two vegetative organs, roots and stems, anatomical correlations which appear to be due in part to the ontogenetic evolution of the plant. Under the conditions stated for *Iriartea*, where both these organs are formed at the same time from connected meristems, we offer the suggestion, that the parallel variations of structure may be explained by the modifications of the physiological conditions which surround the meristem in the course of development.

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