Abstract
The shoot apical meristem generates stem, leaves, and lateral shoot meristems during the entire shoot ontogeny. Vegetative leaves are generated by the meristem in the vegetative developmental phase, while in the reproductive phase either bracts subtending lateral flower primordia (or paraclades), or perianth and strictly reproductive organs are formed. Meristem growth is fully characterized by the principal growth rates, directions, volumetric, and areal growth rates. Growth modelling or sequential in vivo methods of meristem observation complemented by growth quantification allow the above growth variables to be estimated. Indirectly, growth is assessed by cell division rates and other cell cycle parameters. Temporal and spatial changes of growth and geometry take place at the meristem during the transition from the vegetative to the reproductive phase. During the vegetative phase, meristem growth is generally indeterminate. In the reproductive phase it is almost always determinate, but the extent of determinacy depends on the inflorescence architecture. In the vegetative phase the central meristem zone is the slowest growing region. The transition from the vegetative to the reproductive phase is accompanied by an increase in mitotic activity in this zone. The more determinate is the meristem growth, the stronger is this mitotic activation. However, regardless of the extent of the activation, in angiosperms the tunica/corpus structure of the meristem is preserved and therefore the mitotic activity of germ line cells remains relatively low. In the case of the thoroughly studied model angiosperm plant Arabidopsis thaliana, it is important to recognize that the flower primordium develops in the axil of a rudimentary bract. Another important feature of growth of the inflorescence shoot apical meristem is the heterogeneity of the peripheral zone. Finally, the role of mechanical factors in growth and functioning of the meristem needs further investigation.

Key words: Flower primordium, geometry, growth, inflorescence, shoot apical meristem, transition from vegetative to reproductive phase.

Introduction
The shoot apical meristem (SAM) is a non-differentiated portion of the shoot apex, located above the youngest leaf primordium. The SAM generates stem, leaves, and also lateral shoot meristems during the entire shoot ontogeny. The course of morphogenesis at the SAM depends on the developmental phase, which particularly affects the identity of primordia produced at its periphery. In the vegetative phase, the SAM produces vegetative leaves, while in the reproductive phase, the SAM produces either bracts subtending lateral flower primordia (or paraclades), or perianth and reproductive organs (stamens and carpels). Only in a few angiosperms, like a number of members of the Nymphaeaceae family, flowers completely replace some leaves, thus appearing without subtending bracts (Cutter, 1957). The switch from the vegetative to the reproductive phase is related to temporal and spatial changes of growth at the SAM and to corresponding changes in its geometry.

The notion of growth used in the title of this review can have two general meanings. In kinematics it means a displacement velocity of material points or elemental growth rates (Green et al., 1970; Gandar, 1983). The term growth, however, is also used in ecology in reference to an increase in biomass or the size of a population. In this review the former meaning is adopted. The term growth dynamics refers to temporal changes resulting from growth, or to temporal changes in growth of a living...
structure. Such changes take place at the SAM during the developmental transition from the vegetative to the reproductive phase (VR transition).

In the present paper, the available methods that can be used for studying shoot apical meristem growth are reviewed first. Then, what is known on meristem growth during the vegetative phase is briefly presented. The discussion on changes in SAM growth in the course of the VR transition and on the growth of the inflorescence SAM will follow. Finally, there will be a focus on the mechanical factors shown to affect reproductive morphogenesis.

How to characterize meristem growth?

Variables directly quantifying growth

Growth of cells in apical meristems is symplastic, i.e. all the contacts between cells are preserved since no displacement or sliding takes place at middle lamellas by which neighbouring cell walls are joined (Priestly, 1930; Erickson, 1986). This means that growing plant cells observe the continuum condition of solid body mechanics (Hejnowicz and Romberger, 1984; Kwiatkowska, 2004a). Another fundamental feature of plant cell growth is its anisotropy (Baskin, 2005), i.e. the directional variation in growth rates at a point. Because of these two features, in order completely to characterize meristem growth it is feasible to use the tools of continuum mechanics and compute variables characterizing plastic strain, i.e. the irreversible deformation (Goodall and Green, 1986). These are strain rates, principal directions of strain rates, and strain rate anisotropy. In the case of the meristem, the strain rates are growth rates. In particular, the aim is to estimate the relative elemental rates of growth (RERG) in length, area (areal growth rates), or in volume (Richards and Kavanagh, 1943; Silk, 1984). Fundamental for anisotropic growth characterization are the principal growth rates and their directions (Hejnowicz and Romberger, 1984). Principal directions of growth rates (for convenience, from now on these will be referred to as principal directions of growth) are those particular directions in which growth rates attain their extreme values. These are maximal, minimal, and the saddle type growth rate directions. The latter is the direction of maximal growth in a plane perpendicular to the maximal growth direction, and at the same time the direction of minimal growth in a plane perpendicular to the minimal growth direction. As a rule, the three principal directions are mutually orthogonal.

Since leaf primordia are cyclically produced at the SAM periphery the SAM growth and geometry are changing in plastochron cycles (a plastochron is a time interval between the initiation of two consecutive primordia; Erickson, 1976). A given meristem shape can be achieved by various growth patterns (Green et al., 1970). Therefore, ideally, meristem growth is quantified with the aid of a non-invasive method of sequential in vivo meristem observation with high spatial and temporal resolutions, performed for a number of plastochrons (Dumais and Kwiatkowska, 2002). Suitable methods available at present are in vivo confocal laser scanning microscopy (CLSM) and the sequential replica method.

The in vivo observation in the CLSM has been applied to Arabidopsis thaliana (L.) Heynh. inflorescence SAM (Grandjean et al., 2004; Reddy et al., 2004). This method requires access to the meristem, which is normally overtopped by lateral organ primordia (in this case young flower buds). The obstacle has been overcome in two different ways. Grandjean et al. (2004) used plants initially grown on medium supplemented with naphthylphthalamic acid (NPA), an inhibitor of Polar Auxin Transport (PAT), that were moved to NPA-free medium before observation. Arabidopsis plants grown on NPA in the reproductive phase produce apices virtually devoid of flower primordia, mimicking pin-like shoots of a pin-formed1 (pin1) mutant in which PAT is also impaired (Okada et al., 1991). Such plants were used for observation with the CLSM during the period when, after the transfer to NPA-free medium, the SAM have started to produce flower primordia that for a certain time remained small enough to make the meristem accessible. In the second in vivo CLSM method, overtopping older flower primordia were removed from the plants used for the SAM observations (Reddy et al., 2004). When using these in vivo CLSM methods one needs to keep in mind that meristems recovering from the NPA treatment may not represent normally growing meristems. Primordia removal, in turn, may affect mitotic activity of some meristem portions, as indicated by experiments with vegetative SAM of a sunflower Helianthus annuus L. (Davis et al., 1979). One more factor that may influence morphogenesis is tissue scanning with the laser beam. The fact that it causes damage to the meristem at longer exposure time prevents obtaining in vivo images at higher resolution. The in vivo CLSM, however, has a unique advantage in that the data on SAM growth can be combined with data on in vivo gene expression patterns in the same meristem if adequate reporter gene constructs are used (Grandjean et al., 2004; Heisler et al., 2005; Reddy and Meyerowitz, 2005).

The sequential replica method (Williams and Green, 1988) is based on the preparation of dental polymer moulds of an individual apex surface at various time intervals. They are later used to prepare epoxy resin casts. The casts are sputter-coated and examined in the scanning electron microscopy (SEM), while the apex remains intact. This method has been used successfully for a number of species (reviewed by Green, 1999), including Arabidopsis (Kwiatkowska, 2004b, 2006). The major limitation of this method is that it is only the apex surface that can be examined. Another weak point is a possibility
that mechanical stress or other kinds of stresses resulting from dental polymer application may influence morphogenesis. In addition, the polymer application may affect the superficial walls of the meristem cells, as indicated by desiccation in some meristems, especially in exposed apices of *pin1* *Arabidopsis* (Kwiatkowska, 2004b). Nevertheless, despite major differences in the empirical protocols of *in vivo* CLSM and sequential replicas, the results obtained with the two methods are similar (Carraro et al., 2006). Ideally, the data obtained from the two types of experiments should be combined since their weak points are exclusive.

**Methods of indirect growth assessment**

Indirect ways to assess growth are based on rates of cell divisions and other cell cycle parameters, like cell cycle duration. Since cell sizes in meristems are roughly uniform, it can be assumed that these parameters are a representation of growth rates (Lyndon and Cunningham, 1986; Lyndon, 1994). Various techniques of quantitative analysis of cell divisions, also in the shoot apex, have been recently discussed in details by Fiorani and Beemster (2006). Parameters employed for this analysis are: cell division rate (mean for a population of cells), Mitotic Index (MI – percentage of cells undergoing mitosis at the moment of preparation), cumulative Mitotic Index (cumulative MI – percentage of cells that divided within a given time frame), and cell cycle duration (also mean for a cell population). The cell division rate parallels the rate of growth in volume (Lyndon and Cunningham, 1986; Lyndon, 1994), and higher values of MI or cumulative MI are related to faster growth. At the same time the cell cycle duration is inversely proportional to the volumetric growth rate. These relationships hold even if cell size in various meristem regions varies to a limited extent (Lyndon, 1994).

A number of methods exist that are suitable for the collection of data necessary to estimate the above-mentioned cell proliferation parameters. More recently developed methods enable an examination of large material, making use of automated microtechnique and advanced image analysis protocols (Sundblad et al., 1998). Various techniques of labelling of dividing cells (Clowes, 1959; Breuil-Broyer et al., 2004) have been used as well as cell cycle-blocking methods (Clowes, 1978; Marc and Palmer, 1984). The insight into the duration of cell cycle stages can also be obtained with the aid of flow cytometry (Fiorani and Beemster, 2006). Some conclusions on the relative intensity of mitotic activity of cells in different regions of the apex can be drawn with the aid of cytohistological techniques applied to fixed plant material, as has been done in numerous early investigations of shoot meristem function (reviewed by Cutter, 1965; Gifford and Corson, 1971; Buvat, 1989). The limitation of the use of the cell cycle parameters for growth assessment is that they only provide information on volumetric growth rates. It should also be noted that values of variables like MI are usually obtained as averages from a large number of meristems. Moreover, borderlines between various meristem regions for which cell cycle parameters are quantified are not clear-cut, which may cause additional inaccuracy. A more detailed quantitative analysis of cell divisions, for example, accounting for temporal and spatial variation of mitotic activity in individual cells, can be performed only on the basis of data obtained from *in vivo* sequential observation techniques.

The parameters described above that were used for cell division quantification do not provide information on principal growth directions. Nevertheless, the distribution of growth, also in the SAM interior, can be reconstructed on the basis of an analysis of cell wall patterns (the method available again thanks to the symplastic mode of plant cell growth) as long as the growth field can be regarded as steady in time as in the root apex (Silk et al., 1989) or some special cases of SAMs. For example, estimation of growth anisotropy by means of the comparison of shapes of cell packets visible in preparations of fixed meristem surface allowed Nakielksi (1987) to compute the principal growth directions for the SAM of spruce *Picea abies* (L.) Karst. seedling. For this computation the growth tensor model was used. Using the same model the distribution of growth within the SAM of barley *Hordeum vulgare* L. has been assessed (Hejnowicz et al., 1988). Though not directly referring to the principal directions of growth, in a series of investigations Lyndon and collaborators (reviewed in Lyndon, 1994, 1998) recognized changes in maximal growth direction on the basis of new cell wall orientation in the interior of pea *Pisum sativum* L. vegetative SAM and both vegetative and floral meristems of *Silene coeli-rosa* L. Gordon. Such methods allowed them to discover the changes in growth accompanying the primordium formation.

**What is the growth pattern at vegetative shoot apical meristem?**

**Cytohistological zonation and mitotic activity of the SAM**

Cytohistological zonation of the vegetative SAM recognized by Foster (1939, 1943) for the SAM of gymnosperms, among others points to differences in rates of cell divisions between various meristem zones (Fig. 1A). This zonation, based on the interpretation of the median longitudinal SAM section, focuses on the central mother cells which, according to Foster, were giving rise to most of the internal portion of the subapical shoot region. The apical-initial zone is distal to the central mother cells. Proximal to the central mother cells there is the transition zone, analogous to the shell zone of lateral vegetative
shoot apical meristems. Still more proximally, the rib meristem (which sometimes used to be referred to as the central meristem) is located, while the peripheral zone surrounds the central mother cells and the rib meristem. It is worth noting that this elaborate zonation has been recognized in large SAMs, in particular those of cycads, while the zones may be not so apparent in more common smaller meristems (compare apices in Fig. 2A–D).

Numerous later studies showed similar zonation of the angiosperm vegetative SAM (reviewed by Clowes, 1961; Romberger et al., 1993). These observations were based on cytohistological analyses, MI assessment, and estimation of cell cycle duration. It is generally accepted that the vegetative angiosperm SAM can be differentiated into three zones differing in growth and mitotic activity among others (Fig. 1B). The central zone of low mitotic activity (i.e. slowly growing) occupies the distal SAM portion. The rib meristem, located basipetally with respect to the central zone, is characterized by higher mitotic activity, similar to the peripheral zone, which surrounds both the central and rib meristem zones.

Fig. 1. Systems of cytohistological zonation of SAM in the vegetative phase shown in outlines of median longitudinal sections of an apex. (A) Foster’s zonation of the SAM in cycads and Gingko. (B) Angiosperm SAM. (C) Functional domains in the SAM of Arabidopsis defined by gene expression patterns. CLV3 domain corresponds to putative stem cells; WUS domain is the organizing centre, while UFO domain covers both the peripheral zone and rib meristem. Apical-initial zone (ai), zone of central-mother-cells (cmc), peripheral zone (pz), central zone (cz), rib meristem (rm), and leaf primordium (lp) are outlined. The thin shell-like zone between central mother cells and rib meristem in the Foster’s zonation (A) is the transition zone (tz).

The zones distinguished within the vegetative meristem participate to various extents in fulfilment of the two fundamental functions of the SAM. The central zone contributes mainly to the self-perpetuation of the meristem, i.e. the maintenance of meristem size and general shape. Noteworthy in Arabidopsis SAM in the vegetative phase, it is distinguished also by the expression pattern of genes regulating the SAM self-perpetuation. These are CLAVATA1, CLAVATA3 (CLV1, 3), and WUSCHEL (WUS) acting in a negative feedback loop involved in maintenance of the proper SAM size (Barton, 1998; Traas and Doonan, 2001; Veit, 2006). On the basis of the gene function, the CLV3 expression domain, overlaying the zone of apical initials mentioned above, is often referred to as the stem cells domain (Fig. 1C), while the WUS domain, corresponding most likely to the central mother cells, is called the organizing centre (Brand et al., 2001; Fletcher, 2002; Baurle and Laux, 2005). The peripheral zone is the site of the formation of leaf primordia, which is the second SAM function. Together with the rib meristem, it is distinguished by expression of UNUSUAL FLOWER ORGANS (UFO) (Brand et al., 2001).

French school concepts and biological role of the central zone

The differences in cell division rates and growth between the central zone and the other two SAM zones in some species are profound (Clowes, 1961; Cutter, 1965), especially in trees (Romberger et al., 1993). However, although cell divisions in the central zone are infrequent, the division rate is high enough to result in a basipetal ‘flow’ of cells from the meristem summit, to the region where organogenesis (differentiation) takes place, i.e. leaves and stem tissues are formed. The contribution of the central zone to the formation of leaves has been questioned by researchers of the so-called French school (reviewed by Buvat, 1955, 1989; Cutter, 1965; Gifford and Corson, 1971). They postulated that the SAM is functionally divided into ‘l’anneau initial’ (the initial or
initiating ring) corresponding to the peripheral zone, and ‘méristème d’attente’ (the waiting or resting meristem), i.e. the central zone. During the vegetative phase of development the organogenetic activity was attributed exclusively to ‘l’anneau initial’, but ‘méristème d’attente’ was to play the special role during reproductive organogenesis (see below). Although the non-quiescence of the central zone and its contribution to vegetative morphogenesis has been proved by studies using methods based on the incorporation of radio-labelled DNA precursors and the French school concept of SAM zone function was thoroughly criticized (Wardlaw, 1957; Gifford and Tepper, 1962; Gifford and Corson, 1971), the significance of numerous cytohistological studies of the SAM in various species published by the French school has to be acknowledged (Wardlaw, 1957; Buvat, 1989). The terminology referring to the SAM zones introduced by the French school turned out to be troublesome since the term ‘méristème d’attente’ itself assigned the complete absence of mitotic activity and the notion of ‘not completely waiting “méristème d’attente”’ could not be used. Nevertheless, the generalization of the French school concepts is true and the concepts adopted by Anglo-Saxon researchers are in fact a milder version of the French school concepts.

A biological role attributed to the slow growth and infrequent cell divisions at the central zone is the lower probability of defects in genetic material in cells, which will later contribute to the formation of gametes, i.e. the germ line (Ruth et al., 1985; Klekowski, 1988). This is true especially for angiosperm SAMs with tunica/corpus organization, where the germ line is the L2 (the second tunica layer). In such SAMs not only the cell growth rates in the L2 are low but also the accompanying cell divisions are limited to anticlinal divisions, i.e. periclinal divisions are excluded so that the layered structure is maintained (reviewed in Kwiatkowska, 2004a). The superficial, first tunica layer (L1), in turn, protects the germ line from the external environment.

Formation of leaf primordia

A special region of the peripheral zone is the site of leaf primordium formation. The first event at this site is a local increase in cell division and growth rates. However, the temporal and spatial relationships between the increase in division rate and the primordium initiation are not straightforward. It has been shown on the basis of division distribution in sections of fixed material that growth and cell divisions in other meristem regions contribute to increased cell numbers in the primordium (Lyndon, 1994). Moreover, the region of increased growth on the meristem surface can be larger than the region actually contributing to the primordium formation such as, for example, in Anagallis arvensis L. (Kwiatkowska and Dumais, 2003).

The early protrusion of a leaf primordium is accompanied by periclinal divisions in cells located beneath the L1, while L1 cells divide only anticlinally. The exceptions are some monocots where periclinal divisions occur also in L1 (Clowes, 1957, 1961). Therefore, another event regarded as characteristic for the primordium formation site is the occurrence of periclinal divisions in L2 and the corpus. The significance of periclinal divisions has been questioned. Foard (1971) demonstrated that, in wheat Triticum vulgare Vill., the divisions are not necessary for the early stages of leaf primordium formation. Also a number of studies led by Lyndon and collaborators showed that there is no clear evidence that periclinal divisions are causative for primordium initiation (Lyndon, 1994, 1998). It has thus been suggested that they are rather permissive in that they allow growth in a new direction. It may also be that they are necessary for cells to remain isodiametric in the meristem, though why this is a requirement is not clear.

Growth of the SAM surface

SAM surface growth in the vegetative phase has been examined with the aid of the sequential replica method for Anagallis shoots exhibiting decussate and spiral Fibonacci phyllotaxis. The decussate vegetative apex of Anagallis has two axes of activity corresponding to arms of a cross described by the pairs of consecutively formed primordia (Green et al., 1991). The growth (cell divisions and extension) is faster along this axis where new leaf primordia arise, in particular at meristem periphery. At the centre growth is very slow. Growth variables (principal growth rates and directions) were quantified only for apices exhibiting spiral Fibonacci phyllotaxis (Kwiatkowska and Dumais, 2003). The regions of different growth at the SAM are the slowly and nearly isotropically growing SAM centre (probably the surface of the central zone), and SAM periphery where growth rates are not uniform, but in general higher than in the centre. Within the SAM periphery there are wedge-like sectors of position and growth pattern dependent on the position and age of adjacent leaf primordia. The sectors are growing faster where a new primordium is initiated, as well as at contact with the older leaf primordia. The latter are regions where the SAM periphery is being rebuilt. There the growth is strongly anisotropic with the meridional direction of maximal growth rate. The primordium initiation site is, in turn, characterized by nearly isotropic growth. The SAM surface region of the slowest growth is that where an adaxial leaf primordium boundary (the region referred to as a crease by Green et al., 1991), a future leaf axil, is formed (Kwiatkowska and Dumais, 2003). There, not only the areal growth rates are the lowest but also growth is strongly anisotropic, with the latitudinal direction of maximal growth rate, i.e. along the primordium boundary, and meridional direction of minimal growth rate. The rate
in the latter direction is usually nearly zero; sometimes even the contraction can be detected. This does not necessarily mean that the cell area is decreasing, since the areal growth rate is the sum of the minimal and maximal rates. Rather the shape of the boundary cells is changing, as if the cells were stretched in one direction. Because at the primordium boundary there is virtually no growth in the meridional direction, starting from this stage of primordium development there is no displacement of its boundaries with respect to cells (cells do not ‘pass’ the boundary).

How do the meristem growth and shape change when the reproductive phase begins?

In the course of the VR transition the remarkable morphological changes are brought about at the shoot apex by the interplay between meristem-derived and non-meristem factors (recently reviewed by Chuck and Hake, 2005). Physiology of the VR transition has been thoroughly reviewed by Bernier and collaborators (Bernier, 1988; Bernier et al., 1993; Bernier and Pérelleux, 2005). Apart from changes in growth rates and mitotic activity of the SAM, the transition is also characterized by reorganization of symplasmic communication between the meristem cells (Ormenese et al., 2000, 2002). In Sinapis alba L. temporarily the frequency of plasmodesmata dramatically increases in the whole SAM (Ormenese et al., 2000). Also a pattern of symplasmic fields of the SAM is different in vegetative and reproductive phases: a central symplasmic field in the vegetative phase is smaller than in the reproductive phase and is of a different shape (Ormenese et al., 2002).

It is logical to consider the transition events with the preceding vegetative phase and the established reproductive phase, since these events depend on the reproductive shoot architecture. In the course of the VR transition the vegetative SAM is transformed either to a flower meristem giving rise to a terminal flower, or to an inflorescence SAM. In principle, growth of the SAM in the vegetative phase is fully indeterminate as exemplified by SAMs in trees like Sequoiadendron giganteum (Lindl.) Buchh. The flower meristem growth is, in turn, determinate (for a review on flower meristem determinacy see Sablowski, 2007), with only a few exceptions such as the unique proliferated flowers of Nymphaea prolifera Wiersema (Grob et al., 2006). The inflorescence SAM can retain indeterminate growth for a period of time the length of which depends on the inflorescence architecture, i.e. its growth is to various extents determinate. The present review does not deal with growth of the SAM leading directly to formation of a terminal flower. The growth of the inflorescence SAM and the early stages of formation of the lateral flower primordia, excluding the development of strictly generative organs, are discussed in more detail.

**Classical studies on mitotic activity and SAM zonation**

Early during the VR transition, the mitotic activity of the meristem (cell division rate) usually increases. This has been demonstrated in plants with terminal flowers or various inflorescence types also showing different photoperiodic preferences, such as in the extensively studied model species of an obligatory long day plant Sinapis alba L. (Bodson, 1975), a short day plant Chenopodium album L. (Gifford and Tepper, 1961, 1962), or the day neutral sunflower (Steeves et al., 1969; Marc and Palmer, 1982, 1984). Elegant studies of Sinapis reviewed by Bernier (1988) showed that early during the VR transition the cycle of meristem cells becomes synchronized. This phenomenon leads to the occurrence of two successive waves of mitoses (mitotic peaks) in the meristem (Gonthier et al., 1987; Bernier, 1988; Lyndon, 1998).

The division rates and cell cycle duration are affected to various extents in different meristem zones (Gifford and Corson, 1971; Bernier, 1988; Buvat, 1989). The most dramatic changes take place in the central zone where mitotic activation is most marked (reviewed by Cutter, 1965). This observation led the investigators from the French school to the conclusion that the ‘méristème d’attente’ of the vegetative meristem (central zone of the SAM in general) plays a major role in reproductive development, i.e. it is the central zone exclusively, which gives rise to all the reproductive shoot structures. Such conclusion, however, is an exaggeration of the role of ‘méristème d’attente’. For example, in a number of not related species with different types of inflorescence and photoperiodic preferences, the early sign of the VR transition in the SAM is a considerable increase in a number of cells below the central zone, suggesting that portions of SAM other than the central zone contribute to reproductive structure formation (Wetmore et al., 1959). Nevertheless, is has to be recognized that the concept of ‘méristème d’attente’ is a good and accurate caricature of the important role played by the central zone in shoot ontogeny.

The fact that at the onset of flowering the central zone, previously often mitotically almost silent, becomes active, usually leads to the disappearance of the significant difference in mitotic activity between central and peripheral zones (Fig. 3). Also the sizes of cells in different zones are usually changing. In the vegetative phase cells of the central zone are often somewhat larger than cells of the peripheral zone, while in the reproductive phase the central zone cells are no longer larger but the size of rib meristem cells is increased. These enlarged cells, which give rise to the central core, are still active mitotically as a consequence of symplasmic growth. The changes in mitotic activity and cell size are often so profound that the new SAM zonation is defined. It should be noted, however, that the tunica/corpus SAM organization is nevertheless
A strong activation of the central zone (Steeves et al., 1987), and for species in which the vegetative SAM changes into floral meristem like Silene coeli-rosa (Nougare`de et al., 1991) forming a cyme, an inflorescence with sympodial type of branching, or Datura stramonium L. with a terminal flower (Corson, 1969). The increase in mitotic activity of the central zone accompanying the VR transition has been reported also for monocots, like banana (Fahn et al., 1963), and ‘primitive dicots’ like Drimys winteri var. chilensis (Tucker, 1959).

In an obligatory long day plant Anagallis arvensis (Ballard, 1969; Brulfert et al., 1985) the inflorescence is of a frondose raceme type exhibiting virtually indeterminate axial growth. It closely resembles a vegetative shoot, the difference being mainly in replacement of vegetative axillary shoots by flowers (Green et al., 1991). During both the vegetative and reproductive phases, Anagallis SAM exhibits cytohistological zonation into central, peripheral, and rib meristem zones, originally described by Vaughan (1955) as central initial cells, flank meristem zone, and the file meristem, respectively. The central zone is more apparent in median sections of the vegetative meristem, which has been interpreted according to the French school concept by Brulfert (1962). Periclinal divisions accompanying primordium initiation are in L2 in case of leaf-like bract primordia, but in the corpus in the case of flowers (Vaughan, 1955). Studies of SAM surface growth with the aid of the sequential replica method (Green et al., 1991) show that in the reproductive SAM of Anagallis, two primordia, instead of a single one, are formed successively at the meristem along a meridian (one above the other) as visible in the top view of the SAM. The first is the leaf primordium (leaf-like bract), while the second is the flower primordium. In inflorescence SAM exhibiting decussate phyllotaxis, the centre of the SAM surface still grows slower than the periphery, similar to the SAM in the vegetative phase, but the growth rate was not quantified. The directional growth in the peripheral region of the meristem is stronger (higher anisotropy) than in the SAM in vegetative phase. Although the flower primordium originates from only a narrow row of cells located along the leaf primordium boundary, the area of rapid periphery extension includes a flower primordium, its adaxial boundary (referred to as a crease by Green et al., 1991), and also the recovering (rebuilding) portion of the meristem.

Quantification of surface growth variables (principal rates and principal directions) performed for reproductive Anagallis apices exhibiting spiral Fibonacci phyllotaxis (D Kwiatkowska and A-L Routier-Kierzkowska, unpublished data) shows that the difference in growth rates at the meristem centre and periphery is less apparent than at the SAM in the vegetative phase. The most characteristic pattern of the SAM growth is at the stage when the flower...
primordium is formed in the axil of two plastochrons old leaf primordium. The region where the flower primordium is formed, as well as the region of the future boundary between this primordium and the SAM, grow with a high areal rate and strong anisotropy. The direction of maximal growth is meridional. This observation points to two important differences between the formation of flower and leaf primordia. Firstly, the flower primordium bulges in the lateral direction (Fig. 4A), while the leaf primordium bulges upward (Fig. 4B). Also the growth at the site of the formation of the adaxial boundary of the flower primordium is relatively fast and with a meridional direction of maximal growth rate, unlike the growth at leaf (or leaf-like bract) primordium boundary.

Classical concepts applied to the SAM of Arabidopsis: a model plant for molecular biology

Cytohistological zonation of vegetative Arabidopsis SAM, recognized by Vaughan (1955) on the basis of cell stainability, resembles that of Anagallis in that it exhibits an apparent central zone. For the SAM of Anagallis in the vegetative phase it has been shown that such distinguished central zone is also characterized by lower growth rates, which may also be true for Arabidopsis. The assessment of cell division rates by tritiated thymidine incorporation allowed Miksche and Brown (1965) to distinguish a distally located group of slowly dividing cells in Arabidopsis plants grown in vitro. When the reproductive phase begins, the cytohistological zonation becomes less distinct (Vaughan, 1955; Miksche and Brown, 1965).

As a model plant for contemporary genetic research Arabidopsis has also been the subject of more recent studies on meristem mitotic activity, as a necessary complementation to mutant phenotype characterization. Breuil-Broyer et al. (2004) show median longitudinal sections of the Arabidopsis inflorescence SAM labelled with the 5-bromo-2'-deoxyuridine (BrdU) incorporation/immunodetection method in which the central zone can be recognized as a region of lower labelling than the surrounding SAM periphery. Laufs et al. (1998) compared cellular parameters of the vegetative and inflorescence SAMs, in particular estimating the MI. They used a 3D representation of SAM and its interior reconstructed on the basis of optical CLSM sections of fixed material. In the study of SAM zonation within the L1 and L2, the border between the slower dividing distal part of a putative central zone, and a surrounding peripheral zone was estimated as a circle crossing the SAM dome meridian (which is the radius in a top view) at a certain quotient. In the case of inflorescence SAM the differences in MI of the two zones were statistically significant for some quotient values. Interestingly, such a method of zone assessment did not allow the authors to recognize significantly different zones in the vegetative Arabidopsis SAM. This could be because of either the variability of the examined meristems (a sample of a large number of meristems has to be used for the MI assessment) or the small number of cells comprising putative zones in the vegetative SAM. For the inflorescence SAM statistically significant differences in the MI value have also been found between the angular meristem zones. These zones, defined with respect to flower primordia of different age, presumably correspond to the wedge-like sectors in the Anagallis SAM described above.

Jacqmard et al. (2003) also assessed the MI for both vegetative and inflorescence Arabidopsis SAM, with the aim of the labelling method (tritiated thymidine incorporation) and cytohistological staining of longitudinal sections. The differences in stainability within the vegetative SAM allowed them to distinguish the central, peripheral, and rib meristem zones, while in the inflorescence meristem another zonation pattern was apparent, namely the mitotically active meristematic mantle and a less active central pith core. The values of labelling indices changed as expected at the transition to flowering. However, the zonation of the vegetative meristem has not been confirmed by statistically significant differences in labelling indices or MI of the zones although some expected differences were observed.

Comparison of the above-described results with the observations of Reddy et al. (2004) are yet another example on how much depends on the method employed. In this study, the estimation of cumulative MI from in vivo CLSM did not allow the authors to recognize the central and peripheral zones in the L1 and L2 of the inflorescence SAM. The two zones, however, differed in cell cycle duration. The in vivo analysis also suggests that location of slowly dividing central zone with respect to cells is not stable. This is in agreement with observations from sequential replicas showing that the position of the central

Fig. 4. Two types of bulging of the SAM surface leading to formation of a primordium. Apex outlines before (left) and after (right) the bulging are shown. Arrows point to the bulging direction, which is either lateral (A), like in the inflorescence SAM of Arabidopsis during the putative rudimentary bract formation, or upward (B), as in the case of vegetative Anagallis SAM during the formation of leaf primordium.
region of slow growth is not stable with respect to cells (Kwiatkowska, 2004b). Such a ‘wandering’ central zone may be detected only with the aid of in vivo observations of high temporal resolution. The recognition of the central zone, based on the estimation of MI and cumulative MI, averages various locations of such a ‘wandering’ zone into a larger and less homogenous region.

Summarizing, the detection of a mitotically less active central zone depends on the method used, but the existence of the central zone of lowered mitotic activity in the inflorescence SAM of Arabidopsis is supported by empirical data. Location of this zone is to some extent related to the CLV3 expression domain. Some discrepancy of the results discussed above may be caused by significant differences in SAM growth between individual plants (Grandjean et al., 2004). Moreover, the heterogeneity in cell cycle duration within the Arabidopsis inflorescence SAM has been observed (Grandjean et al., 2004). In addition, in vivo study allowed Reddy and collaborators (2004) to detect peaks in mitotic activity of the inflorescence SAM cells, which were not related to any particular plastochron stage. An interesting interpretation is that they may occur due to WUS activity participating in regulation of the SAM self-perpetuation (Reddy et al., 2004).

**Geometry of the SAM**

It is convenient to recognize two types of changes in the SAM geometry (Fig. 5): a change in the meristem height not accompanied by a change in its shape, and a change in shape, which may be accompanied by a height change. For the SAM in the vegetative phase, geometry changes of the first type are typical. In particular, changes accompanying leaf primordium formation can be interpreted as fluctuations in meristem height only, in plastochron cycles. Such interpretation is supported by observations of the apex of a pin-like shoot in pini Arabidopsis. In this apex, where the geometry analysis suggests that, exclusively, the earliest stages of the formation of lateral organ primordia take place, the apex maintains roughly steady height and shape (Kwiatkowska, 2004b).

Both types of SAM geometry changes may accompany the VR transition. These changes take place at or just before the beginning of flower initiation (Lyndon and Battey, 1985; Bernier, 1988, 1997). Their type and extent depend on the species, in particular, on the habitus of the flowering plant (whether the terminal flower or inflorescence is formed, and what is the inflorescence type). In dicots, the SAM usually enlarges, especially in plants with a capitulum type of inflorescence, such as sunflower (Steves et al., 1969). Since the meristem is often increasing more in height than width, the change in SAM geometry is usually described as meristem doming (Bernier, 1988). It can be related to the vacuolation and elongation of cells originating from the rib meristem of the vegetative SAM. The increase in the SAM height without the shape change is exemplified by Ranunculus repens var. glabratu DC (Meichenheimer, 1979), height increase accompanied by a change in SAM shape, by Chenopodium rubrum L. (Albrechtová et al., 2004).

Profuse changes in meristem shape and the meristem enlargement have also been reported for monocots, such as the grass Pennisetum americanum (L.) K. Schum. (Metcalfe et al., 1975). However, it should be noted that the meristem enlargement has not been observed in some plants. For example, in Impatiens the SAM size actually decreases at the onset of floral morphogenesis (Bernier, 1988).

An almost universal feature of the VR transition is also precocious initiation of axillary meristem producing lateral inflorescence or flower (Bernier, 1988, 1997). In Sinapis after the transition, meristems of axillary inflorescence shoots appear one or two plastochrons earlier than in the vegetative phase (in the axil of seven instead of eight or nine plastochron old leaf; Bernier, 1997). In Anagallis the change is still more striking, since in the reproductive phase, axillary meristems, which in this phase are flower meristems, arise when the subtending leaf (leaf-like bract) primordium is still in direct contact with the SAM. Similar to Sinapis, also in Anagallis, flower meristems become apparent in the axils of leaf primordia one or two plastochrons younger than leaf primordia subtending vegetative axillary meristems (Vaughan, 1955).

**Phyllotactic pattern**

Presumably due to the typical increase in meristem size, shape, and growth, as well as the switch in identity of the lateral organs produced, changes at the VR transition are also in some parameters characterizing phyllotaxis (Lyndon and Battey, 1985), i.e. the pattern of lateral organ arrangement. In particular, the rate of primordium initiation increases and the plastochron duration decreases, also resulting in a decrease in the plastochron ratio (the ratio of distances from the meristem centre to the centres of two successively initiated primordia, older over the younger; Richards, 1948). Thus the phyllotactic pattern becomes

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**Fig. 5.** Various types of differences in SAM geometry shown in outlines of median longitudinal sections of an apex. The meristem (A) differs from (B) in its height but not shape. Meristems in (C) and (D) differ from (A) in their shapes.
more complex, i.e. higher numbers of contact parastichies become apparent, as in *Ranunculus repens* var. *glabratu* DC (Meicenheimer, 1979) or *Clethra barbinervis* Sieb. et Zucc (Hara, 1977). This may be explained by the fact that lateral organ primordia become smaller with respect to the SAM, either due to SAM enlargement before the lateral organ identity has changed, or afterwards also due to the decrease of absolute primordium size accompanying the change in identity (Bernier, 1988, 1997). Such changes in relative sizes of primordia and the SAM are known to accompany quantitative or even qualitative changes in the phyllotactic pattern (Meicenheimer and Zagórška-Marek, 1989; Meicenheimer, 1998; Kwiatkowska and Florek-Marwitz, 1999), and explain a phenotype of certain mutants (Golz and Hudson, 2002). It has therefore been suggested that it is the change in relative size of primordia that is important for VR transition rather than the absolute change in the SAM size (Lyndon and Battey, 1985).

In other species, such as *Anagallis*, the relationships between changes in phyllotaxis and the VR transition are not straightforward (Kwiatkowska, 1995). *Anagallis* phyllotaxis in the vegetative phase is most often decussate and rather stable, while in the reproductive phase it is variable and changes during the individual shoot ontogeny. This is despite the virtually identical size and shape of leaves and leaf-like bracts, as well as the similarities between shoot development in both the phases described above. The ontogenetic changes in phyllotactic pattern are not coinciding with the VR transition. Rather the probability of the pattern change increases at the onset of flowering.

**Formation of lateral flower primordia at the Arabidopsis inflorescence SAM**

It may seem that the typical raceme inflorescence of Brassicaceae lacks bracts. It could thus be expected that in reproductive phase the *Arabidopsis* SAM produces flower primordia in place of leaves, i.e. the lateral organs produced by the SAM are flowers. Accordingly the notion of ‘the inflorescence meristem’ generating ‘flower meristems’ is often used in the literature. This, however, is not precise, since the flower primordium in *Arabidopsis* is in fact formed in an axil of a rudimentary bract (Long and Barton, 2000; Hepworth *et al.*, 2006; Kwiatkowska, 2006).

Studies of the early stages of flower development in *Arabidopsis* with the aid of *in vivo* observation methods (*in vivo* CLSM and sequential replicas) generally show a significant increase in the mitotic activity (estimated as an increase in cell number per 24 h, cumulative MI, or areal growth rates) at the primordium formation site (Grandjean *et al.*, 2004; Kwiatkowska, 2004b, 2006; Reddy *et al.*, 2004). However, during these early stages of flower development periclinal divisions occur in corpus, while L1 and L2 cells divide only anticlinally (Vaughan, 1955). Therefore, although the whole flower meristem is mitotically active, the two-layered tunica organization is preserved.

Smyth *et al.* (1990) divided flower development in *Arabidopsis* into 15 stages (later stages distinguished by these authors comprise the development of a siliqule), which are used as a framework for developmental studies. Consecutive initial stages are: arising of flower buttress (stage 1), flower primordium formation (stage 2), and arising of sepal primordia (stage 3). Studies of early flower morphogenesis with the *in vivo* techniques (Reddy *et al.*, 2004; Kwiatkowska, 2006; Fig. 6) allowed the authors to detect the primordium formation earlier than in this classical study, and to distinguish substages within stage 1 of Smyth *et al.* (1990). The first sign of primordium formation is the initial bulging of the SAM periphery surface (P1–2 in Fig. 6), taking place in the lateral direction (referred to as P1 stage by Reddy *et al.*, 2004; Fig. 4A). It probably leads to the formation of

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**Fig. 6.** Schematic representation of growth pattern in early stages of lateral flower development in *Arabidopsis*. Scanning electromicrograph of the inflorescence SAM in the top view is shown in the centre. Primordia are labelled as P1–6 with a number increasing with the primordium age. Growth pattern on the apex surface is shown for the outlined regions as crosses with the arms pointing to the principal growth directions. Arm lengths are proportional to the corresponding principal growth rates. Areas shadowed in red point to the regions where the axes of putative rudimentary bracts (boundaries between the bracts and the SAM) are formed, green areas point to boundaries between the SAM and flower primordia proper. For each primordium the outline of the corresponding median longitudinal apex section is shown. P1 and P2 are in the stage of lateral bulging leading to the shallow crease formation (P3). In P3 and P4 the upward bulging at the bottom of the shallow crease takes place. P6 is in the fast growing bulge stage.
a rudimentary bract. Growth at this earliest stage is fast and strongly anisotropic, with a meridional direction of maximal growth (Kwiatkowska, 2006). Such a growth pattern is accompanied by cell divisions in planes perpendicular to the maximal extension and thus leads to the formation of longitudinal cell files along the meridional direction, which are referred to as column-shaped lineages by Reddy et al. (2004). This specific growth pattern is of short duration and ends by the formation of a shallow crease (Kwiatkowska, 2006; P3 in Fig. 6), also called the first groove visible at the P2 stage of Reddy et al. (2004). The shallow crease is a putative axil of the rudimentary bract (Kwiatkowska, 2006). Soon after the bract formation at the bottom of the shallow crease the next bulging, now in an upward direction (Fig. 4B; P4 in Fig. 6), takes place, leading to the formation of a flower primordium proper (the P3 stage of Reddy et al., 2004). Starting from this stage, when the flower primordium proper is already well delineated from the SAM, the cell cycle duration in the flower primordium cells decreases (Reddy et al., 2004) and the areal growth rates of the surface of the flower primordium proper are very fast without preference for any growth direction, i.e. no strong anisotropy (P6 in Fig. 6; Kwiatkowska, 2006). This is the stage 2 of Smyth et al. (1990).

Interesting and instructive is a comparison of these quantitative data on the SAM surface expansion with dynamics of gene expression patterns (Long and Barton, 2000; Heisler et al., 2005). The rudimentary bract in wild-type Arabidopsis flower primordium development has been recognized by Long and Barton (2000) on the basis of changing expression patterns of SHOOTMERISTEM-LESS (STM) and AINTEGUMENTA (ANT). This rudimentary structure is visualized for a short time also with the aid of sequential replicas (Kwiatkowska, 2006) complementing the genetic approach.

LEAFY (LFY) and ANT were used by Grandjean et al. (2004) as markers of the future primordium cells. Based on changes in their expression pattern the early flower formation has been divided into two stages. In the course of the first stage a rapid recruitment of cells to those already committed for the primordium formation takes place, the number of these cells at the end of recruitment stage being several tens. During the next stage the number of primordium cells also increases, but only due to proliferation of cells already committed for the primordium. The first stage lasts for a short time and may possibly correspond to the upward bulging at the shallow crease described above. If this were the case, the LFY cells would first correspond to the rudimentary bract (excluding its axil, i.e. the shallow crease) and afterwards LFY expression domain would expand to include cells of the flower primordium proper (Kwiatkowska, 2006). Such interpretation could also explain the discrepancy in the number of the so-called founder cells estimated by the sector boundary analysis (Bossinger and Smyth, 1996) and by the in vivo LFY examination (Grandjean et al., 2004). The former study led the authors to proposition that a flower in Arabidopsis ultimately develops from a block of four cells on the flanks of SAM surface. This was further supported by clonal analysis based on in vivo CLSM showing that flower progenitor cells comprise one to two rows of cells in a radial progenitor (Reddy et al., 2004). However, the number of LFY cells described above at the end of recruitment stage is much higher. The difference between the two estimates may be because only a subset of LFY cells, i.e. the flower primordium proper cells, is actually used for formation of the flower (Grandjean et al., 2004; Kwiatkowska, 2006). Another explanation could be that the activation of LFY takes place later than the cell commitment. This however, would not explain the observed recruitment stage.

It is important to note that during the early morphogenesis of flowering in Arabidopsis, two types of primordium boundaries are formed. The first is between the SAM and the rudimentary bract, originally specified at the SAM periphery. This first boundary is formed during the short period of fast and strongly anisotropic growth, with a meridional direction of maximal growth rate (Kwiatkowska, 2006). This is unlike the growth pattern described for adaxial boundary formation at the leaf primordium in Anagallis (Kwiatkowska and Dumais, 2003), but surprisingly resembles that of the flower primordium boundary in this species. The second boundary in Arabidopsis reproductive development is the boundary between the SAM and flower primordium proper. It has been detected by a BrdU incorporation procedure as a narrow band region of non-dividing cells (Breuil-Broyer et al., 2004). This domain overlaps with the CUP-SHAPED COTYLEDON2 (CUC2) expression (Breuil-Broyer et al., 2004) and its formation is known to be regulated by the CUCs and interacting genes as well as miRNA (Laufs et al., 2004; Aida and Tasaka, 2006). Cells of this second boundary expand along a ‘lateral axis’ (latitudinal direction) and divide less frequently (Reddy et al., 2004). They grow slowly and with strong anisotropy, similar to the described above axil of Anagallis leaf primordium (Kwiatkowska and Dumais, 2003; Kwiatkowska, 2006).

Mechanical factors related to reproductive development

Evidence exists that chemical and biophysical systems most likely complement each other in a mechanism of primordium formation at the SAM (reviewed by Green, 1999; Lyndon, 1994; Kwiatkowska, 2004a). Putative auxin efflux carriers PIN, proteins of the plasma membrane, are hypothesized to provide a link between the chemical and mechanical factors controlling morphogenesis (Carraro et al., 2006). Processes involved in primordium formation
control traits like growth rate, division plane, surface microstructure, and surface extensibility. The first two processes are probably themselves not causal for the primordium formation but the control of cell wall microstructure and extensibility, which are biomechanical traits, may be necessary to delimit incipient primordium (Lyndon, 1994), as shown by elegant experiments with expansins (Pien et al., 2001).

There are experiments demonstrating the role of mechanical factors (osmotic pressure, cell wall structure, and elasticity) in the VR transition. Albrechtová et al. (2004) showed that, in Chenopodium rubrum, local changes in cell wall properties on the SAM surface take place in the course of the transition, during which SAM geometry changes were also recorded. They postulate that the geometry changes are due to water uptake, which may be connected with a change in osmotic pressure, and modifications of cell wall elasticity. This is in support of the importance of tension differences in morphogenesis.

Elegant experiments performed by Palmer and Marc (1982) show that wounding of the receptacle in a young sunflower capitulum, up to the stage when only the first row of disc floret primordia has been initiated, results in the formation of involucral bracts and ray floret primordia in place of disc florets. The reason may be that wounding creates regions of localized stress in the receptacle at the wound edges (like at crack edges; Wainwright et al., 1976). In turn, compressive forces applied to the young sunflower capitulum cause changes in floret primordium arrangement and in the identity of some primordia (Hernández and Green, 1993).

Mechanical factors have also been incorporated in models. A finite element model of the SAM shows that lateral bulging of the meristem surface leading to the primordium formation results in a gradient of shear stresses with high shear at the next, i.e. future primordium site (Selker et al., 1992). The occurrence of compressive stresses in the superficial cell layer of the meristem is one of the assumptions in the buckling model of phyllotaxis, applied in particular to the sunflower capitulum, and can explain some mutant flower phenotypes in Antirrhinum majus L. (Green et al., 1996; Green, 1999; Dumais and Steele, 2000). The occurrence of mechanical stresses in the meristem cell walls may be due to differential growth. If the tendency for periclinal growth is stronger in the superficial meristem layer than in its interior, the compression can be expected in the superficial layer while there is tension in the interior SAM walls (Schüepp, 1926). These are tissue stresses of the growth stress type (Romberger et al., 1993). Tissue stresses can also be of a turgor type (Hejnowicz et al., 2000). They originate from differences in the elastic properties of the cell walls. If turgor of all the meristem cells is the same, but the surface cell walls are thicker (with an additional layer of cuticle) than other walls, the surface walls are under tension while the interior walls are under compression. Still other factor affecting stress distribution in superficial meristem cell walls is SAM geometry. The real distribution of stresses in the walls of SAM superficial cells, however, remains disputable. A thorough discussion of empirical data on stresses in SAM surface has been presented by Dumais and Steele (2000).

**General conclusions**

During the vegetative developmental phase, growth of the SAM is, in principle, indeterminate. In the reproductive phase it is almost always eventually determinate, and the extent of determinacy depends on the inflorescence architecture. In the vegetative phase, the most distal portion of the SAM (the central zone) is the slowest growing SAM region. The VR transition (the transition from the vegetative to the reproductive phase) is accompanied by the increase of mitotic activity of the central zone. Generally, the more determinate is the SAM growth in the reproductive phase, the stronger the mitotic activation of the central zone takes place during the transition. Although it has been shown that in the vegetative phase the distal portion of the SAM is not completely quiescent, and in the reproductive phase the distal portion is not the only SAM region contributing to formation of a flower or an inflorescence, the French school concept of ‘l’anneau initial’ and ‘méristème d’attente’ is a good and accurate caricature of growth distribution in the SAM.

Regardless of the extent of the mitotic activation of the angiosperm SAM in the course of the VR transition, the tunica/corpus SAM structure is preserved. In particular, periclinal cell divisions are restricted in the L2, i.e. the germ line, which is covered by L1 protecting it from the environment. Therefore, the mitotic activity of germ line cells remains low, and it can be estimated that, for example, a number of cell generations in the germ line of a 50-year-old tree would be as little as 100 (Romberger et al., 1993). Only during the later stages of flower development do the cells of this line become active, which presumably enables elimination of genetically defective cells (Klekowski, 1988). The L1 cells, in turn, divide periclinally, producing outer tissues of various functions during the development of strictly generative organs (ovules, anthers).

In the case of a thoroughly investigated model species Arabidopsis it is important to recognize that various types of investigation showed the existence of a rudimentary bract in the development of the Arabidopsis flower. Therefore, the often used terminology of the inflorescence meristem generating the flower meristems is a simplification, since the flower primordium in Arabidopsis develops in the axil of a rudimentary bract. Another important feature of the inflorescence SAM growth is the heterogeneity of the peripheral zone. In particular, the behaviour...
of the peripheral zone cells is related to their location with respect to primordia of various ages surrounding the SAM.

Finally, the role of mechanical factors in the growth and functioning of the SAM in the reproductive phase have not been sufficiently explored. This is despite the existence of numerous premises suggesting the significance of mechanical factors.

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References


