



# The shoot concept of the flower: Still up to date?☆



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## ABSTRACT

The shoot concept of the flower suggests that flowers correspond to vegetative short-shoots except the fact that their lateral appendages are floral and not vegetative leaves. However, in view of the different properties of vegetative and flower meristems, this concept should be questioned. Differential meristem activity resulting in tubes, hypanthia and inferior ovaries, continuous meristem expansion providing space for stamen fascicles and additional structures and the process of (repeated) fractionation using a given space completely, are characteristics of flower meristems hardly explainable with the shoot concept. Linking instead flower development with recent findings in molecular biology and computational modeling widens the view to the fundamental relation between growth and form. Given that the same general principles characterize plant growth at all life stages, the loss of apical growth appears to play the major role in changing geometry, space availability and genetic regulation in flower meristems. The flower, thus, turns out to be the sporangia bearing tip of a shoot.

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## 1. Introduction

von Goethe (1790) was one of the first scientists interpreting floral organs as modified leaves. Since his time, the definition of flowers as ‘short shoots bearing reproductive organs’ (Wagenitz, 2003) has been widely accepted. It also underlies the concepts of ‘euanthium’ (anthostrobilus sensu Arber and Parkin, 1907), ‘strobilus’ (e.g., Zimmermann, 1930) and ‘neotenous strobilus’ (Takhtajan, 1973). Though the peculiarities of flowers are always mentioned, be it determinate growth, dense packing of organs, formation of reproductive structures or high structural and functional plasticity (Weberling, 1992; Endress, 1994; Ronse de Craene, 2010), terms like ‘sporophylls’, ‘floral axis’, ‘floral leaves’, ‘shoot apical meristem (SAM)’ or ‘short-shoot’ indicate that, subliminally, the flower is compared with the vegetative shoot.

The shoot concept of the flower suggests that flowers correspond to vegetative shoots except the fact that their lateral appendages are floral and not vegetative leaves. Comparing a flower with a vegetative shoot is mainly based on the position of flowers at the end of shoots, the evident phyllotactic patterns seen in most flowers (see e.g., Ronse de Craene, 2010) as well as the presence of elongated receptacles (e.g., *Magnolia*) and transitional

forms between vegetative leaves and floral organs (e.g., *Helleborus*, *Nymphaea*; Troll, 1927). Triple mutants in *Arabidopsis* form leafy buds (Coen and Meyerowitz, 1991) and fossils of *Archaeofructus* (Sun et al., 2002) indicate that the angiosperm flower may indeed have evolved from a shoot with reproductive organs.

These arguments being highly convincing corroborate the shoot concept of the flower and prevent alternative thinking. Moreover, pseudanthia theories proceeding from a multiaxial nature of the flower also refer to the shoot concept (e.g., Delpino, 1890, 1892; von Wettstein, 1901–1908; Neumayer, 1924; Lam, 1950; Nozeran, 1955; Melville, 1960; Meeuse, 1972). As a consequence, no competing flower theory exists allowing a scientific dispute on the nature of flowers. In the present paper, some observations on flower meristem development are summarized questioning the shoot concept of the flower and aiming to stimulate discussion on a revised concept of the angiosperm flower.

## 2. Material and methods

Based on literature and experience in floral morphology, the shoot concept of the flower is critically questioned. To illustrate specific developmental stages, scanning electron microscopic (SEM) images are included from *Ammobium alatum* R. Br. (Asteraceae), *Anemone hupehensis* (Lemoine) Lemoine (Ranunculaceae), *Garcia nutans* Vahl (Euphorbiaceae), *Hypericum perforatum* L. (Hypericaceae), *Orlaya grandiflora* (L.) Hoffm. (Apiaceae), *Pavonia multiflora* A. St.-Hil. (Malvaceae), *Passiflora foetida* L. var. *hispida*

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Killip (Passifloraceae), *Pycnosorus globosus* F.L. Bauer ex Benth. (Asteraceae) and *Ricinus communis* L. (Euphorbiaceae).

Plant material was taken from the Botanical Garden at Mainz University, dissected, critically point-dried (BAL-TEC CPD 030), sputtered with gold (BAL-TEC SCD 005) and analyzed under an ESEM XL-30, Philips scanning electron microscope. All steps were conducted according to the manufacturer's protocols.

The following terms and definitions (based on Claßen-Bockhoff and Bull-Hereñu, 2013) are used and explained in the text. For better understanding, they are summarized here (see also Table 1).

- Reproductive meristem: all meristems producing flowers solitarily or in inflorescences or floral units; they are determinate, and differ morphologically and in their genetic regulation from vegetative meristems.
- Inflorescence meristem: reproductive meristems with apical growth; they produce primordia by segregation and form all basic types of inflorescences.
- Flower and floral unit meristem: reproductive meristems lacking apical growth; they produce primordia by fractionation; if they fractionate once, floral organs are formed (flower meristem), if they fractionate repeatedly, submeristems are formed finally merging into flowers (floral unit meristems).

### 3. Results and discussion

If flowers are short-shoots with floral leaves, they should develop like shoots. However, comparing vegetative and flower meristems, we observe considerable and fundamental differences (Table 1).

#### 3.1. Vegetative meristems

Vegetative meristems are indeterminate. They permanently produce leaves by the process of segregation. This means that a lateral part is separated from the apical meristem ('segregated'), subsequently developing into a leaf, while simultaneously, the apex continues growth. Due to this apical growth, the sequence of segregation is always acropetalous. Leaf primordia originate from the apical meristem in specific phyllotactic patterns. Axillary meristems persist in each leaf axil possibly developing into lateral shoots. However, vegetative branching usually appears late, i.e., lateral buds only appear several nodes below the shoot apical meristem (Claßen-Bockhoff and Bull-Hereñu, 2013).

From the histological point of view, vegetative meristems show a characteristic zonation (Kwiatkowska, 2004). A central zone is flanked by peripheral meristem from which the leaf primordia originate. Molecular studies in the model organism *Arabidopsis thaliana* (L.) Heynh. show that the continuous growth of the shoot apical meristem is maintained and regulated by the antagonistic activities of WUSCHEL (WUS) and CLAVATA3 (CLV3) gene products (Bäurle and Laux, 2003). Cells in the central zone are a bit larger than the peripheral cells, which show a higher mitotic activity than the cells in the central zone (Sharma and Fletcher, 2002). The sequence of the formation of leaf primordia and their position follow Hofmeister's rule (Hofmeister, 1868), predicting that the next primordium appears in the largest gap between the two next older primordia. Most likely, phyllotaxis is based on physical meristem conditions and hormonal control (Smith et al., 2006). According to Reinhardt et al. (2003), local auxin accumulation plays a dominant role.

#### 3.2. Flower meristems

Flower meristems differ from vegetative meristems in almost all aspects (Table 1). They are larger than the vegetative meristems of the same individual and usually start with a naked phase.

This means that a flower meristem enlarges to a considerable size before floral organ primordia are formed (Figs. 2A, C and 3A, B). This meristem enlargement concurs with the loss of apical growth, the process of fractionation and ongoing intercalary activity.

##### 3.2.1. Loss of apical growth

Molecular studies in *A. thaliana* give a first insight into the transition from the vegetative to the flowering state. According to the present view (Turck et al., 2008; Zeevaart, 2008), light stimulates the synthesis of FLOWERING LOCUS T (FT) in the leaf which is then upwards transported to the shoot apical meristem. Here, it interacts with FLOWERING LOCUS D (FD) and induces the expression of SOC1 (suppressor of overexpression of CO). This causes the meristem to change from vegetative to reproductive development. Reproductive meristems usually enlarge thus providing a morphological character for their identification (Claßen-Bockhoff and Bull-Hereñu, 2013). The antagonism between FT and TERMINAL FLOWER 1 (TFL1) determines the further meristem fate (Turck et al., 2008; Zeevaart, 2008). As long as FT/TFL1 suppresses the expression of the floral meristem identity gene, APETALA 1 (AP1), the meristem remains an inflorescence meristem continuously segregating reproductive primordia. When FT/FD assisted by LEAFY (LFY) suppresses TFL activity, the meristem merges into a flower meristem. The WUS/CLV3 antagonistic loop collapses, the central zone disappears and the meristem gets completely determinate.

Histologically, flower meristems have a homogenous mantle core zonation (Grégoire, 1938; Kwiatkowska, 2008). A central zone is lacking and the whole meristem surface is covered by mitotically active cells.

##### 3.2.2. Process of fractionation

Due to meristem determinism, apical growth and segregation of leaf primordia end. No new nodes and internodes can be produced any more. Only the already existing meristem can be used for further development. The process subdividing the meristem into primordia is called fractionation (Claßen-Bockhoff and Bull-Hereñu, 2013). Fractionation is restricted to determinate meristems lacking apical growth (Table 1). It is defined as the complete subdivision of an already existing 'naked' meristem. Such naked meristems either produce flowers or floral units (e.g., heads in Asteraceae, umbels in Apiaceae). In flower meristems, fractionation usually proceeds only once resulting in the formation of floral organ primordia. In floral unit meristems, the process repeats and results in submeristems (Claßen-Bockhoff and Bull-Hereñu, 2013). This way, flowers (Figs. 2 M and 3 A–E), simple (Fig. 3I–K) and compound heads (Fig. 3L–O) can originate from the same type of naked meristem by the same process of fractionation, differing in the number of fractionation steps.

Due to the lack of apical growth, space is limited. This changes the conditions at the meristem and the process of primordia initiation. Computational models (Runions et al., 2014) confirm the molecular view that phyllotactic patterns arise due to a self-organizing process responding to local auxin maxima. Auxin accumulation depends on the dimension of the meristem and the speed of its flow through the tissue. In the vegetative condition, leaves are formed at the permanently active SAM by segregation. They are separated from each other by internodes which originate from the peripheral and rib meristems below the central zone of the SAM. Spatial constraints thus play a minor role. Instead, flower and floral unit meristems are space limited. Fractionation follows the changed spatial conditions and determines the position of newly generated primordia.

Hypothesising that developing flower meristems maximize the use of space (Prusinkiewicz and Barbier de Reuille, 2010), fractionation may result in diverse patterns. Though centripetal organ formation is common, centrifugal (Rudall, 2010), divergent (Api-

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