The vegetative bud as the structural basis of the flower

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Abstract
The role of the vegetative bud in the structural development of the flower has received little research attention to date. The bud is an independent organ composed of mature scale leaves enveloping young, immature cauline leaves. There are some obvious parallels between vegetative buds and reproductive, or flower buds. It is generally accepted that the leaf serves as the morphological and genetic basis for the various flower organs. The term 'leaf' normally refers to a traditional foliage leaf. Study of the vegetative bud reveals that the leaf assumes two basic forms, namely those of the scale leaf (cataphyll) and the cauline leaf (trophophyll). This paper posits that the vegetative bud is the structural basis for the flower. The scale leaf serves as the basis for the first three categories of organs in the flower: the sepals, petals and stamens. The foliage leaf, on the other hand, serves as the basis for the carpels. The prevailing model used to elucidate the structure of the angiosperm is based on annual flowering plants. This paper proposes the use of a perennial, woody plant as an alternative, complementary model. This model draws from the primary organ concept proposed by Julius Sachs and Karl Goebel, which differentiates between the primary vegetative and reproductive organs. The two sporophylls – the stamen (microsporophyll) and the carpel (macrosporophyll) – are produced by the interactions between these two classes of primary organ. In this context, the stamen can be described as a catasporophyll, while the carpel can be described as a trophosporophyll. The morphological significance of the vegetative bud in defining the basic structure of the plant has been habitually overlooked, a fact which is reflected in the lack of genetic models focused on the development of the vegetative bud and the differentiation between the scale leaves and the cauline leaves.

Key terms: vegetative bud, flower, scale leaf (cataphyll), foliage leaf (trophophyll), primary organs, stamen (catasporophyll), carpel (trophosporophyll).

Introduction

The first angiosperms (*Magnoliopsida*) were perennial woody plants. They were small trees. Ancestral angiosperms formed both bud scales (scale leaves) and foliage leaves. Stipules developed later on. Angiosperm flowers consist of short shoots and a perianth, which comprises both sterile organs and the male and female reproductive organs.

Plants are able to generate innumerable forms from just a few basic organs. These organs are referred to as 'primary organs'. By definition, primary organs are organs with no morphological relationship to one another that carry out different functions. The most commonly cited concept, originated by Wilhelm Troll, recognises three primary organs: the root, the stem and the leaf.[1] Troll uses the scheme of an annual herbaceous plant as a model for illustrating angiosperm arrangement and structure.

But what if we replaced the model of an annual with a perennial plant capable of producing both woody tissue and buds? This type of model combines the formation of buds and woody shoots, meaning perenniality or secondary growth, with annuality, or the formation of inflorescences and flowers.

The reference model for an annual plant depicts a linear sequence of leaf organs, from the cotyledon to the carpel. Goethe (1790) originally based his work on linear metamorphosis. The model of the woody plant exposes the possibility that the vegetative bud as a whole may serve as the structural basis for flower development. This would shift our focus to the metamorphosis from vegetative bud to flower. Adolph Hansen (1907) defines metamorphosis as a change in form in an organ accompanied by a concurrent change in function. This paper employs a broader understanding of the term, defining metamorphosis as a process capable of influencing both individual organs and organ systems.

Wilhelm Troll uses his primary organ concept, which is based on vegetative structure, and differentiates between roots, stems and leaves in order to describe the structure of the flower, emphasising the leaf-like nature of the reproductive organs. Unlike Sachs (1874, 1882) and Goebel (1884), Troll does not differentiate between primary vegetative and reproductive organs.[2][3] According to Sachs and Goebel, the primary reproductive organs comprise the sporangia and gametangia. Goebel defines a sporangium as any organ that produces spores. This organ may be sunk into the leaf or shoot tissue or protrude from the same tissues in the form of a tiny capsule.[4] According to Goebel (1884), stamens and carpels are the products of interactions between both types of

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1 Troll (1954)

2 Sachs (1874) pp 151-153 and Sachs (1882) p 15
3 Goebel (1884) p 127 ff.
4 Goebel (1884) p 130

organs.[5] This would imply that, when acted upon by the plant's impulse to produce spores, the vegetative bud undergoes metamorphosis, resulting in the flower.

There is a plethora of research focused on the genetic basis for diversity of leaf form within the same plant (heteroblasty, heterophylly). Zotz et. al (2011) provide a review of the literature. However, these studies concentrate exclusively on the different forms occurring in foliage leaves rather than the obvious differences between scale leaves and foliage leaves.

Genetic science has developed the (A)BCE model for flower development, which describes the genetic preconditions that trigger the specialisation of flower organs into sepals, petals, stamens and carpels.[6] However there are no existing genetic models for the development of vegetative buds. There are models describing the proximal-distal structure of the foliage leaf. These models focus on the junction between the petiole and the lamina. There are no existing models for describing the differentiation of the leaf base and the lamina.[7]

Morphology is based on a comparative analysis of forms. When describing a mature plant, one might start by observing the whole and subdividing it step by step into its constituent parts. This method is referred to as 'top-down'. Alternatively, one might begin by describing the individual components and use these to construct a model of the whole organism. This method, which is the dominant approach, is referred to as 'bottom-up' and is based on the assumption that organisms are made up of building blocks or modules. This paper applies both approaches in a complementary manner.

Bud and shoot

Herbaceous, annual plants are the phylogenetic descendants of perennial, woody plants. Ancestral angiosperms were small trees and shrubs. A tree is organised into underground parts, meaning the roots, and above-ground parts. The above-ground portion of the tree can be organised into the vegetative components, or the shoots and buds, and the reproductive components, or the flowers. The shoot is the organ of the active phase, in which assimilation and respiration take place. The bud is an organ which exemplifies the resting phase, in which life processes slow down, allowing the plant to remain dormant during unfavourable growing conditions. Buds possess a short shoot. The mature leaves of the bud are scale leaves (cataphylls) that envelope and protect the developing foliage leaves. The shoot is composed of an elongated stem with foliage leaves (trophophylls). Organisms alternate between bud and shoot phases. Buds give way to shoots and shoots develop new buds which give way to further shoots, etc. Growth is indeterminate.

The reproductive organs of the flower are subject to determinate growth. Growth ceases with the development of fruit and seeds. Inflorescences and flowers comprise the herbaceous, annual part of the tree. Shoots, which develop into branches and trunks, comprise the perennial part. Flowers develop from reproductive buds, which are similar to vegetative buds, however tend to be somewhat larger.

Vegetative bud and flower

What are the similarities between a bud and a flower, and what are the differences? The vegetative bud is encased by strong, coarse, mature scale leaves. Thinner, more membranous scale leaves make up the next layer. The scale leaves form a protective enclosure surrounding the developing foliage leaves. At this stage, it is possible to recognise the folded lamina of the developing foliage leaves. The petiole has not yet begun to extend, and the primordial lamina appear to be sessile. The bud scales and lamina primordia are arranged densely along the short shoot. Growth has paused (Fig. 1).

Stevens (2017) provides the following definition of a flower: "the characteristic reproductive structure of angiosperms, a heterosporangiate strobilus, typically consisting of androecium, gynoecium, usually surrounded by a perianth and borne on an axis or receptacle, the parts showing various kinds of symmetry relationships to each other and to the inflorescence axis, also often with a distinctive merism, see also euanthial and pseudanthial, theories on the evolutionary origins of flowers, also meranthium and pseudanthium, flowers that are not quite what they seem to be."

The closed flower bud is enveloped by leaves that are finer in texture than the course scale leaves. These provide a protected enclosure for the stamens and carpels. The stamens are fully mature. For the purpose of ovule fertilisation, the carpels are fully mature; however, they will continue to develop into the seed capsules.

Compared to the pedicel, the receptacle is broader, short and compact. In morphological terms, 'receptacle' refers to the vegetative tissue located at the base of reproductive organs. The flower's organs are tightly arranged on the receptacle.

Vegetative and reproductive buds also exhibit similarities in the opening process. This process occurs very rapidly. First, the outer, course scale leaves are pressed apart; they are shed as soon as the shoot begins to undergo secondary growth. The inner, finer and more membranous scales expand and abscise like their courser predecessors. The internodes expand, with the most pronounced expansion exhibited in the internodes between the foliage leaves. Leaf primordia develop into mature foliage leaves with a leaf base, petiole and lamina. The petiole is the last part of the leaf to develop. Foliage leaves supply the next generation of buds with assimilates. These foliage leaves die at the end of the season and fall off. The buds enter the rest period.

Flower buds open very rapidly. The perianth is divided into the calyx and the corolla. Soon after the flower blooms, its petals and stamens dry out. The immature carpels and ovules grow to their final size. The carpels

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[5] Goebel (1884) pp 110-112
[6] For a review, see Ambrose et. al. (2013)
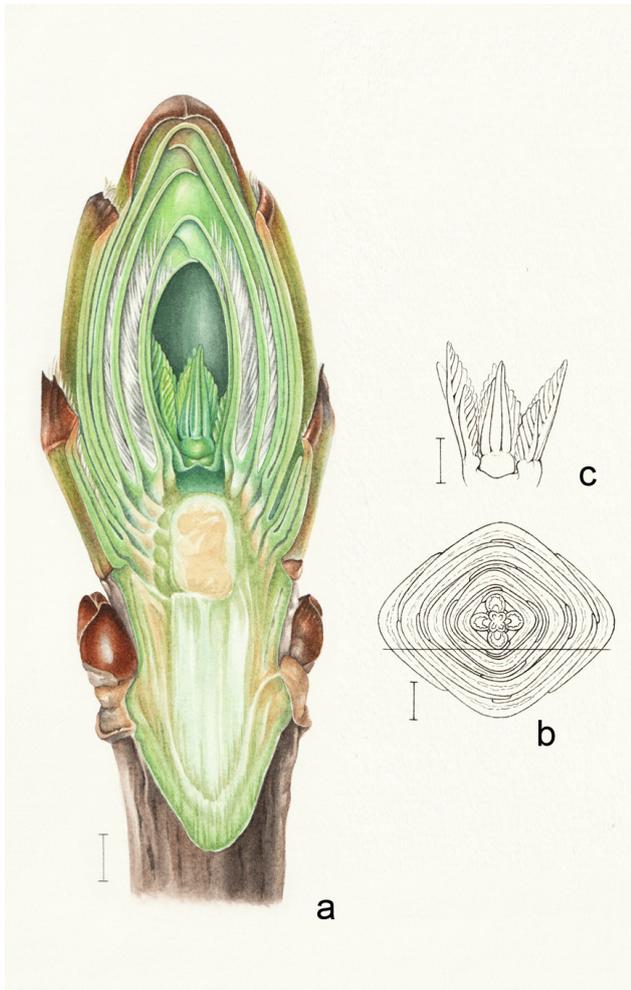[7] Ichihashi et al. (2011); Toriba et al. (2019)

Fig. 1 a) Longitudinal section of a terminal bud of the sycamore maple (*Acer pseudoplatanus*); b) Cross-section of the terminal bud at the level of the foliage leaf primordia; c) Foliage leaf primordia separated from the bud. a) The large, outermost scale leaves to the left and right exhibit residual, undeveloped lamina. Subsequent scales do not exhibit residual lamina. The inner scale leaves are linked together via their hood-shaped apices. The bud is clearly divided into an inner chamber which houses the foliage leaf primordia and a closed casing made up of scale leaves. b) The cross-section illustrates the opposite phyllotaxis with two leaves per node exhibited by the scale leaves and the foliage leaves. c) The margins of the young lamina face one another; the lamina primordia give the appearance of being folded. Bars = 1 mm. Watercolour: Jasmin Huber. © Peer Schilperoord

supply the ovules with assimilates. The fruit capsule dies. The seeds enter the rest period.

The difference between the vegetative bud and the flower lies in the flower's ability to produce spores and seeds. In morphological terms, the scale leaves are known as 'cataphylls'. Foliage leaves, which are capable of respiration, assimilation and nutrient production, are known as 'trophophylls'. The morphological term for the stamens is 'microsporophylls', while the carpels are designated as 'macrosporophylls'. Stamens are incapable of assimilation, while the carpels are able to carry out assimilation. Due to their ability to carry out assimilation, carpels may

also be designated as 'trophosporophylls'.[8] Accordingly, stamens can also be defined as 'catasporophylls'.

Woody plants may skip the budding stage during the production of lateral shoots (syllepsis). Proleptic lateral shoots, on the other hand, are formed from a bud. The vegetative bud serves as both the first and final stages; it facilitates all forms of plant reproduction. The flower is the terminal stage, after which reproduction continues via the seeds. Flower bud positioning on the shoot – terminal or axial – corresponds to the position of the vegetative buds.

Formal comparison between a flower and a vegetative bud yields more similarities than a comparison between a flower and a shoot with leaves and short internodes. According to a generally accepted definition, a flower is a short shoot bearing sporophylls which serves the purpose of reproduction.[9] Leins and Erbar (2008) decline to provide a definition, as the flower is too diverse a structure and too little is known about its phylogenetic origins. Their description of a flower's constituent parts, however, aligns with the generally accepted definition: as comprised of the perianth, androecium, gynoecium and receptacle with a determinate growth pattern. Greyson and McDaniel (1994) reserve the term 'flower' for: "the characteristic aggregation of sterile and fertile reproductive organs of the angiosperms." None of these definitions or descriptions account specifically for the vegetative bud; however, emphasis is placed on the short internodes, which are characteristic of both structures.

Internal conditions

Plants are adapted to their external conditions. There are numerous ways in which they can adapt both form and function to suit these external conditions. However, the plant is also subject to internal conditions that affect the structural potential of its shoots and leaves. The differences in form between the woody shoot, the herbaceous shoot and the flower are expressions of different developmental phases, which are generally termed 'woody growth', 'herbaceous growth' and 'reproductive growth'. Each phase has its own basic structure, its own preconditions and its own internal conditions. When applied to woody growth, the pattern of alternating shoot and bud formation presents structural limitations for stem and leaf growth. Foliage leaves allow buds to form and buds enable rapid shoot development given favourable external conditions. The leaves abscise while the stem remains. Flowers are subject to determinate growth, and their development ends with the production of fruit and seeds. Seeds represent the beginnings of a new plant. Here, elimination of the imperative to

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8 In the morphological literature, the term 'trophophyll'(nutrient-producing leaf) is generally used to refer to the fronds of ferns that carry out assimilation and do not produce spores. Conversely, the spore-producing fronds that do not carry out assimilation are referred to as 'sporophylls'. Hagemann (1984, p 349) refers to fronds that both produce spores and carry out assimilation as 'trophosporophylls'.
9 Kadereit et al. (2014)

repeat certain processes gives way to new structural possibilities.

In the case of herbaceous annual or biennial plants, the entire plant dies after fruiting. There may be a clear division between the stem and the foliage leaf, although it is no longer required. The same applies to perennial plants with annual, determinate, deciduous vegetative and reproductive shoots. In these cases, any restrictions associated with woody growth, or the persistence of the stem, are eliminated.

Exclusively herbaceous plants enjoy a whole new range of structural possibilities. The herbaceous shoot itself constitutes a structural element. Leaf and stem are correlative terms: The leaf can perform the functions of the stem while the stem can perform the functions of the leaf. One common example can be seen in grasses. The leaf sheath of a wheat plant (*Triticum aestivum*) forms a pseudo-stem during emergence. The culm and ear then push out through the pseudo-stem. During emergence, the internodes and leaf sheaths display interrupted, or intercalary, growth. This type of growth gives grasses their unique structure, in which leaf and culm form a single unit. Another example can be seen in Scotch thistle (*Onopordum acanthium)* from the Asteraceae family. In Scotch thistle, both sides of the leaf base extend down the stem like a ribbon. In this way, the leaf is connected to the stem both horizontally, in the usual pattern, as well as vertically down the sides of the stem.

Less diversity is observed in the leaves of the woody shoots on shrubs and trees than in the leaves of persistently herbaceous shoots. Herbaceous plants also exhibit a wider range of shoot structures than do woody plants. Flowers display even more diversity. As previously shown by Goebel, diversity in flower structure can be linked to the fact that a flower is a shoot with a determinate growth pattern. This means that the receptacle not only serves as a juncture for connecting the lateral organs; it also plays a role in determining the structure of the flower itself.[10] For example, the receptacle may deepen into a bowl-shaped structure and subsequently form the wall of an inferior ovary. The organs are densely arranged, internodes are extremely short and apical growth ceases with the development of the carpels. Lateral shoot growth is suppressed. Sporangia formation is an additional element affecting the internal conditions of the plant.

Studies on the diversity of leaf shapes generally tend to focus on the ways in which external biotic and abiotic environmental factors interact to determine the shape of the leaf.[11]

The leaf as scale and foliage leaf

Scale leaves and foliage leaves are the two types of leaves that grew on the stems of the very first flowering plants. But how are these two leaf types related? Throughout the history of plant morphology, scale leaves have fre-
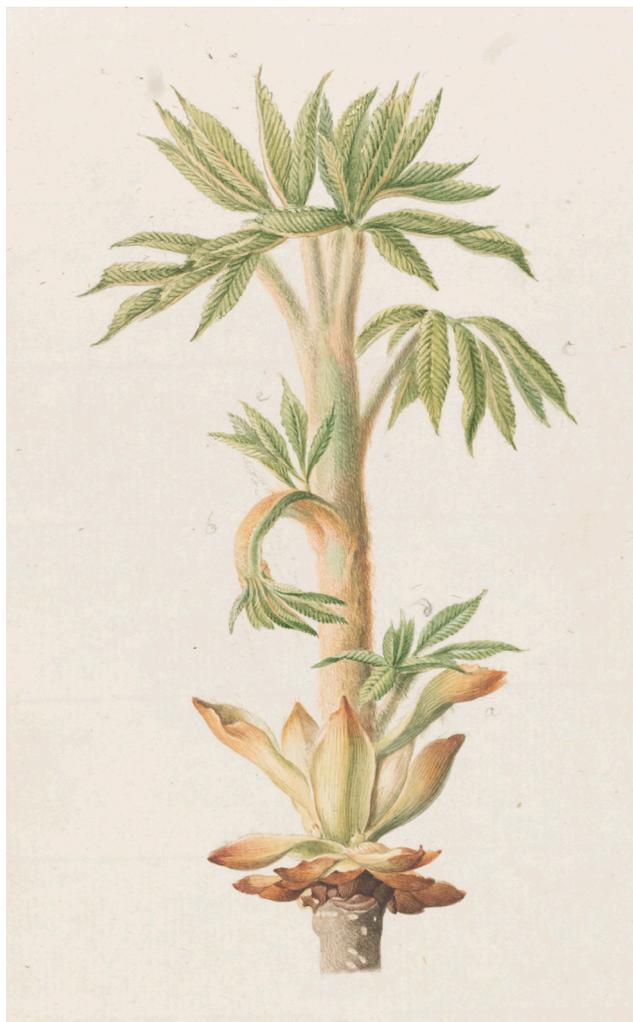

Fig. 2 Illustration of a young horse chestnut shoot (*Aesculus hippocastanum*) with the transitional form between scale leaf and foliage leaf depicted in the centre. This form has a broadened leaf base and a lamina positioned directly on the leaf base which will exhibit little additional growth. The outer brown bud scales have spread back while the inner scales have elongated. Goethe compares the outer and inner scale leaves with a calyx and a corolla from which the shoot emerges. The image was originally a copper plate engraving intended as an illustration to accompany Goethe's Metamorphosis of Plants. Adolph Hansen first published this watercolour in 1907. Johann Wolfgang Goethe, © Klassik Stiftung Weimar GSA_26_LIV. 8

quently been studied and described. Detailed analysis of buds and the bud opening process dates back to Marcello Malpighi, who studied species such as *Acer* sp., *Juglans* sp., *Prunus domestica*, *Quercus robur*, *Rosa canina* and *Ulmus* sp.[12] Among other things, Malpighi determined that the apices of the (inner) bud scales of the maple display a hood-like shape and that these cucullate apices cause the scales to interlock. Johann Wolfgang Goethe also studied bud production and the opening process. Yet, in his best-known work focused on the metamorphosis of plants (1790), these investigations are limited to descriptions of the development of herbaceous plants and do not include observations of scale leaves and their transitional forms to foliage leaves. The watercolour il-

10 Goebel (1884) p 278
11 Kidner & Umbreen (2010)

12 Malpigin (1675; 1679)

lustration (Fig. 2) of a young horse chestnut shoot (*Aesculus hippocastanum*) shows Goethe's intense interest in the relationship between scale leaves and cauline leaves as well as their intermediate anatomies. In its original form as a copper plate engraving, this watercolour was intended to illustrate the process of metamorphosis in plants.[13]

Alexander Braun inventoried and categorised diversity in leaf shapes.[14] Braun's scale leaf category included both scales and sheaths as well as underground buds, bulbs, stolons and tuberous rhizomes. According to Braun, these forms all display a "broad base, reduced height and highly simplified form and ribbing; they lack lamina, petioles and lobes, are thus never accompanied by stipules and always possess an entire margin. They frequently exhibit a fleshy, cartilaginous or leathery texture and infrequently exhibit a delicate or membranous texture, [...] they are never explicitly green in colour and are frequently white, yellowish, flesh red, brown or even blackish." Braun interprets the scale as a morphological reversion away from the more highly developed form of the foliage leaf.

August Wilhelm Eichler (1861) studied the ontogenesis of the leaf with a special emphasis on the development of the stipule. He referred to the leaf base as the 'lower leaf zone' and the lamina as the 'upper leaf zone'. Eichler originated the term 'leaf primordium', which refers to the earliest developmental stage of a young leaf prior to its differentiation into lower and upper zones. This differentiation into lower and upper leaf zones is distinguished by a minor acceleration in the growth of the middle section of the young leaf primordium, which results in a slight narrowing of the marginal meristem. This narrow section may develop into a petiole later on via intercalary growth. The basal section, or lower leaf zone, develops into the leaf base either with or without stipules, while the apical section, or upper leaf zone, becomes the lamina. Eichler viewed the petiole as part of the upper leaf zone. Due to its position, the petiole forms the link between the leaf base and the lamina.

Karl Goebel (1880) lamented Braun's failure to produce a more detailed comparative ontogenetic description of the two leaf forms. Goebel therefore came to the conclusion that the development of bud scales was the result of foliage leaf primordia remaining in an earlier developmental stage, remarking that "the scales are nothing more than a highly developed leaf base." According to Goebel (1880), "the first developmental stages of the bud scale and the foliage leaf are completely identical, i.e. a broad leaf base produces a small lamina primordium." Goebel describes these leaf forms with small lamina as occurring in the basal scales on the terminal buds of *Acer*, *Juglans* and *Fraxinus*. Later on (1913) he emphasises that not all scale leaves are required to possess residual lamina primordia.[15] Goebel views the foliage leaf as the primary

form and describes the scale leaf based on the model of the foliage leaf. Accordingly, he interprets the scale leaf as an arrested foliage leaf produced by accelerated development of the leaf base accompanied by reduced lamina growth occurring early on in the development of the foliage leaf.[16] Goebel also considered juvenile leaves, which occur between the cotyledons and the first mature foliage leaves, and bracts to be modifications of the foliage leaf.[17] Juvenile leaves are scale-shaped, yet they grow individually from the stem and are capable of assimilation. They share certain similarities with bracts, which are also scale-shaped and individually positioned on the stem. Adriance S. Foster composed a 1928 summary of contemporary scale bud research and studied scale formation in *Aesculus* and *Paeonia*.[18] [19] Foster confirms Goebel's observation that young scale primordia often display primordial lamina which fail to develop. He goes further than Goebel in emphasising the unique dynamic of scale development and the ways in which it differs from the dynamics involved in the development of foliage leaves. Foster identified a reversal in the rate of growth, a type of 'polarity' in the development of the scale leaf and the foliage leaf.[20] [21] Scale leaves that do produce a lamina primordium exhibit very slow growth in that area. Conversely, the basal section of the leaf primordium displays far faster growth and subsequently develops into the scaly part of the leaf. Foster reiterates that scale leaves do not represent an arrested form of the foliage leaf. He goes on to elucidate the ontogenetic, morphological, seasonal and functional distinctions between both leaf forms.[22] According to him, both forms are of equal value. He describes a fork in the developmental process. A leaf primordium may develop into either a scale leaf or a foliage leaf; this determination is made early on in the leaf's development.

Foster (1929) distinguishes between two different transitional forms linking the scale leaf and the foliage leaf. He calls these the lower and upper transitional forms. During the budding phase, the lower form is located between the final scale and the first foliage leaf while the upper form can often be found at the terminus of a larger shoot, where it serves as the first leaf of the terminal bud. Upper transitional forms can frequently be observed in the terminal buds of *Acer pseudoplatanus* as well as in the terminal buds of epicormic shoots in *Fraxinus excelsior*. The lower transitional forms have a more scale-like appearance, whereas the upper forms resemble foliage leaves. These two types of transitional forms stem from two different physiological states, which, ac-

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13 Hansen (1907)
14 Braun (1851) p 66
15 Goebel (1913) p 315

16 Goebel (1879) p 125
17 Goebel (1884) p 251
18 Foster (1928; 1929)
19 Foster and Barkley (1933)
20 Foster (1929) p 494; Foster and Barkley (1933)
21 Foster and Barkley (1933): "The primordia of cataphylls and foliage leaves in *Paeonia* exhibit a similar 'polarity' which is expressed by segmentation into lamina and basal regions. Differences in the rate and type of growth in these two regions are responsible for the divergence in form between the adult cataphyll and foliage leaf."
22 Foster (1931)

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cording to Foster, exert some kind of control over the annual, seasonal alternation between scale leaves and foliage leaves.

Wilhelm Troll considered bud scales, which he also termed 'tegmina', to be juvenile leaves in a morphological sense. Juvenile leaves are scale-like leaves that often serve as developmental successors to the cotyledons.[23][24] Juvenile leaves differ from subsequent cauline leaves in that the later exhibit a fully mature lamina. The characterisation of the bud scales as a specialised form of juvenile leaf appears to arbitrarily reference studies by Goebel and Foster. Troll selects a perennial, vegetative plant that produces both buds and wood as a model for angiosperm structure (Fig. 3). Juvenile leaves are not illustrated in the model. He uses the model of the broad bean (*Vicia faba*) to describe the juvenile leaves. The juvenile leaf should be considered as an intermediate form between scale and foliage leaves. The juvenile leaf is not the primary form and the scale leaf not a special form of a juvenile leaf.

Both Goebel and Troll use the foliage leaf as a starting point for their analyses and underline the structural differentiation between the lower leaf zone and the upper leaf zone. Troll's objective is to "so thoroughly parse the diversity of form that all variations may be traced back to size differences in the individual components." Troll's principle of variable proportions provides a mathematical framework for the transitional forms.[25] Thompson (1917) and recent computer models developed by Coen et. al. (2017) and Runions et. al. (2017) provide even more precise mathematical models than those proposed by Troll in his principle of variable proportions.

Troll's principle of variable proportions grants only a secondary importance to qualitative differences. Consequently, in a morphological sense, the model is more abstract than the precise descriptions provided by Goebel (1880), Foster (1929), Foster and Barkley (1933), Schuepp (1929), Steingraeber (1982), Jones and Watson (2001), Pabon-Mora and Gonzalez (2012), Antonova and Popova (2014), Barykina and Churikova (2014) and Troll (1954). Barykina and Churikova describe the wide variety in scales observed in woody plants as opposed to herbaceous species. Pabón-Mora and Gonzalez (2012) describe the scale leaves, foliage leaves, short shoots and striking thorn-like leaves of the long shoots observed in the genus Berberis.

When we compare Troll's preferred approach with the generally accepted definition of metamorphosis as a change in form corresponding to a change in function, then it becomes clear that Troll reduces the core of morphology to its quantitative aspects.[26] Scale leaves are diametrically opposed to juvenile leaves in terms of their arrangement, function and substantial qualities. Troll's
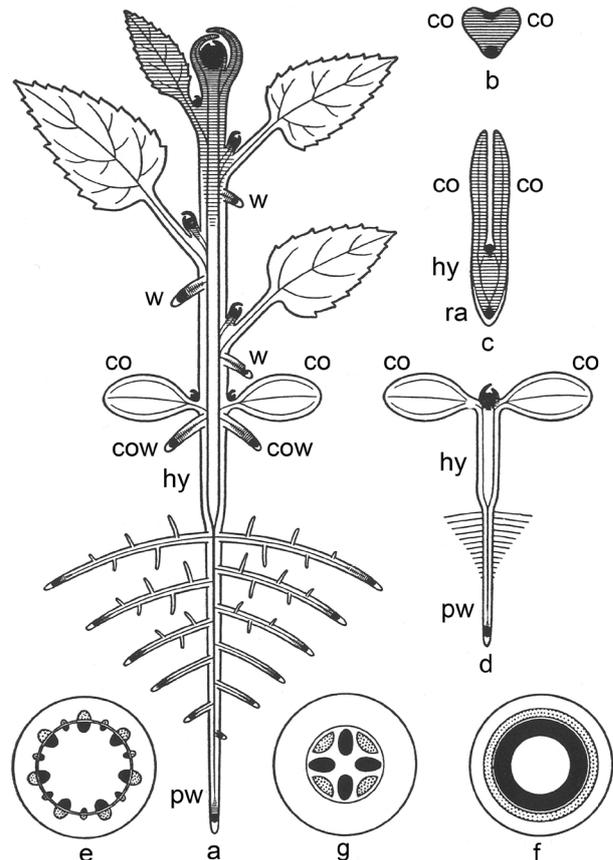

Fig. 3 Model of the seed plant, vegetative. Diagram by Wilhelm Troll from 1954. Unlike his model from 1937, this illustration includes root hairs, the development of lateral roots from the shoot and also secondary woody growth. (a) Schematic model of the seed plant. (b), (c) Embryo, young (b) and developed (c). (d) Embryonic plant. (e-g) Stem (e, f) and root sections (g). co cotyledons; hy hypocotyl; ra radicle; pw primary root in (d) with root hairs; w adventitious roots; In (a-d) meristematic zones (black), growing sections (shaded). Troll (1954)

morphological characterisation of scale leaves as an arrested form of foliage leaves therefore falls short.

Today, the physiological states affecting seasonal changes acknowledged in Foster's work are more widely recognised (Janssen and Douglas, 2007). Antonova and Popova (2018) refer explicitly to a genetic threshold in *Ulmus glabra* that must be crossed in order to catalyse a transition from scale leaves to foliage leaves. Pabón-Mora and Gonzalez (2012) add to this findings in the field of molecular genetics regarding the formation of foliage leaves and apply these discoveries in their inquiry into the developmental differences between scale leaves and foliage leaves. To date, no molecular genetic investigation of bud formation has been conducted.

The bud inside the bud

It is generally recognised that the bud scale serves a protective purpose. Karl Mikosch (1876) was one of the first to conduct a thorough investigation of the anatomy, morphology and function of the bud scales. The bud enables the plant to suspend its growth and subsequently survive during unfavourable conditions. It also allows for rapid development in the presence of

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23 Wilhelm Troll (1937; 1939; 1954)
24 Troll (1954) p 141
25 Troll (1954) p 2
26 Hansen (1907)

Fig. 4 *Helleborus foetidus,* Voigt (1817). The stinking hellebore is a perennial that overwinters as a rhizome and forms annual, herbaceous shoots at the beginning of the growing season. Its highly robust shoot exhibits an array of transitional forms between the cauline leaves and the perianth. These transitional forms demonstrate that the organs are homologous, meaning that they belong to the same class of primary organs. See also Figure 5 with *Helleborus niger*.© BayerischeStaatsbibliothekbvb: 12-bsb10076691-2

favourable conditions. Thus, plants are able to optimise their growth during (short) growing seasons. Buds provide plants with a measure of independence from their external environment. Foster (1929), in his investigations of the mature terminal buds of *Aesculus hippocastanum*, determined that the buds contained seven to eight pairs of scale leaves and three to four pairs of foliage leaf primordia for shoots in the current growing season. He then often found one to two pairs of scale leaf primordia for buds that would mature the following year. Foster referred to this phenomenon as preformation. Sabatier and Barthélémy (2001) identified preformation in *Juglans regia*, while Studer and Schilperoord (2015) identified the phenomenon in *Quercus robur*. The terminal bud may contain the first scale primordia for the next terminal bud. This phenomenon occurs in a slightly modified form for reproductive buds, which contain the entire flower primordium or the primordium of the inflorescence. The anatomy of the transitional zone between the bud scales and the flower primordium can take on various forms. The area between the bud scales and the

flower primordia may contain a section of shoot with foliage leaves. However, there may also be an immediate transition without foliage leaf development.

Transitional forms between the leaves on the shoot and the flower occur most frequently on larger shoots with terminal buds. One classic example is the stinking hellebore (*Helleborus foetidus*), drawn by Voigt (1817) showing a case example of *Goethe's Metamorphosis of Plants* (1790) (Fig.4). *Helleborus* exhibits a graduated series of transitional forms reminiscent of the transitional forms observed in *Aesculus hippocastanum* (Fig.2). Transitional forms between foliage leaves and the sepals and petals of the perigonium are known as bracts.

The Paeoniaceae family yields another classic example. The tree peony (*Paeonia suffruticosa*) is a perennial woody plant. It produces robust reproductive buds which develop into leafy inflorescences with terminal flowers. *Paeonia suffruticosa* produces the same transitional forms as *Helleborus foetidus*.

Primary organ concepts

Primary vegetative organs

Wilhelm Troll's concept of primary organs (1926, 1954) is a staple of today's botany textbooks.[27] By definition, primary organs are organs with no morphological relationship to one another that carry out different functions. Troll recognises only three primary organs: the root, the stem and the leaf. He did not adopt the concept propounded by his own teacher, Karl Goebel, or Julius Sachs. Sachs and Goebel describe vegetative plants as possessing four primary organs. Sachs (1874) first differentiates between the root and the shoot as an initial division and then further divides the organs into roots, stems, leaves and trichomes. Sachs defines trichomes (hairs) as all types of hairs found on any part of the plant; his definition explicitly includes root hairs. This concept has recently been adopted by Sattler (1990, 1996), Sattler and Rutishauser (1997) and Rutishauser (2020). These authors, however, explicitly include intermediate forms of the primary organs in exceptional cases, such as in the genus *Utricularia* and the Podostemaceae family.

Hansen (1907) identified only two primary organs. These two primary organs, the root and the shoot, can be found in the embryonic plant. Hansen justified this delimitation to two primary organs by referencing Braun, who makes the assumption that there is no functional boundary between the leaf and the stem that supports it.[28] Hansen compares the initial stages of the embryonic plant with the mature plant and observes that the organs appearing later on in the plant's development (flower and fruit) are produced by a gradual transformation of the root and shoot already present in the embryo.

In this paper, I propose a two-stage differentiation scheme. The root and shoot are the product of the initial stage. By applying the basic concept for shoot diferentia-

27 Kadereit et al. (2014)
28 Braun (1854) p 24

tion to the root, we can further divide the root into the primary root axis and the root hair zone.[29] In contrast to Sachs' concept, which grants each individual hair – regardless of its position on the plant – the status of an organ, I define the entire root hair zone as a single organ. The root hair zone on the root corresponds to the foliage leaves on the shoot. (Scheme 1)

Primary reproductive organs

The morphological literature has characterised the production of sporangia as both an essential structural component of the leaf (Hansen, 1907) and as a structural element with no developmental link to the leaf.

Wilhelm Troll (1957) applies his three-part primary organ concept for the vegetative plant body to the flower as well. Troll views the rosette as possessing the basic form of a flower. A rosette and a flower both exhibit very short internodes. The rosette is a short shoot. The leaves of the rosette are all very similar, unlike stamens and carpels, which display marked differences. Troll nevertheless draws a connection between the stamens and carpels and the inner leaves of the rosette. Over the course of his investigations, he correlates the development of the carpels with the formation of the lamina in foliage leaves. He identifies an additional parallel between the structure of the bracts, which are not present in the rosette, and that of the sepals. Yet, he stops short of equating the stamens with the leaves of the rosette, instead describing only a close relationship between the stamens and the petals, positing that the petals may have originated from the stamens. Baum (1949, 1951) and Leinfellner et al. (1959) proposed the hypothesis that the carpel and the stamen developed from the same ancestral structure. This would seem to align with Troll's rosette model. Within this framework, the carpel and stamen are viewed as modified peltate leaves. This hypothetical derivation of carpels and stamens from a common peltate leaf primordium also appeared in textbooks, such as Weberling (1981) and Strasburger's Textbook of Botany (1991). Henning Kunze (1978) demonstrated that the hypothetical intermediate forms do not appear during stamen ontogenesis. Accordingly, more recent versions of the Strasburger text omit this hypothesis.[30]

Following Wilhelm Hoffmeister's discovery of the alternation of generations (1851), Sachs and Goebel realised that the production of sporangia (and subsequently the production of gametangia) were not processes associated with the basic structures of vegetative plants. The production of sporangia takes place in the basic vegetative structures; however, these structures are not themselves capable of generating the sporangia. Consequently, alongside his (four) primary vegetative organs, Sachs proposes an additional class of primary organs consisting of the sporangia and the gametangia. This classification of sporangia and gametangia as primary organs

Primary organ model		Differentiation model
I Root		Ia Root organ
	I Root	(Root hairs)
		....
....		Ib Root axis
II Stem		....
		IIa Stem
....	II Shoot	....
III Leaf		IIb Leaf

Scheme 1 Primary organ model for the vegetative plant. Three-part organisation (left) and four-part differentiation (right). Traditional primary organs (left) and two-part differentiation (right)

emphasises their uniqueness and independence from the vegetative organs.

Sachs' primary organ concept leads to the conclusion that the stamen (microsporophyll) and the carpel (macrosporophyll) result from the interaction between two organs. This view is shared by Goebel, who provides examples in ferns (e.g., *Blechnum* sp.[31] and *Botrychium* sp.) demonstrating that the transmutation of a sterile frond (trophophyll) to a fertile frond (sporophyll) is catalysed by the appearance of sporangia. The appearance of the sporangia changes the structure of the frond. Goebel applies his fern-related discoveries to the development of sporangia in spermatophytes. In Coniferopsida (gymnosperms), the anthers are part of the stamens, whereas the ovules are located on seed scales, which are modified lateral shoots. In Magnoliopsida (angiosperms), leaf and spore formation together precipitate the development of the stamen and carpel organ classes. Thus, there is a partial homologous relationship linking stamens and carpels to leaves. The term catasporophyll, which refers to the stamen, and trophosporophyll, which refers to the carpel, illustrates the respective relationships of these organs to the cataphyll (scale leaf) and trophophyll (foliage leaf) (Scheme 2). There are no regular, aesthetically compelling transitional forms between stamens and carpels. These teratological forms have the quality of intermediate forms, and they may be referred to as 'catatrophosporophylls'.

Ectopic positioning in ovules, for example the formation of ovules on petals[32], confirms Goebel's previous morphological findings (1884).

Stamen and carpel

The basic framework for describing the evolution of the organs (organogenesis) of the stamen and carpel had already been established during the second half of the 19th century. Goebel penned a summary of the state of this research in 1884. These findings are in line with current research and imagery produced with the help of cutting-edge technology such as the scanning elec-

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29 Schilperoord-Jarke (1997)
30 Schilperoord (2011)
31 Goebel (1884) pp 110-112
32 Gasser et al. (1998)

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Bud with stem
   1. Scale leaf (cataphyll)
   2. Foliage leaf (Trophophyll)


Flower with receptacle
   1.1 Sepal
   1.2 Petal
   1.3 Stamen (Katasporophyll)
   2.  Carpel (Trophosporophyll)
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Scheme 2 Link between bud and flower

tron microscope. See Greyson (1994), Leins and Erbar (2008), etc. This information is also available in textbooks. See Kadereit et al. (2014).

Carpels exhibit a pronounced basic tubular or ascidiate-plicate structure. The basic ascidiate-plicate structure of the carpel indicates the action of developmental processes similar to those present in shield-shaped (peltate) lamina, tubular (ascidiate) lamina and in the commonly observed longitudinally pleated and laterally folded (plicate) primordia of foliage leaf lamina. Normally, no stalk is formed. These descriptions are reminiscent of young foliage leave primordia in which the elongation growth required to form the petiole fails to take place. Occasionally, however, some carpels do possess stalks, for example members of the Fabaceae family. The stalk, or gynophore, exhibits intercalary growth like the petiole of a foliage leaf. In this case, no broad leaf base develops.[33] Even fully mature foliage leaves sometimes fail to produce a broad leaf base. Troll (1954) refers to such leaves as 'base-less' leaves.

The young stamen primordium initially takes on a more or less triangular shape. The basic components of the stamen are the filament and the anther.[34] Anthers consists of two thecae bound together by a connective. Each theca is composed of two fused pollen sacs. The connective is the extension of the filament. The filament may be flattened like a leaf.

Goebel (1884) determined that the traditional school of morphology habitually overlooked the fact that a stamen is composed of two different components. Findings from the molecular genetic research conducted by McConnell and Barton (1998) confirm the leaf-like character of the stamens. One notable characteristic of leaves is their adaxial-abaxial polarity. This polarity is encoded in the leaf primordia before it is even visible as a miniscule bulge under a scanning electron microscope. These two researchers investigated the appearance of PHABULOSA mutants in *Arabidopsis*.[35] The mutant plants are no longer capable of developing the ventral side of the leaf. The plant produces spike-like structures. In addition, there is

a modification in the connective of the flower's anthers which changes the orientation of the thecae. In the carpels, this loss-of-function mutation causes the ovules to develop on the outside base of the carpels.

According to morphological criteria, all flower organs are considered to be leaf organs, as they fulfil the main criterion, which is positioning. The morphological literature determines the homology of organs or parts of organs based on three criteria. The main criterion states that the organs or components must exhibit identical relative positioning with respect to other structures.[36] If it is not possible to draw a conclusion based on this criterion alone, homology can also be proven by a secondary criterion, which requires a continuous series of transitional forms linking the two organs (Fig. 5). The third criterion is special quality, or a characteristic shared by the two organs. The dorsal-ventrality of a leaf primordium qualifies as a special quality. Thanks to molecular genetics, the criterion of special quality can be applied starting at a very early stage in the organ's development.

Modules

The primary organs – and the leaf in particular – had been viewed as central structural units and afforded prominent consideration in the field since the time of Goethe. However, even higher-level organs and organ systems, such as the flower, can serve as basic structural elements in the development of compound flowers. They are made up of numerous simple flowers. The leafy shoot and the bud each has its own modular character, and these structures play a substantial role in determining the architecture of woody plants.

Development of the bud, the vegetative shoot, the inflorescence and the flower itself all require modified regulation of molecular-genetic processes. The basic plant body, composed of an axis with lateral organs, remains unchanged.

The flower, with its four floral organs, constitutes a higher-level morphological and genetic unit. The vegetative bud, with only two leafy organs, constitutes a higher-level morphological and genetic unit too. Although the genetics of bud-formation are unknown. *Arabidopsis thaliana* does not produce vegetative buds, yet bud formation in Brassicaceae does sometimes occur, for example in sea kale (*Crambe maritima*).

Metamorphosis sequences

Based on the primary organ concept, it is possible to construct a metamorphosis sequence illustrating plant development from cotyledon to carpel (Fig. 5). This sequence corresponds to the successive positioning of the organs on the stem. The cauline leaf serves as the reference organ. The sequence, with its transitional forms, illustrates the homologous relationships between the different leaf organs. Sequences such as this can be found throughout the history of morphology, employed by Johann Wolfgang Goethe, Karl Goebel and Wilhelm Troll.

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33 Leins and Erbar (2008)
34 Leins und Erbar (2008); Kadereit et al. (2014)
35 Eshed et al. (2001)

36 Eckardt (1964) p 85

Fig. 5 Overview of common examples of transitional forms frequently cited in the literature. The sequence begins bottom left with the cotyledon of a wild strawberry (*Fragaria vesca*) and ends upper right with the carpel and leafy carpel of the East Asian cherry (*Prunus serrulata*). A simple rose leaf is depicted between the stamen and the carpel. The rose leaf points to a partial homology between the carpel and the leaf base of the foliage leaf as well as to a partial homology between the stamen and the leaf base. Based on drawings by Troll: (1939, 1954) Wild strawberry, a selection of leaf forms from cotyledon to bract; (1928) Christmas rose (*Helleborus niger*) with two bracts and a tepal from the outer perianth; (1928) Waterlily (*Nymphaea* sp.) with a selection of forms ranging from petal to stamen; Troll based on Rauh (1957) East Asian cherry with a carpel (left) and a leafy carpel (right). Watercolour: Franziska Fahrni, © Peer Schilperoord (2018)

Figure five shows a juxtaposition of leaves from the wild strawberry (*Fragaria vesca*), the Christmas rose (*Helleborus niger*), the waterlily (*Nymphaea* sp.) and the East Asian cherry (*Prunus serrulata*). These leaf sequences drawn from individual species are textbook examples. There is no single species that exhibits all forms and transitional forms. Such a plant would indeed be the ultimate model organism. The sequence shown here, which contains all leaf types except for the juvenile leaves, does not in fact appear in this form anywhere in the literature. A foliage leaf has been inserted between the stamen and the carpel; naturally, this positioning does not occur in nature.[37] The foliage leaf with a broadened leaf base serves as a central element in the sequence. It stands as evidence that the sequence through to the development of the stamen can undergo a series of transformations. The contraction of the lamina and expansion of the leaf base makes it possible to deduce the presence of a relationship between the foliage leaf and the bracts, sepals and petals. The leaf base provides the structural foundation for the stamen. There are no consistently structured or established transitional forms linking the stamen and the carpel. The lamina of the foliage leaf serves as the structural foundation of the carpel, as illustrated in the example of *Prunus serrulata*. Differentiation of the foliage leaf into the leaf base and the lamina serves as the basis for the development of the highly differentiated stamens and carpels. Sequential illustrations of the leaf organs from cotyledon to carpel do pose one disadvantage: They allow for the impression that the transformations illustrated take place step by step with the exception of the aforementioned discontinuity in the transition from stamen to carpel.

Figure 6 shows the model of an annual plant. An abrupt transitional zone can be seen between the final cauline leaf and the flower: Here, something new is afoot, a new chapter is about to begin. This occurrence is not depicted in the sequence in Figure 5.

Instead of searching for the cause in the primary organs, it is reasonable to localise this culmination in the higher-level organ systems, in the modules of the bud, the leafy shoots and the flower. The comparison between the bud and the flower illustrates the diametric opposition between the scale leaves and the foliage leaves in the

37 Schilperoord-Jarke (1997)

bud as well as between the sepals, petals and stamens and the carpels in the flower (Fig. 7). The transition between the vegetative bud and the flower is non-linear; it is based on simultaneity. The overarching *gestalt* of the bud must be compared with that of the flower.

Both comparisons – the leaf sequence (Fig. 5) and the comparison between the bud types – yield the same conclusion: Each confirms the validity of the other. The difference lies in the fact that the leaf-based comparison proposes the leaf base as the structural origin of the sepals, petals and stamens whereas in the bud-based comparison, the scale leaf serves as the origin. Considering that the first angiosperms were indeed woody plants, the bud-based comparison presents the more historically compelling approach. It takes the historical context into account.

The first sequential model (Fig. 5) can be presented without consideration of the historical context and corresponds with observations (Fig. 6). The second model in Figure 7 encourages comparison between the vegetative bud and the flower. Production of the sporangia catalyses a transformation in the entire organism. Figure 8 depicts a schematic drawing of the lifecycle of a plant with shoots and buds.

Genetic models

Goethe established the leaf-like quality of the flower organs in 1790. Conclusive molecular-genetic confirmation of his observation came at the very latest with the discovery of the SEPALLATA subfamily of the MADS-box gene. SEPALLATA mutants produce flowers in which the flower organs are replaced by leaf-like organs.[38] Conversely, by forcing expression of the SEP genes in the shoot, it was possible to induce replacement of the cauline leaves with flower organs. Regine Claßen-Bockhoff (2016) proposes a different view, in which stamens represent an entirely separate class of organs. She justifies this approach by citing the unique type of primordium exhibited in stamens, which is not comparable to the foliage leaf primordia that develop from the shoot meristem. However, this thesis does not account for the dorsal-ventrality that the stamens share with all types of leaves and the myriad transitional forms occurring between petals and stamens.

Based on the hypothesis that the vegetative bud serves as the basis for the flower, the question becomes whether or not there are any correlations in the genetic framework controlling the formation buds and flowers, respectively. Foster describes an antagonism in the development of scale leaves and foliage leaves. The development of the lamina results in the loss of the scale-like character of the leaf base. A mature lamina and a mature scale must be considered mutually exclusive. The plant abhors intermediary forms; yet, they can still occur (Fig. 3). Zotz et al. (2011) summarised the results of molecular-genetic research on the topic of heteroblasty. Heteroblasty refers to the diversity in leaf forms

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38 Goto et al. (2001); Zahn et al. (2005)

Fig. 6 Model of an annual flowering plant with all leaves, from cotyledon to ovary. The shoot was based on garlic mustard (*Alliaria petiolata*), the flower was based on the medium-flowered winter-cress (*Barbarea intermedia*) and the root hair zone was based on embryonic wheat (*Triticum aestivum*). Watercolour: Franziska Fahrni, © Peer Schilperoord (2015)

occurring in a single plant. As is commonly the case, the authors rely on a narrow view of heteroblasty. For whatever reason, they choose to omit scale development in their definition. Stevens (2001): "Heteroblastic: having the adult parts of the plant (especially the leaves) distinctly different in form from the juvenile parts, differences sometimes to be seen in the leaves produced during the course of a single season (scale leaves are not normally taken into consideration)."

Major leaps have been made in decoding the genetic basis underlying the development of compound leaves. This research mainly focuses on the development of cauline leaves with simple lamina. Some examples include the research of Ichihashi et al. (2011) on *Arabidopsis* and Toriba et al. (2019) on rice. These studies point to the role of the BLADE-ON-PETIOLE gene family, which is central to the development of the petiole and lamina in *Arabidopsis* and the development of the leaf sheath and

Researchpaper

Fig. 7 Model of a woody flowering plant .The young shoot was based on Rhododendron, the flower was based on the marsh-marigold (Caltha palustris) with additional sepals in the calyx. The colour of the petals was adapted based on the colour of the bud scales. Watercolour: Franziska Fahrni, © Peer Schilperoord (2015)

lamina in rice. It is unknown whether this gene class is involved in bud formation and differentiation between scale leaves and foliage leaves.

Long and Barton (2000) focus on the close link between axillary meristems and the leaves that produce meristems in their axils. An axillary meristem can be a floral meristem (FM), an inflorescence meristem (IM) or a shoot apical meristem (SAM). *Arabidopsis* forms lateral shoot meristems in the axils of the leaves forming the basal rosette. Inflorescence meristems form in the axils of the cauline leaves. In Arabidopsis, floral meristems do not tend to be accompanied by a leaf. In exceptional cases, floral meristems can sometimes be found in the axils of bracts in mutant forms (Grbic and Bleecker, 1996). *Arabidopsis* always develops bract primordia; however, further development is suppressed, so that bracts never form (Long and Barton, 2000). Hempel et al. (1998) view the SAM - IM - FM sequence as the transition from a vegetative to a reproductive phase. The genetic

basis for the sequence is unknown. *Arabidopsis*, like all herbaceous plants, exhibits sylleptic growth in its lateral shoots, meaning that no buds are produced as part of an intermediate growth phase.[39] I propose the addition of a fourth type of meristem, the bud meristem (BM) to the three meristem types listed above. This would yield the sequence: BM - SAM - IM - FM, which begins with the vegetative bud and ends with the flower bud.

The review authored by Wellmer et al. (2014) "Flower Development: Open Questions and Future Directions" does not address the vegetative bud in any way. On the one hand, the authors point to the fact that many mutations that cause developmental defects in the flower organs can also affect foliage leaf morphology, which indicates a shared architecture between the leaf and flower organs: "supporting the idea of the common basic developmental plan of the lateral organs, on top of which floral organ identity is laid. [...] The leaf 'factors' could physically interact with ABC factors, or with the few floral specific factors directly downstream of them [...] and thus generate new functional domains." The authors do not explore the fact that the scale leaf and foliage leaf represent two fundamentally different types of leaves; their work is based on a very general understanding of the leaf. Later on, in the description of the perianth, the authors do emphasize that: "the outer perianth of the angiosperm flower is morphologically distinct from leaves suggesting that their identity as such must be specified by some means. Despite some initial skepticism, it is becoming apparent that AP1 orthologs have a relatively conserved function with respect to floral organ identity in eudicots: loss of AP1 ortholog function results in conversion of sepals into bracts- or leaf-like organs and a loss or partial loss of flower meristem identity." Furthermore, "one idea is [...] that the default state of organs produced by a floral meristem is a sepal-like organ, whose identity can be modified by the additional expression of B and C class genes." This statement is almost diametrically opposed to the previously cited assertion by Baum (1949, 1951) and Leinfellner (1959) that the peltate leaf serves as the common architecture for the stamen and carpel.

What is required is a genetic model describing the development of vegetative buds and the differentiation between the primordia of scale leaves and foliage leaves.

Conclusion

The annual plant appears simpler than the woody plant, hence its selection by Goethe as a model organism for illustrating the structure of angiosperms. Yet, the model of the annual plant is missing a leaf organ – the scale leaf – and an organ system – the bud. Goehte's model is based on a type of growth that evolved from a woody ancestor. A model based on a woody plant would be better suited for analysing the morphological commonalities observed at both the level of the individual organ as well as the level of the organ system.

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39 Wellmer et al., (2014)

Fig. 8 Schematic diagram of a plant lifecycle with shoots and buds. Clockwise starting at the bottom: 1 Embryonic plant; 2 Shoot with a sprouting vegetative bud; 3 Resting vegetative bud prior to sprouting; 4 Cross-section of a flower with sepals, petals, stamens and carpels; 5 Germinating pollen grain; 6 Longitudinal section of the upper part of an ovary with germinating pollen grains and ovules, fertilisation. Based on an SEM image (Bowman, 1994); 7 Fruit with seeds; 8 Seeds. Drawings: Evelyn Lengler, ©Peer Schilperoord (2018)

The scale leaf and the foliage leaf exhibit a polar developmental dynamic. They are complementary; the scale leaf is not an arrested form of the foliage leaf. Troll's characterisation of the scale leaf as a juvenile leaf and his derivation of the juvenile leaf from the foliage leaf based on the principle of variable proportions does not account for the developmental dynamics described by Foster. The position and arrangement of the scale leaves and their special quality indicate that the scale leaf represents an independent form. Scale leaves and cauline leaves are two basic leaf forms.

The traditional primary organ concept dividing a plant into the leaf, shoot and root is too static. This paper proposes replacing these three categories with a two-stage differentiation scheme. In this differentiation model, the root and shoot are considered primary organs that can be further classified into lower-level primary organs, with the shoot and leaf on one side and the root axis and root hair zone on the other. This differentiation model differs from Sachs' model, which also identifies four primary organs. Sachs' fourth organ is the trichome rather than the root hair zone. The proposed differentiation model defines the shoot as a structural unit. Depending on the plant's current developmental phase, whether vegetative perennial, vegetative herbaceous or reproductive, the development of the shoot is subject to different internal conditions. These internal conditions affect the available options for the plant's structural development. Woody shoots and buds are subject to the most rigid architectural limitations, herbaceous vegetative shoots have increased flexibility and flowers exhibit the greatest degree of structural freedom.

The traditional primary organ concept requires the production of sporangia. In this vegetative concept, the sporangia are already accounted for. Sachs' expanded concept defines the sporangia and gametangia as primary reproductive organs. The stamen and carpel are produced by the combined action of the primary vegetative organs and the developmental process that yields the sporangia. Stamens and carpels are partially homologous with the leaf.

The plant exhibits a modular organisational structure. This modular structure applies not only to the traditional primary organs but also to the higher-level organs

such as the vegetative bud, the woody shoot and the flower. Organ systems are capable of undergoing metamorphosis, as illustrated by the well-known example of the compound flower of the Asteraceae, which employs the organisational unit of the flower as a structural element.

Research has yet to produce a molecular-genetic model describing the differentiation between the scale leaf and foliage leaf or illustrating the transitions between the bud phase and the leafy shoot phase through to the phase of the inflorescence and the flower.

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