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review

# Plant architecture

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**Plant architecture is species specific, indicating that it is under strict genetic control. Although it is also influenced by environmental conditions such as light, temperature, humidity and nutrient status, here we wish to focus only on the endogenous regulatory principles that control plant architecture. We summarise recent progress in the understanding of the basic patterning mechanisms involved in the regulation of leaf arrangement, the genetic regulation of meristem determinacy, i.e. the decision to stop or continue growth, and the control of branching during vegetative and generative development. Finally, we discuss the basis of leaf architecture and the role of cell division and cell growth in morphogenesis.**

## Introduction

Plant architecture is defined as the three-dimensional organisation of the plant body. For the parts of the plant that are above ground, this includes the branching pattern, as well as the size, shape and position of leaves and flower organs. Plant architecture has long been the only criterion for systematic and taxonomic classification, and, even today, it is the best means of identifying a plant species. But it is also of major agronomic importance, strongly influencing the suitability of a plant for cultivation, its yield and the efficiency with which it can be harvested. Notably, one of the great successes of the Green Revolution, which led to major increases in productivity, was based on the modification of plant architecture: the selection of wheat varieties with shorter and sturdier stems resulted in plants that can carry more yield while still resisting damage from wind and rain (Peng *et al.*, 1999). Thus, a better understanding of the molecular-genetic regulation of plant form will help us to modify specifically agronomically relevant traits. During the past decade, studies on the model plants *Antirrhinum majus* and *Arabidopsis thaliana*, and on crop plants such as maize and tomato, have furthered our understanding of the genetic basis of plant architecture.

## Phyllotaxis

During vegetative development, plants continuously form new leaves that are arranged in regular patterns (phyllotaxis), with defined divergence angles between successive leaves (Steeves and Sussex, 1989). The most prevalent phyllotactic patterns are distichous (Figure 1A), decussate (Figure 1B) and spiral (Figure 1C). Leaves are initiated at the shoot tip in the shoot apical meristem (SAM; M in Figure 1D). In order to achieve defined divergence angles, the SAM must integrate spatial information from pre-existing leaf primordia, and it has been proposed that such information could be mediated by the release of inhibitors of leaf formation (reviewed in Steeves and Sussex, 1989). Depending on its range and stability, such an inhibitor could create a field that constrains the formation of new leaves to positions with defined minimal distances (Figure 1E). Here, we focus on recent studies that illustrate a crucial role for auxins, related plant hormones whose most important representative is indole-3-acetic acid (IAA). A broader discussion of models and classical work in phyllotaxis research has been given in several previous reviews (Steeves and Sussex, 1989; Lyndon, 1998; Reinhardt and Kuhlemeier, 2001).

Phyllotaxis is thought to be a multigenic trait because, although many genetic screens have identified genes with a regulatory function in leaf formation and positioning, they have mostly failed to yield mutants with specific phyllotactic phenotypes (i.e. 'homeotic' transformations of one phyllotactic pattern into another). Nevertheless, several mutants that exhibit defects in organ initiation, separation, spacing or arrangement have been described in *Arabidopsis* (reviewed in Reinhardt and Kuhlemeier, 2001). Among these, *pin-formed1* (*pin1*), *pinoid* (*pid*) and *monopteros* (*mp*) all carry mutations in genes that play a role in the transport of, or the response to, auxin (Gälweiler *et al.*, 1998; Hardtke and Berleth, 1998; Christensen *et al.*, 2000; Benjamins *et al.*, 2001). Inhibition of auxin transport, either by a mutation in the auxin transport protein PIN1 or by chemical

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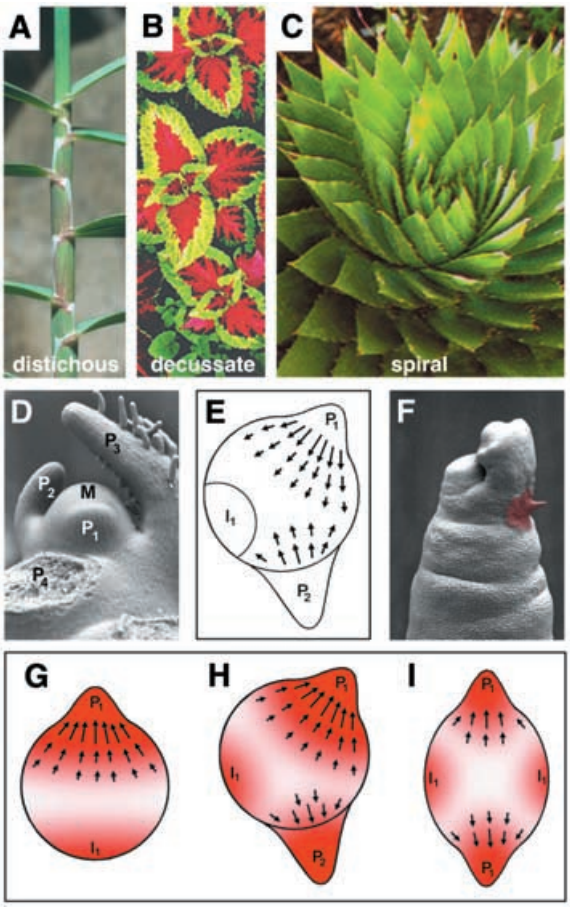


**Fig. 1.** Regulation of phyllotaxis. (**A**) Distichous phyllotaxis in *Trisetum distichophyllum*. Leaves diverge by 180° and alternate in two opposite rows. (**B**) Decussate phyllotaxis in *Solenostemon scutellarioides*. Pairs of opposite leaves are formed. Successive leaf pairs diverge by 90°. (**C**) Spiral phyllotaxis in *Aloe polyphylla*. Successive leaves are initiated with a divergence angle of 137°. Note that apparent spirals (parastichies; see Steeves and Sussex, 1989) are due to dense packing rather than the sequence of leaf formation. (**D**) The shoot apex of a tomato plant with the youngest leaf primordia in spiral succession ($P_1$, $P_2$, $P_3$ and the base of $P_4$) and the shoot apical meristem (M). (**E**) Model of phyllotactic regulation by an inhibitor (arrows) emanating from young primordia ($P_1$ and $P_2$). $P_2$ is surrounded by a weaker inhibitory field than $P_1$; thus $I_1$, is initiated closer to $P_2$. (**F**) Local administration of IAA (red paste) to the tip of an *Arabidopsis pinformed1* mutant apex induces organ formation. (**G–I**) Model of auxin transport in phyllotaxis. Auxin is transported into the meristem, where it is absorbed by the pre-existing primordia, leading to accumulation of auxin and, consequently, organ formation at a certain minimal distance ($I_1$). If only the youngest primordium absorbs auxin, distichous phyllotaxis is established (G). If mainly $P_1$ but also, to a lesser extent, $P_2$ absorb auxin, spiral phyllotaxis results (H). If the size of the meristem allows for two auxin maxima to coexist, then pairs of opposite leaves are formed, resulting in decussate phyllotaxis (I). Subsequent pairs of leaves will diverge by 90°. (D) and (F) reprinted with permission from Reinhardt *et al*. (2000) © 2000 American Society of Plant Biologists.

inhibitors of auxin transport, specifically abolishes organ formation at the SAM, whereas stem growth and meristem perpetuation are not affected, resulting in the formation of pinlike stalks (Okada *et al.*, 1991; Reinhardt *et al.*, 2000). This defect can be restored by exogenous application of IAA directly to the meristem of such pins (Figure 1F; Reinhardt *et al.*, 2000). Thus, auxin is an inducer of organ formation, and, based on these findings, we have proposed a model in which the distribution of auxin in the meristem regulates phyllotaxis (Kuhlemeier and Reinhardt, 2001; Figure 1G–I). We assume that auxin is transported into the meristem from developing leaf and stem tissues. At the flank of the meristem, the youngest pre-existing primordia absorb the auxin in their vicinity, thus depleting the hormone from the surrounding meristem tissue. According to this model, auxin can only accumulate to levels necessary for organ initiation at a characteristic distance from these primordia, resulting in the regular organ patterns found in nature. This model is conceptually similar to the classical model (Figure 1E), but differs from it in that it is based on an activator absorbed by primordia, rather than on an inhibitor that they have released.

## Branching and apical dominance

Plants produce lateral shoots (branches) from so-called axillary meristems that are initiated in the axils of the leaves (Figure 2A). Therefore, the branching patterns essentially reflect the phyllotactic pattern of the main shoot axis. In most plants, the growth of axillary meristems is initially suppressed by the shoot tip, a phenomenon known as apical dominance (Davies, 1995). Decreased branching (i.e. increased apical dominance) has been one of the major traits to be selected for during the domestication of maize from its ancestor teosinte. Increased apical dominance in maize is mediated primarily by the gene *TEOSINTE BRANCHED1* (*TB1*) (Doebley *et al.*, 1997). In the *tb1* mutant, all axillary meristems grow out, leading to highly branched plants (Figure 2C versus B).

Conversely, in the tomato mutant *lateral suppressor* (*ls*), the vegetative axillary meristems are suppressed and no lateral branches are formed (Schumacher *et al.*, 1999). Decreased branching is of prime interest to tomato breeders, since manual pruning is labour intensive.

The existence of specific mutants in branching and apical dominance demonstrates that these traits are under tight genetic control.

## Flowering: determinate and indeterminate growth

The onset of flowering affects plant architecture in many ways. For instance, in some plants with decussate phyllotaxis (e.g. *Antirrhinum*) it is associated with a transition to spiral phyllotaxis (Carpenter *et al.*, 1995). It also affects the fate and identity of the meristems. In many plants (e.g. *Arabidopsis* and *Antirrhinum*), the SAM of the main shoot is indeterminate, i.e. it is active during the entire life span of the plant, producing first leaves and later flowers (Figure 2A). This growth behaviour is referred to as monopodial (Schmitz and Theres, 1999). In contrast, the SAM of plants from the *Solanaceae* family (e.g. tomato) is determinate, i.e. it terminates in a single flower, and development continues from lateral meristems. This growth behaviour is referred to as sympodial growth (see below; Schmitz and Theres, 1999).

Mutations in the *Antirrhinum* gene *FLORICAULA* (*FLO*) and in the *Arabidopsis* orthologue *LEAFY* (*LFY*) transform flowers into indeterminate axillary branches (Figure 2D; Coen *et al.*, 1990; Weigel *et al.*, 1992). Hence, a developmental switch mediated by *FLO* and *LFY*, is sufficient to transform indeterminate axillary meristems into determinate floral meristems. Based on these

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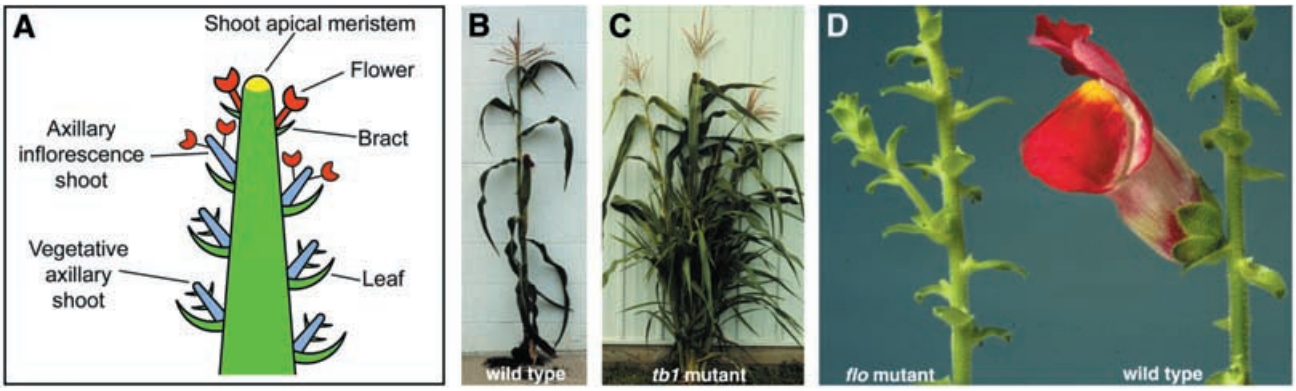


**Fig. 2.** Regulation of branching, apical dominance and determinacy. (**A**) Organisation of a prototypical monopodial plant. The SAM (yellow) remains active during the entire life span of the plant. Depending on the developmental stage of the plant, axillary shoots (blue) form leaves or flowers; later, they are entirely transformed into flowers (top part). (**B**) Wild-type maize plant. (**C**) The maize mutant *teosinte branched1* (*tb1*) [reprinted with permission from Doebley *et al.* (1997) © 1997 Macmillan Publishers Ltd]. (**D**) The *flo* mutant (left) versus wild type (right) [reprinted with permission from Coen *et al.* (1990) © 1990 Elsevier Science].

findings, it has been hypothesised that flowers could have evolved from axillary shoots (Coen and Nugent, 1994). Conversely, in the mutants *centroradialis* (*cen*) of *Antirrhinum* and *terminal flower* (*tfl*) of *Arabidopsis*, the SAM terminates prematurely with the formation of a flower. Thus, the program of the SAM is transformed from indeterminate to determinate, rendering it similar to that of the axillary flower meristems (Bradley *et al.*, 1996, 1997). Overexpression of the *CEN* gene in the determinate plant tobacco dramatically extends the indeterminate (vegetative) growth phase (Amaya *et al.*, 1999).

The orthologous *CEN* and *TFL* genes can be considered to play a functionally antagonistic role to the *FLO* and *LFY* genes, although they act in different domains. Whereas *CEN* and *TFL* prevent termination and flower formation in the main meristem, *LFY* and *FLO* promote determinacy and flower formation in lateral meristems. It is likely that *CEN* and *TFL* function by repressing *FLO* and *LFY*, respectively, in the indeterminate SAM to avoid termination (Bradley *et al.*, 1996).

## Playing with branching and determinacy: sympodial development in the *Solanaceae*

In the *Solanaceae*, inflorescence architecture exhibits remarkable diversity (Danert, 1958; Huber, 1980). In general, the apical meristem of solanaceous plants forms a terminal flower after the onset of flowering (Figure 3A–E). Axillary meristems grow out and develop for a certain period before they also terminate their own development and initiate new axillary inflorescences (Figure 3F–H). This reiterative growth behaviour is sympodial growth, and the shoot segment that is formed by an individual lateral meristem before it itself terminates is called a sympodial unit (Schmitz and Theres, 1999).

The related solanaceous species tobacco, tomato and petunia establish different body plans because of their varying basic sympodial growth pattern. Tobacco initiates several sympodial shoots (Figure 3A and C), each consisting of one leaf (called bract in this case), a new sympodial meristem and the terminal flower (Figure 3F and H). In tomato, only two sympodial meristems are initiated (Figure 3B and D), the lower of which forms three leaves before flowering, whereas the upper splits repeatedly, each time forming a terminal flower and a new sympodial meristem (Figure 3H). In petunia, only one sympodial shoot is initiated (Figure 3E), which forms two leaves, one new sympodial meristem and a terminal flower (Figure 3G and H). Taken together, the differences between tobacco, tomato and petunia can be explained by the number of sympodial shoots initiated (Figure 3C–E) and the degree to which the sympodial units are reduced (Figure 3H).

Genetic analysis of branching in the *Solanaceae* has identified genes that regulate sympodial development. In the tomato mutant *self-pruning* (*sp*), the sympodial units are reduced successively. Only one leaf is formed between the first two inflorescences rather than three, the following sympodial unit has no leaf at all, and the plant terminates after the third inflorescence (Pnueli *et al.*, 1998). The recessive *sp* gene was important in the development of modern agrotechniques in tomato (Pnueli *et al.*, 1998). Interestingly, *SP* is the tomato orthologue of *CEN* and *TFL*, whose wild-type function is to confer indeterminacy to the inflorescence meristems of *Antirrhinum* and *Arabidopsis*, respectively (see above).

The species variability in sympodial development, and that between different sympodial meristems of the same plant (e.g. tomato), is likely to be caused by differential fine tuning of genes that control meristem identity and determinacy (e.g. *SP*). Differential regulation of meristem fate is inferred from the occurrence of mutations that affect only a subset of the lateral meristems. For example, the *ls* mutation in tomato (see above) affects vegetative axillary meristems but not inflorescence and sympodial meristems (Schumacher *et al.*, 1999). On the other hand, the *exp* mutation in petunia inhibits development of the axillary inflorescence meristem but not of the terminal flower meristem or the vegetative axillary meristems (Souer *et al.*, 1998).

## Leaf architecture

The shapes and sizes of leaves and flower organs are major determinants of plant architecture. Leaves can be either simple, as in *Arabidopsis* and tobacco, or composed of several subunits, the leaflets, as in tomato and pea (reviewed in Sinha, 1999). A

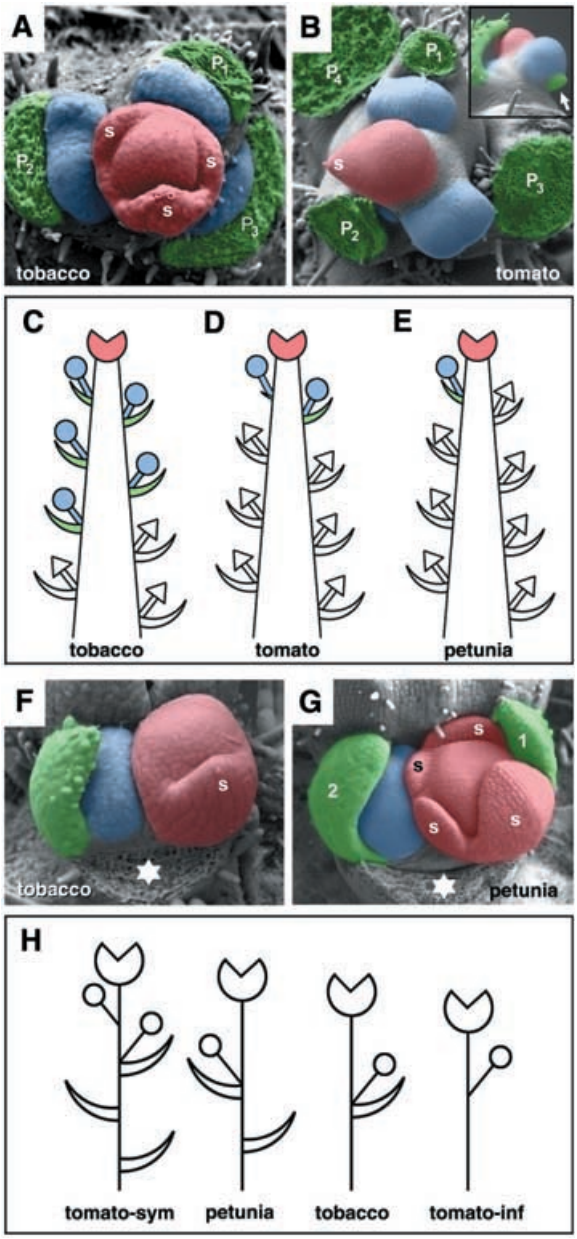


**Fig. 3.** Sympodial growth of the shoot apex in the *Solanaceae*. (**A**) Apex in the top view of a tobacco plant at the onset of flowering. The SAM (red) has undergone floral determination. Axillary meristems (blue) from the youngest leaves (green; removed) grow out in spiral succession. (**B**) Tomato apex as in (A). Note that the inflorescence meristem is subtended only by a rudimentary primordium (inset, arrow). (**C**–**E**) Schematic representation of sympodial development in tobacco (C), tomato (D) and petunia (E). (**F**) Sympodial unit of tobacco, consisting of one bract (green) in the axil of which the next sympodial unit is initiated (blue), whereas the apex terminates as a flower (red). The star denotes the position of the subtending leaf that was removed. (**G**) Sympodial unit of petunia as in (F). The new sympodial meristem is initiated in the axil of the younger bract (2). (**H**) Schematic representation of sympodial organisation in tomato, tobacco and petunia. Differences are interpreted as variations on a basic theme. The lower sympodial unit of tomato (tomato-sym) has four nodes with three leaves and two new sympodial meristems. In petunia, the sympodial unit has two nodes and one new sympodial meristem. In tobacco, it has only one node. The end-point of this progressive reduction is represented by the tomato inflorescence (tomato-inf), which consists of sympodial units with only one node that lacks a leaf. s, sepals.

prototypical leaf has three axes: the proximodistal axis (tip–base), the dorsiventral axis (upper side to lower side, or adaxial–abaxial) and the lateral (left–right).

Genetic analysis has identified several mutants in which the leaves are radially symmetric, i.e. no leaf blade is formed and the primordia lack dorsiventral pattern (reviewed in Bowman *et al.*, 2002). Classical experiments have shown that surgical separation of incipient primordia from the meristem also leads to radially symmetric leaves, indicating that a signal from the meristem is required to establish dorsiventrality (Sussex, 1955). These findings have led to the following model. A signal emanating from the meristem induces dorsal identity in the adaxial side of the primordium (which is closer to the meristem), whereas, in the abaxial tissues of the primordium (more remote from the meristem, and thus not reached by the signal), a default mechanism establishes ventral identity. The dorsal and ventral identities suppress and exclude each other, leading to the establishment of two sharply separated domains. At the lateral edge of the primordium, the interaction between the domains leads to outgrowth of the blade (Bowman *et al.*, 2002).

The development of compound leaves has been studied mostly in tomato and pea (reviewed in Sinha, 1999). The *lanceolate* mutation in tomato results in a loss of meristem activity in the SAM and leads to the suppression of lateral leaflets (Mathan and Jenkins, 1962). Conversely, the overexpression of *KNOX* genes, which confer meristem identity, promotes the reiterative formation of excess lateral leaflets, resulting in supercompound leaves (Hareven *et al.*, 1996). Hence, in tomato, the formation of lateral leaflets is associated with extended meristematic activity at the base of leaf primordia.

## The cellular basis of growth and morphogenesis

During the early phases of leaf development, growth is accompanied by intense cell division activity. At later stages, starting from the tip of the leaf, cell divisions become less frequent, and the cells enter into a phase of expansion and differentiation (Donnelly *et al.*, 1999). Based on the above observations, it has been concluded that two parameters determine the final organ dimensions and organ size: the length of time over which cell division is sustained, and the amount of expansion of the cells after they have ceased to divide. The fact that cell size is usually quite uniform over the area of a leaf suggests that cell number, rather than cell size, determines the dimensions of an organ. Does this mean that the number and direction of cell divisions define organ shape and size, whereas expansion only increases organ size? Such a view basically reflects the 'cell theory', which states that the development of the organism can be understood as the sum of the development of all its constituent cells (Kaplan and Hagemann, 1991). Indeed, cell division patterns are often highly stereotyped during plant development. In *Arabidopsis*, the number, timing and direction of cell division are strictly controlled during several stages: early embryogenesis (Jürgens, 1996), post-embryonic development of the root (Benfey and Scheres, 2000) and stomate formation (Larkin *et al.*, 1997).

However, it should be emphasised that growth is, by definition, mediated by expansion rather than division (Lyndon, 1998). Cell division in the absence of coordinated expansion will only lead to subdivision of an existing volume, as is the case for cleavage

divisions during early amphibian development (Slack, 1991). Therefore, precise control of expansion is required at all stages of leaf development. In fact, in lower plants such as green algae (*Chlorophyceae*), morphogenesis can occur in the absence of cell division, merely by regulation of cell wall expansion (Kaplan and Hagemann, 1991; Mandoli, 1998).

Several lines of evidence also point to a pivotal role for cell expansion in the morphogenesis of higher plants. (i) When cell division in young wheat leaves was blocked by γ-irradiation, leaf growth and morphogenesis continued and cell size increased dramatically compared with that in non-irradiated controls (Haber, 1962). (ii) Mutations in the *TANGLED* gene of maize lead to irregular cell division patterns, but the size and the shape of the leaves are close to normal (Smith *et al.*, 1996). (iii) The extracellular protein expansin, which regulates cell wall extensibility (Cosgrove, 2000), is expressed both in elongating and meristematic tissues (Cho and Kende, 1998; Reinhardt *et al.*, 1998), and it has been shown that local induction of an expansin gene in the apical meristem is sufficient to induce organ formation (Pien *et al.*, 2001), whereas local induction of cell division did not induce organogenesis (Wyrzykowska *et al.*, 2002). (iv) In tobacco plants in which the cell cycle was slowed down experimentally, the rate of leaf formation, as well as leaf shape and size, was normal, whereas cell size was increased (Hemerly *et al.*, 1995). (v) Again in tobacco, if the cell cycle was accelerated, the rate of organ formation was increased, although phyllotaxis as well as the shape and size of the leaves was normal (Cockcroft *et al.*, 2000), as was cell size. (vi) Finally, mutants such as *angustifolia* and *rotundifolia*, whose organ shape is altered, appear to be compromised in cell expansion, rather than in cell division (Tsuge *et al.*, 1996).

These observations demonstrate that growth and morphogenesis are not controlled directly by the number and direction of cell divisions. Rather, it is likely that growth is regulated at a supercellular level, possibly through differential expansion of the apoplastic cell wall 'exoskeleton' at the tissue/organ level. According to this idea, cell division would be a consequence, rather than a cause, of growth (Lyndon, 1998).

## Conclusions

Plant architecture is regulated at numerous levels involving phyllotaxis, apical dominance, meristem determinacy and differential growth of stems and lateral organs. Genetic analyses have identified regulatory proteins that control meristem identity and determinacy. In addition, plant hormones have been implicated in the regulation of plant architecture. The current challenge is to reveal how the actions of regulatory proteins tie in with hormonal regulation and, ultimately, how the control of growth at the cellular level allows the genetically determined plant form to be realised.

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