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Constitution of Organs of the Higher Plants

The multiple secondary axis theory

Translated by Yang Yen

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Preface

Agriculture is the foundation of national economy. This is because at present organic matters can only be produced by photosynthesis, which converses energy from light (mainly sunlight) and stores it in organics biosynthesized from inorganics. The organics needed by humans for survival and conducting activities are also produced mainly by crops via photosynthesis. The organics produced by green plants via photosynthesis are the essential resources of the most essential substances needed for life by all organisms including humans. Before humans can imitate photosynthesis using sunlight to produce organics, photosynthesis in green plants that produces organics from inorganics is absolutely the only means to store solar energy. Even when the secret of photosynthesis is completely revealed and artificial photosynthesis could be used to produce organics for storing light energy, agriculture will always be the foundation of national economy; and green plants will still be an important component of the physical world and a part of the material cycle in the eco-environment which humanity is also a part of, and thus is vital to humans for their survival and living. Of course, this is the reality that cannot be changed unless the sun dies, and the solar energy completely disappears.

Crop varieties are the fundamental means of agricultural production. The quality and quantity of agricultural products are directly determined by the economic traits of crop varieties. Therefore, improving crop varieties by breeding is the most important way to increase agricultural productivity. For a long time, selection of new varieties during agricultural production, as Darwin summarized, was unconscious. It had become modern, scientific, and conscious only after the function of artificial selection of improved varieties was recognized. Therefore, spontaneously occurred beneficial genetic variations that met humans' needs were collected, gathered, preserved, selected, and utilized in a relatively short period of time in recent centuries. For instance, some famous varieties of crops, poultries, and live-stock bred at that time basically had met the needs by the booming, flourishing, large-scale agricultural production at the early stage of capitalism.

On the other hand, people had recognized, in the practice of artificial selection, that sexual hybridization can produce more variations in the offspring for the

benefits of selection. In addition, various good traits can be combined into the offspring through hybridization. A new era of hybridization breeding then began. As a result, genetics was established in the late nineteenth century for the study of the laws of inheritance and variations created by hybridization.

Since the beginning of the twentieth century, due to the advances in genetics, cytogenetics, and molecular genetics, the laws and mechanisms of inheritance and variations of organisms have been understood better and more thoroughly. Development and applications of artificial mutagenesis, chromosome engineering, and DNA engineering and the application of these technologies have started to advance breeding from being just waiting for spontaneous variations and genetic recombinants to occur into a new area of controlling genetic variations. The use of germplasm has been broadened beyond the boundaries of species and genera by wild hybridization to utilize germplasm from related species and by genetic transformation that artificially transfers cloned genes. Now we can create a new crop with brand new traits that have never been seen in nature before by controlling DNA expression and creating new genes via reformatting DNA base pairs. In 2012, approved by USDA and FDA, a new transgenic soybean cultivar Plenish was released by Pioneer Hybrid, which marks the creation of a new soybean cultivar by regulating DNA with transgenic technology. A brand new high-quality plant oil that had not been seen previously in nature has been produced by regulating DNA to suppress the activity of FAD2-1, a key enzyme in oil metabolism in soybean. This new oil contains more oleic acid, but less linoleic acid and linolenic acid, and thus has higher nutrition value and stronger antioxidization activity and is more heat stable. Consumption of this oil can reduce triacylglycerol in the blood; frying food with this oil can greatly reduce carcinogens in the food. Therefore, Plenish is incomparable with any nontransgenic soybean at the time.

From unconscious selection to conscious selection of crop varieties and from hybridization breeding to transgenic breeding, humans have journeyed four stages. The first stage lasted about 10,000 years. The second stage probably started at the beginning of the seventeenth century. Therefore, it has been less than 200 years since humans understood hybridization breeding. Transgenic crops were born in the late twentieth century. Hybridization breeding had led to the understanding of the laws of inheritance and variations, and intensive studies of the fundamentals of genetics has led to the application of transgenic breeding.

On the one hand, modern agricultural production is no longer satisfied with just waiting for random emergence of new types; it demands scientific design of "ideotypes." This requires that breeding evolves from comparative appraisal of the types already in hand with statistical analysis to a new realm of modern scientific breeding that new types are designed to better meet the demands of production. Modern scientific breeding has similar requirements just as other engineering works do. Therefore, breeding new improved crop cultivars this way requires a thorough understanding of the genetic material from molecules to chromosomes, organelles, cells, tissues and/or organs, of the biochemical and physiological pathways they reflect or derive from, and of the laws that govern the evolution of morphological constitution from micro to macro levels and vice versa. Only when we understand all

these can we design the new types of cultivars under the guidance of these knowledges, foresee the possibilities of breeding new cultivars and the rationality of their organ constitution and their trait specifications, and can we decide the specific approaches, steps, and technologies used for the creation of such a cultivar. The products of agricultural production are particular organ(s) of the crops, not all organs. However, the product organ is associated with all other organs. After all, improved crops are abnormal plants. The demands by the new designing work for improved new cultivars will never be met if we only understand the initial molecular structures and mechanisms of the genetic materials but not the laws of the organ evolution reflected by the genetic traits, the physiology and biochemistry of the functional processes, and the organogenesis initiated by the genetic materials under the specific environment conditions. From our basic understanding of the evolutionary patterns of organs and without a thorough understanding of this knowledge, it is impossible to foresee the possible organ variations and the potential breeding process, to make effective designing of reasonable organ structures, or to select the related traits predictably and effectively; it will also not be possible to predict the occurrence of new organ traits beforehand or to reach the goal of breeding the new cultivars according to the design plan.

Investigating the evolution of plant organ structures is the task of modern plant developmental morphology. Before modern breeding starts to design new crop structures, there is no immediate need for the study of the basic theory of this branch of science because it apparently does not have a close tie with breeding. When breeders start to analyze and design reasonable organ structures for creating a new cultivar, the theory of the organ morphology of higher plants will become a fundamental knowledge of breeding. Unfortunately, when this basic theory is in need of application, we not only find that the current research status of this ancient branch of botany is too far behind the needs, but also identifies conflicts in principles between the breeding practice and the current theories of organogenesis. Practice is the sole standard for testing the correctness of a theory. Practices have revealed many errors in the current theories of the organ morphology of higher plants. Only conducting further research to correct these errors can we provide reliable scientific basis for new cultivar design and more freedom for the designing and analysis. In his practices, the author has reviewed, re-analyzed, and re-investigated questions about the structural unit of organ morphology and the mechanisms of organogenesis in higher plants. On the basis of these studies, a multiple secondary axis theory has been formed to describe the structural unit of organ morphology and the mechanisms in organogenesis in higher plants.

During the “Great Cultural Revolution,” the author overcame interferences and completed two big tasks. The first is the improvement of the low-yield, poor-quality wheat in Sichuan by breeding high-yield, high-quality wheat cultivars that were suitable to grow in the Sichuan wheat production region. Guided by my improved convergent hybridization plan, the author released the stripe rust-resistant, high-yield Fan 6/Fan 7 sister lines in 1969 after 5 years of breeding efforts. These cultivars increased the wheat yield in the Sichuan wheat production region from 3000–3750 to 5250–6000 kg ha hm² and thus lifted the wheat yield in the region one stage

higher. Multiple resistance genes were converged together to form the resistances against 13 races (CRY17 to CRY29) and 20 physiological types of wheat stripe rust pathogen *Puccinia striiformis* Westend. f. sp. *Tritici*. A strong spring type was selected to reduce the first developmental stage of the cultivars, so that sowing can be postponed from “Frost’s Descent” (late September) to “Winter Beginning” (early November) with much reduced risk of getting stripe rust infection before winter. These two measurements enabled the stripe rust-resistant, high-yield wheat cultivar Fan 6 and its sister lines to remain resistant for 20 years, a world record. Genes for high-quality flour were introduced from abroad to improve the flour quality in the Sichuan wheat production region, and were bred into line 70-5858, which was released in 1970. This elite line is the germplasm for a high flour quality that fits to the Sichuan wheat production region. A “70-5858 × Fan 6” cross was then made to improve the flour quality in the Sichuan wheat production region. Offspring of this cross were given to our sister institute Mianyang Agricultural Research Institute to increase the selection population and thus improve the chance of successful selection. Wheat cultivar Mianyang 11 was bred there, which fulfilled our goal of improving the flour quality in the Sichuan wheat production region. To overcome the shortcoming of lacking resistance to pre-harvest sprouting in Mianyang 11, a sprouting-resistant new synthetic common wheat was made by crossing *Triticum taushii* (Cosson) Schmalh. var. *typicum* (Zhuk.) Yen et J. L. Yang with *Triticum turgidum* L. cv. Ailanmai, a landrace from Jianyang that fits to the eco-environment of Sichuan. Rye (*Secale cereal* L.) germplasm that has multi-spikelets per spike but less grains per spikelet was introduced into common wheat, resulting in the common wheat line “10-A,” which has up to 37 spikelets per spike and less grains per spikelet than the ordinary common wheat in the region. All these laid the foundation for further improving wheat in Sichuan.

Another task the author finished during this time was the near completion of the research on the mechanisms in organ constitution of higher plants, the validation of the results, and the writing of the first draft of the manuscript. All these investigations, observations, and thinkings were basically conducted in a “Cowshed” (a kind of informal jail) between events of political criticism and denunciations or reformation through forced labor the authors received there. Here, the author sincerely thanks Ms. Yuzhu Jiang for secretly lending him a microscope disregarding the risks of her own, his lovely wife Prof. Junliang Yang, his son and daughters for secretly providing him the needed books, and papers, pens, and inks for his work, his kindhearted guards for winking at what he was doing. The author could not accomplish this task without these helps. The results of this important research were briefly reported in the *Journal of Sichuan Agricultural University*, 10 (4), 537–565, 1992, under the title “The essential nature of organs in Gramineae, multiple secondary axes theory—A new concept.” However, multiple secondary axes as the common basic organ structure of all the higher plants were not reported there. Also, many data and evidence from the observations and investigations and the complete explanation of them were omitted in that brief introduction. Therefore, the author has taken the time to complete this comprehensive writing after he finished his five volumes of *The Biosystematics of Triticeae* in the USA. The author

is 93 years old now and does not have much time left in his life and is trying to improve the draft he wrote in the “Cowshed” in Sichuan Agricultural University during the “Great Cultural Revolution” and publish it to contribute to the scientific knowledge of mankind and to write a better period to his life.

Revised in 2014 at Davis, California, USA to avoid interferences

Chi Yen

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Chapter 1

The Two Mutually Antagonistic Theories About Organogenesis in the Morphology of Higher Plants



Morphology is a basic science of botany. Before the eighteenth century, it mainly describes the morphological characteristics of plant organs. Morphology served taxonomy as a tool for surveying and organizing plant resources. These surveys have continuously enriched the records and descriptions of the morphological types and characteristics of various plant organs.

For morphology itself, the accumulation of such descriptions and the records of various organ morphologies have inevitably led to comparative studies on the morphological structures of each organ to determine their commonness and the differences in their organogenesis and thus their origin and special individualities (i.e., variations). In other words, it tries to answer how the morphology of plant organs has evolved.

In 1790, Goethe published his book “Versuch die Metamorphose der Pflanzen zu erklären (Studies of the metamorphosis of the plants),” which symbolizes the start of plant morphology as a new research field. His study was based mainly on morphological data. He crafted the term “morphology” for the first time in botanical research. According to Goethe’s theoretic analysis, the organs of higher plants are unified. They are all composed of a basic structure: the leaf. Scales, calyxes, petals, stamens, and carpels are all different metamorphic leaves. Leaves extend downward, becoming petioles; petioles merge to form branches. Flowers are metamorphic branches. A plant body consists of multiple units or segments of leaves and petioles. These units merge to form a stem; the stem extends downward, becoming roots. Each of the “leaf and its downwardly extended petiole” structural units was called “phyton” by Gaudichaud-Beaupré (1841) or “anaphyt” by Schultz (1843). This theory is called “phytonic theory” or “anaphyton theory,” a concept stating that each higher plant body is built up by interconnecting such leaf organs one after another. This theory was also supported by anatomic studies of the vascular bundle system and phyllotaxy, and it regards stems and roots as derived structures of merged leaf bases, not as the basic organs (Celakovský 1901; Velenovsky 1905, 1913). Hofmeister’s hypothesis, as described in his book (Hofmeister 1851) (which

took *Equisetum* as an example and applied it to all higher plants), also falls into this school.

Since the beginning of the nineteenth century, some botanists have believed that axial organs are the basic unit of a plant body and that leaves, which are composed of merged axial branches and webbed structures, are a derivative. This concept was based on palaeobotanical studies of fern (*Polypodiopsida*) and hornwort (*Anthocerotae*) fossils and is antagonistic toward the phytonic theory.

Krüger (1841) suggested that leaves often appear below a growing point and thus are lateral secondary structures and that axial organs are plants' only basic organs. Bower (1884) proposed the concept that the stem is the body axis. Lignier (1903, 1908) hypothesized that original ferns were dichotomously branched and leafless and suggested that because the development of the dominant branch at one side has made it into a sympodial branch, the weak branch changes to a leaf. Therefore, the basic organ is the axial organ, and leaves were transformed from the axes. Bower (1908) proposed his "enation theory," which says that the leaves of *Lycopodiophyta* started from the formation of a thorn-like enation at the side of the stem, which then evolved into flat leaves; the vascular bundles differentiated from the stele reach the bases of the flattened leaf and finally evolve into a single vein structure, extending to the leaf apex. Lang (1931) and Bower (1935) further stated that *Psilophyton* represents the thorn-like enation stage during the leaf evolution, *Thurstophyton* represents the flat-leaf stage, *Asteroxylon* represents the stage when the vascular bundles reach the base of the flat leaf, and *Arthrostigma* represents the stage when the vascular tube extends to the leaf apex.

The concept of axial origin of higher plant organs was adapted to explain *Psilophyton*'s origin in the telome theory of Zimmermann (1930, 1938). Based on the fossil records of *Psilophyton*, he termed the *Rhynia*-like upright branch structure "telome" (terminal branch) and the branch below telome "mesome." Telome and mesome compose the "telome truss" (Fig. 1.1a). A telome can be sterile or fertile if a sporangium developed on the apex. The telome theory states that dichotomous telome trusses become a sympodial branching structure through overtopping (Fig. 1.1b); the dominant branch develops into a stem, while the weak branch stops growing and becomes a dense telome truss through reduction and aggregation (Fig. 1.1c); and then the dense telome truss arranges into a plane with branches webbed together and having parenchyma. This flat, dense telome truss becomes a macrophyll by webbing (Fig. 1.1d), and the aggregated telome truss forms the veins. Therefore, the telome theory believes that primitive veins should be dichotomously open-ended and should be a direct extension of the stem, an equivalent to the stem.

The telome theory believes that *Lycopodiophyta*'s microphyll is also formed from a single flattened telome truss, which is different from Brower's enation theory.

According to the telome theory, macrophylls are formed through planation, aggregation, flattening, and webbing of the weak sympodial branches, and their most primitive phyllotaxy should be alternative. It is aggregation that has made them opposite. Axillary buds are also formed by lowering the position of telome aggregation to the axillaries. Sporangia form at the apexes of telomes. The most primitive sporangium forms at the apex of the marginal vein of the macrophyll during leaf

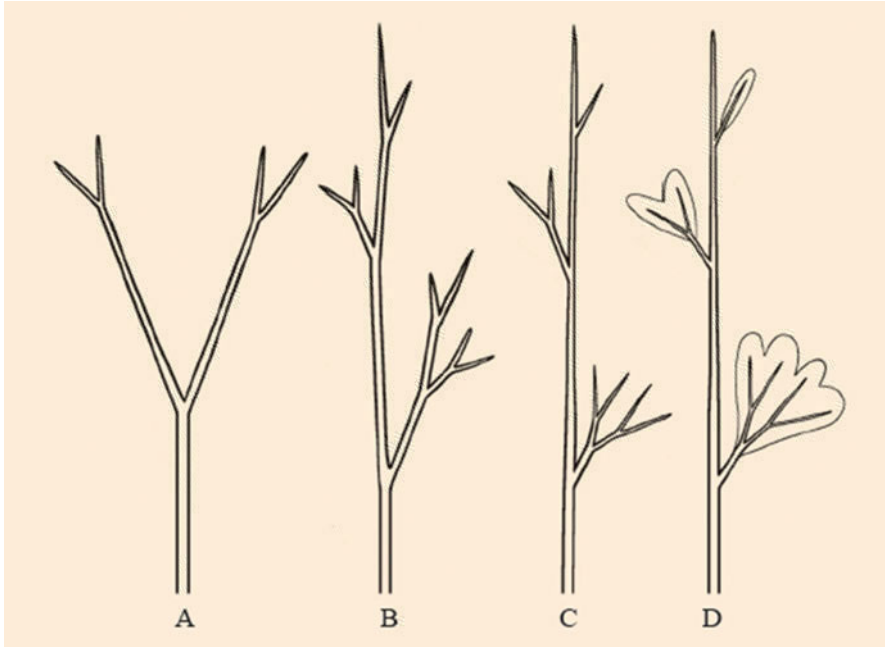


Fig. 1.1 The evolution of macrophyll according to the telome theory. (a) A telome truss consisting of telome and mesome, (b) sympodia formed from weak and dominant dichotomous branches via overtopping, (c) aggregation by shortening lateral branches and the mesomes, and (d) leaves formed by webbing the flattened lateral branches

evolution. In the case of *Lycopodiophyta*'s microphyll, however, they are located anywhere on the leaf surface where single fertile telomes aggregate.

According to the explanation by the telome theory, the sporophyll or the sporangioophore of *Equisetum* form by merging the tops of the outward-turning dichotomous branches, and bracteoles are evolved from sterile telomes (Scott 1900).

Smith (1955), who advocated the telome theory, could not answer how *Equisetum*'s cyclic phyllotaxy has evolved. It cannot be explained by the telome theory, and his only explanation was "do not know yet." *Sphenophyllum* and its relatives have cuneate leaves with dichotomous veins but no petioles. This kind of leaves seem to be cladode. You can see single-veined sterile leaves on many *Equisetum* species. They may be a form of degenerated sterile cladode.

In terms of the morphology of the organs of higher plants, the aforementioned are at present the two main antagonistic viewpoints about the units of organ structure and their basic morphological composition. Although small arguments happen here and there among researchers, in general, there is nothing but the phytonic theory, which regards leaf organs as the basic structural unit for segmental composition, and the antagonistic telome theory, which believes in the continued development of axial organs from the base to the top without segmentation. Currently, the telome theory is adopted by the majority and is the dominant theory in plant morphology.

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Chapter 2

Saunders' Leaf-Skin Theory of the Stem



In 1922, Edith R. Saunders of the University of Cambridge published an article entitled “The Leaf-Skin Theory of the Stem: A Consideration of Certain Anatomico-Physiological Relations in the Spermophyte Shoot” in Volume 36 of *Annals of Botany*. The leaf-skin theory of the stem that he proposed in this article first appeared in his mind in his study of the hairs on the seedlings of *Matthiola incana* and was later concluded after his observations of other spermophytes. This theory states that the surface tissue of the shoot axis of all spermophytes is formed by downward growth and the extension of the leaf petioles, which then fuse around the shoot axis. He believed that this appears to be the case also in some of the Pteridophyta at least. This theory is highlighted here because it is based on objective experimental evidence.

Saunders noticed that the hypocotyl of a *Matthiola incana* seedling was hairless, which differed from the plumule but had the same morphology as the plumule. He further observed similar phenomena on the seedlings of other plants, such as *Veronica hederacfolia*, which has a line of hairs along the edges of the cotyledon extensions of a hypocotyl, but the hypocotyl is morphologically similar to internodes and *Ipomoea sanguinea*, whose cotyledons extend downward and form a furrow on the hypocotyl (Fig. 2.1). He believed that the cotyledons extend downward around the shoot axis, forming the surface of the hypocotyl. The stem above the cotyledons is also formed by the extension of the petiole, which wraps the shoot axis (Figs. 2.2 and 2.3).

Based on these observations and analyses, Saunders made 19 conclusions. The following are the summary and explanations: the surface tissue of the shoot axes of spermophytes are of foliar origin; i.e., the downward extension of leaves is not only observed in those obvious cases but also generally appears in all spermophytes and, at least, in some of the Pteridophyta. In these species, the surface tissues of the hypocotyl are extensions from the cotyledon because they have the same characteristics on their surface. Foliar skin is formed through a downward growth and the extension of the leaf primordium wrapping the shoot axis and forming the surface of the pith. The contact edges of the extensions may be perfectly aligned or deeply