International Journal of Plant Developmental Biology ©2007 Global Science Books

Transition to Flowering and Morphogenesis of Reproductive Structures in Tomato

Muriel Quinet* • **Jean-Marie Kinet**

Unité de Biologie Végétale, Département de Biologie, Université Catholique de Louvain, Croix du Sud 5, boîte 13, B-1348 Louvain-la-Neuve, Belgium

Corresponding author: * **quinet@bota.ucl.ac.be**

ABSTRACT

Flowering in tomato (*Solanum lycopersicum* L.) has long been investigated by plant physiologists and horticulturists aiming to increase productivity of this important fruit crop. The disruption of the sequence of events which give rise to normal development of the reproductive structures by either the manipulation of the environment, hormones or mutations has provided information useful to unravel the complexity of the implicated mechanisms. In this paper, we focus on the early stages of the flowering process, analysing how flowering time and reproductive morphogenesis are regulated. Development of the reproductive structures up to anthesis, having been reviewed on several occasions in the past, is not considered. Tomato is an autonomously flowering plant with a sympodial growth habit, which means that it flowers repeatedly, at the top of an initial segment and of successive sympodial segments. The nature of its reproductive structure, a raceme or a cyme, is still questioned but available evidence supports the view that the tomato inflorescence is racemose. Flowering time is strongly dependent on the daily light energy integral and is regulated by an array of genes among which *SINGLE FLOWER TRUSS* (*SFT*) and *SELF PRUNING* (*SP*) play a major role. *SFT* is a flowering promoter particularly active in the initial segment while *SP* regulates sympodial development by controlling the regularity of the vegetative-reproductive switch of the different sympodial segments. Many genes specifying the identity of the meristems and floral organs interact to regulate the morphogenesis of the reproductive structures, opening a large field for future investigations.

Keywords: environmental regulation, flowering time, genetic regulation, inflorescence structure, *Lycopersicum esculentum* Mill., meristems, mutants, reproductive structures morphogenesis, *Solanum esculentum* L., sympodial growth

Abbreviations: ***AG***, *AGAMOUS*; ***AN***, *ANANTHA*; ***API***, *APETALA1*; ***AP3***, *APETALA3*; ***BL***, *BLIND*; ***CEN***, *CENTRORADIALIS*; **CETS**, *CEN*, *TFL1*, *SP* genes family; ***CRY2***, *CRYPTOCHROME2*; ***FA***, *FALSIFLORA*; ***FLO***, *FLORICAULA*; ***FT***, *FLOWERING LOCUS T*; ***GPI***, *GREEN PISTILLATE*; ***J***, *JOINTLESS*; ***LFI***, *LEAFY INFLORESCENCE*; ***LFY***, *LEAFY*; ***LS***, *LATERAL SUPPRESSOR*; ***MC***, *MACROCALYX*; **PAR**, photosynthetic active radiations; **PEBPs**, phosphatidylethanolamine binding proteins; ***RAX***, *REGULATORS OF AXILLARY MERISTEMS*; ***S***, *COMPOUND INFLORESCENCE*; **SAM**, shoot apical meristem; ***SFT***, *SINGLE FLOWER TRUSS*; ***SP***, *SELF PRUNING*; ***SL***, *STAMENLESS*; ***SL-2***, *STAMENLESS-2*; ***SP***, *SEPALLATA*; ***SVP***, *SHORT VEGETATIVE PHASE*; ***TFL1***, *TERMINAL FLOWER1*; ***TM5***, *TOMATO MADS BOX GENE 5*; ***TM6***, *TOMATO MADS BOX GENE 6*; ***TM29***, *TOMATO MADS BOX GENE 29*; ***UF***, *UNIFLORA*

CONTENTS

INTRODUCTION

The tomato is a member of the Solanaceae which has been known from 1768 as *Lycopersicon esculentum* Mill. However, this denomination has long been disputed and recently, with the support of genomic analyses, its membership of the genus *Solanum* has been confirmed and the latin name *Solanum esculentum* L. has been proposed (Peralta *et al*. 2005).

Received: 27 February, 2007. Accepted: 9 April, 2007.

Invited Review

Tomato originated in the western coastal plain of South America, extending from Ecuador to Chile and was domesticated in Mexico (Harlan 1992). It was first introduced in Europe in the middle of the XVIth century (Rick 1978; Kalloo 1991). An early introduction was probably yellow, since it was named "pomodoro" (golden apple) in Italy. Tomato is now one of the most popular vegetables and one of the most important fruit crops in the world. No horticultural crop has received more attention and detailed study than tomato which became a model crop for many experimental investigations. Knowledge and information gathered from these works have furthered our understanding of flowering in this species. An abundance of applied and fundamental studies, devoted to the development of the flower up to anthesis and of the fruit, have been published, thanks to the economic importance of tomato. They have been summarized on several occasions (Picken *et al*. 1985; Picken and Grimmett 1986; Kinet and Peet 1997) and will not be presented here.

In this review paper, we will focus on the early stages of the flowering process, analysing how flowering time and reproductive morphogenesis are regulated. However, before entering these topics, structural considerations will be developed. The way structures are interpreted has indeed an impact on the way the regulation of their genesis is understood. Tomato is particular in that it grows sympodially; furthermore, the nature of its inflorescence is still a matter of debate.

PLANT ARCHITECTURE

Tomato is a plant with a sympodial growth habit, i.e. after the production of a limited number of leaves, the growth of the primary shoot emerging from the seed is terminated by the initiation of the first inflorescence which is displaced from its terminal position by the active growth of the bud at the axil of the last initiated leaf. This bud continues the plant growth, carrying up the subtending leaf until it occupies a position above the inflorescence which is forced to develop laterally (**Fig. 1**), and producing some leaves and a second inflorescence which is once again rejected laterally by the active outgrowth of an axillary bud. In the so-called 'indeterminate' tomatoes, this process is indefinitely reiterated at initiation of each subsequent inflorescence (Calvert 1965; Sawhney and Greyson 1972; Ecole 1974). The stem portion produced by the vegetative 'shoot apical meristem' (SAM), before the first inflorescence, constitutes the initial segment. Additional stem portions, between inflorescences, are called the sympodial segments; they are produced by precociously activated axillary meristems, referred to as 'sympodial meristems'. Activation of axillary and sympodial meristems is regulated differently since mutations in the *LATERAL SUPPRESSOR* (*LS*) gene that inhibits axillary shoot outgrowth do not prevent sympodial growth (Schumacher *et al*. 1995, 1999; Schmitz *et al*. 2002; Szymkowiak and Irish 2006).

The gene *SELF PRUNING* (*SP*) regulates the sympodial development by controlling the regularity of the vegetative-reproductive switch of the different sympodial segments (Pnueli *et al*. 1998). The *SP* gene has been cloned and is thought to be the orthologue of the *Arabidopsis thaliana TERMINAL FLOWER1* (*TFL1*) and *Anthirrinum majus CENTRORADIALIS* (*CEN*) genes, both acting as inflorescence meristem identity genes (Pnueli *et al*. 1998). A role for *SP* in the regulation of the development of the reproductive structure of tomato is not excluded and will be discussed in the section devoted to the control of the reproductive structure morphogenesis. *TFL1*, *CEN* and *SP* were shown to share sequence identity with a group of mammalian polypeptides designated as phosphatidylethanolamine binding proteins (PEBPs) and are members of a novel *CETS* (*CEN*, *TFL1*, *SP*) family of regulatory genes (Pnueli *et al*. 2001). This family contains five other members in *Arabidopsis thaliana* (Kobayashi *et al*. 1999), among which *FLOWERING LOCUS T* (*FT*) which has been shown to be a major integrator of the genetic pathways to flowering. The *FT* product represents a part of the long distance signal(s) generated in cotyledons and leaves and acting at the shoot apex to trigger floral transition (Abe *et al*. 2005; Huang *et al*. 2005).

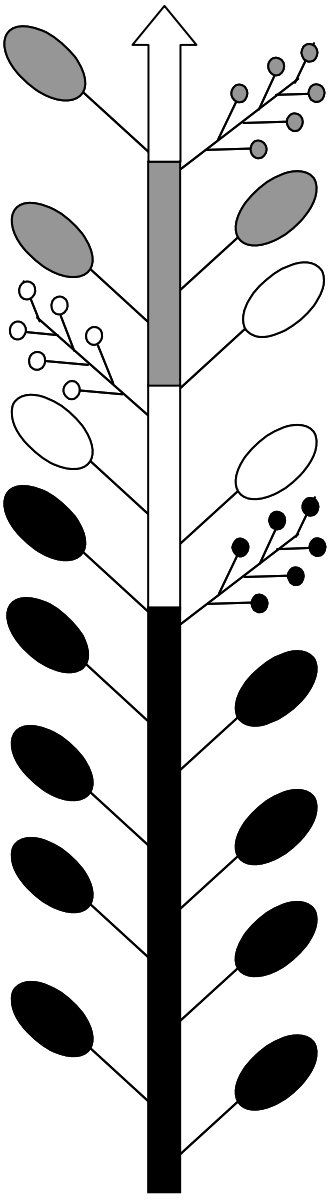

Fig. 1 The sympodial growth of tomato. The initial segment initiated by the SAM is in black. The successive sympodial segments initiated by the successive sympodial meristems are alternatively in white and grey (circle, flower; central column, main shoot; ellipse, leaf).

The *sp* mutant is 'determinate': the number of vegetative nodes arising on successive sympodial shoots is gradually reduced until the vegetative phase is by-passed completely with the production of two successive inflorescences (Pnueli *et al*. 1998). The *sp* mutant allele results from a point substitution (P76L) within a conserved region of CETS proteins (Pnueli *et al*. 1998).

In addition to *SP*, five other members of the *CETS* family were also found in tomato: *SP9D*, *SP3D*, *SP5G*, *SP2I* and *SP6A* (Carmel-Goren *et al*. 2003). Their function is not yet known, except for *SP3D* which was found to be allelic with the *SINGLE FLOWER TRUSS* (*SFT*) gene of tomato and is the orthologue of the *FT* gene of *Arabidopsis thaliana* (Lifschitz *et al*. 2006). The role of *SFT* is further described in the sections devoted to the regulation of the flowering time and of the reproductive morphogenesis.

Additional tomato genes implicated in the formation of the sympodial segments are *BLIND* (*BL*) and *TOROSA*: the mutants *bl-1*, *bl-2* and *to-1*, that lack axillary buds in most leaf axils, have also a tendency to terminate shoot growth after formation of an inflorescence, a feature that is very pronounced in *bl-1*. The *bl* and *to* mutants have been found to be affected in the same gene and *bl-1* also contains a mu-

tant *sp* allele (Schmitz *et al*. 2002). The *BL* gene is a member of the R2R3 class of MYB transcription factors and has at least three *Arabidopsis thaliana* homologues termed *REGULATORS OF AXILLARY MERISTEMS* (*RAX*) which also control the axillary meristem formation (Müller *et al*. 2006).

Both indeterminate and determinate tomatoes – which are incorrectly termed since in both types, the SAM is completely consumed by the production of the first inflorescence (Picken *et al*. 1985) – are economically important. The indeterminate or "vine" tomato, which produces inflorescences and flowers continuously throughout the plant's life, is largely used for production of fresh fruits in greenhouses and home gardens while the determinate or "bushy" tomato, which has one time-limited flowering period followed by a period of fruit development, is ideal for growing unsupported in open and is mainly used for processed food.

INFLORESCENCE STRUCTURE

The inflorescence of tomato has been generally classified as a cyme (Sawhney and Greyson 1972; Chandra Sekhar and Sawhney 1984). However, it has also been viewed as a raceme by some authors (Lewis 1953; Allen and Sussex 1996) and the confusion in the literature concerning the type of inflorescence tomatoes produce remains large. Since ontogenesis of both types of reproductive structures is different (Kinet *et al*. 1985; Weberling 1989), implicating the functioning of an inflorescence meristem in the raceme but not in the cyme – where the vegetative SAM becomes a terminal flower and the subsequent floral meristems are formed successively from the pedicel of the preceding flower – the question thus arises as to whether an inflorescence meristem operates in tomato.

Before trying to answer this question and to understand how these two interpretations of the reproductive structure emerged, it is necessary to analyse precisely (1) the gross morphology of the inflorescence and (2) the way it is initiated by the SAM.

Inflorescence morphology

Looking down on an inflorescence tip, the sequential features of ontogeny are easily observed. When flowers in an inflorescence are numbered in order of their origin, increasing numbers represent younger stages of development of a flower. This progression is called the floral cascade. Flower primordia are in two rows, at right angles and successive older primordia lie in alternate rows, forming a zigzag (**Fig. 2**).

Inflorescence morphogenesis

Dissections under the binocular as well as histological studies showed that, at floral transition, the SAM swells before dividing into two parts which give rise to a first floral meristem on one side and restore a mound of dividing cells on the other side. This latter meristem has a continuous existence and bifurcates repeatedly for the production of each new flower (**Fig. 3A**; Ecole 1974; Dielen *et al*. 1998; Quinet *et al*. 2006b). The successive planes of bipartition are at right angles so that the flower positions form a zigzag (**Fig. 3B**; Allen and Sussex 1996).

Cyme vs. raceme

The development described above is similar to the one observed by Green (1988) in *Echeveria* (except that in *Echeveria*, flowers are associated with 2 bracts). As stressed by Green, such a development "*is unusual for a cymose inflorescence… In a cyme one expects sympodial growth with intermittent renewal of the inflorescence by lateral, subapical, flower initiation*". This would imply that, in *Echeveria* as in tomato, the swelling transitional meristem should be viewed "*as a terminal floral apex which, as it develops…produces a terminal flower and a "renewal" axillary floral bud*". According to Green, "*this notation is awkward*

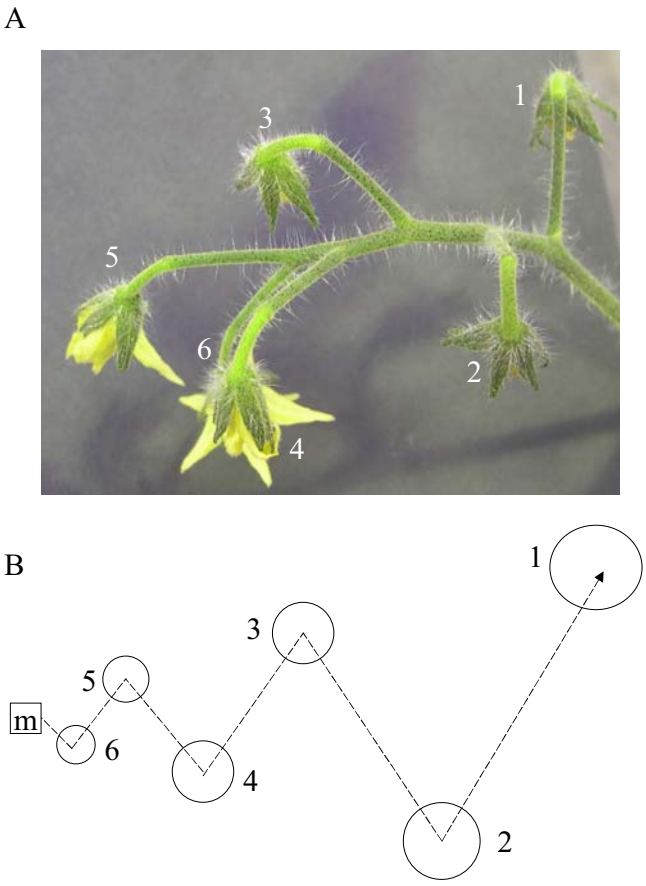

Fig. 2 The tomato inflorescence. (**A**) Top view of a tomato inflorescence. (**B**) the floral cascade showing the zig-zag pattern. The flowers are represented by circles and numbered in order of initiation, the meristem (m) is represented by a square.

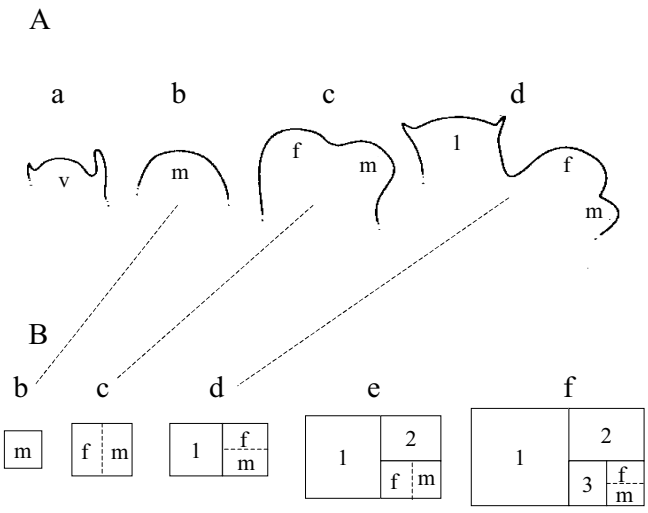

Fig. 3 Schematic representation of (A) longitudinal sections of an inflorescence of tomato during morphogenesis and of (B) top views of the inflorescence of tomato at successive stages of development. In (**B**), flowers and meristems are represented by squares. (a) The vegetative (v) meristem initiates leaves. At floral transition, the shoot apical meristem swells (b) before dividing into two parts (c) which give rise to a first floral meristem (f) and restore a mound of dividing cells (m). (d) The floral meristem gives the first flower (1) and the mound of dividing cells splits then in turn at a right angle of the first division producing a new floral meristem (f) and restoring the mound of dividing cells (m). (e-f) The mound of dividing cells (m) continues to divide repeatedly at right angle and the successive floral meristems (f) develop into flowers (2, 3, …).

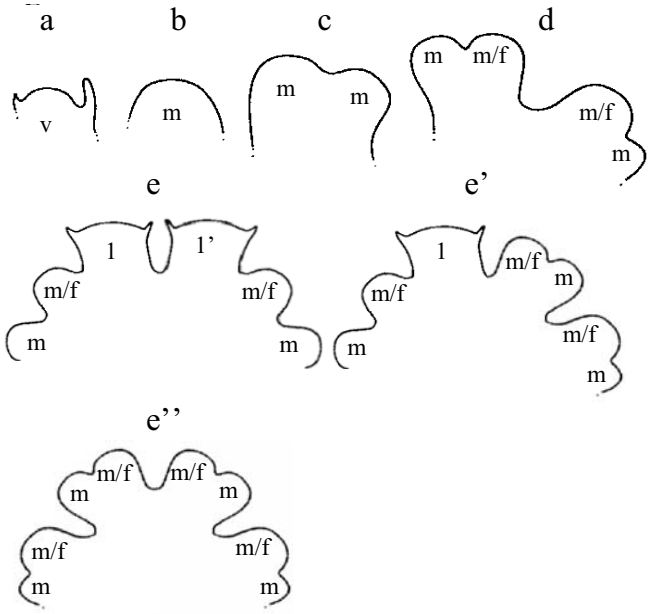

Fig. 4 Schematic representation of longitudinal sections of an inflorescence of the *compound inflorescence* mutant of tomato during morphogenesis. (a) The vegetative (v) meristem initiates leaves. At floral transition, the shoot apical meristem swells (b) before dividing into two parts (c) each giving rise to a mound of dividing cells (m) which divide again into two parts, producing either a floral meristem (f) and a mound of meristematic cells or two mounds of meristematic cells. (e, e', e''). The floral meristem gives the first flower (1) and the mound of dividing cells splits then in turn at a right angle of the first division producing a new floral meristem and restoring the mound of dividing cells or producing two mounds of dividing cells, etc.

Fig. 5 The flowers of the *stamenless* mutant (above) and of the wild type (below). Petals of mutant flower are transformed in sepals and stamens in carpels that fuse with the central pistil in a unique gynoecium.

because it implies that tissue of a terminal flower de-differentiates to make the lateral renewal shoot". It is however the most common view encountered in literature for tomato. The histological study of Ecole (1974) further supports the view that the inflorescence of tomato is not functioning as a cyme because the production of each new flower is not associated with the formation of a shell zone as in the case of flowers produced laterally in the cymes of *Nicotiana glutinosa* (Bonnand 1961), another Solanaceae.

Phenotypes of mutants affected in their reproductive structure also suggest that an inflorescence meristem is operating in tomato. The *compound inflorescence*(*s*) mutant produces a highly branched inflorescence (Rick and Butler 1956) bearing up to 200 flowers, in contrast to the simple type of inflorescence produced by most cultivars. In this mutant, when the swelling transitional meristem divides into two parts for the first time, it generates two mounds of dividing cells which divide again into two parts, producing either a floral meristem and a mound of meristematic cells, or two mounds of dividing cells (**Fig. 4**). This process is frequently, but not systematically, reiterated during the subsequent build-up of the inflorescence resulting in extensive ramification of the inflorescence (Quinet *et al*. 2006b). A similar splitting of the swelling reproductive meristem into two meristematic mounds was observed in the *falsiflora* (*fa*) and *anantha* (*an*) mutants by Allen and Sussex (1996), but the reproductive structures of these 2 mutants markedly diverge from the inflorescence of *s* plants because they are unable to form flowers. The *an* inflorescence consists only of proliferating meristems while in the *fa* mutant, the reproductive meristems ultimately reverts to vegetative meristems. Thus, a common feature of the 3 mutants is that the meristems of their reproductive structure were not determined straightaway to give a flower, but might turn into an inflorescential meristem. The implication of these mutants in flower morphogenesis will be analysed later in this paper.

Finally, it has been observed that, depending on environmental conditions – such as low temperatures (Kinet 1989) – or on position on the plant, branched inflorescences having two or more main axes occur on tomatoes which normally produce the simple type inflorescence indicating once again that the transitional meristem is not readily dedicated to become a flower and that its fate may be dependent on external or internal influences.

In conclusion, the reproductive structure of tomato appears to be of the raceme type, with a persistent inflorescence meristem producing flowers laterally. Several genes controlling identity and/or maintenance of this inflorescence meristem have been identified; they will be presented and their role described in the section devoted to the morphogenesis of the reproductive structure.

If flower positioning in two rows, with successive older flowers lying in alternate rows, is unusual, it is however worth to recall here that raceme organisation in angiosperms is highly variable, including spike, capitulum, corymb, umbell…and very peculiar flower groupings such as in *Convallaria majalis* and various Liliaceae (Kinet *et al*. 1985; Gorenflot 1997).

FLOWER STRUCTURE

Flower morphology

The tomato flower is hermaphroditic and actinomorph (**Fig. 5**). It consists from periphery to centre of (1) a whorl of 5-6 sepals, fused at the base in a short tube; (2) a corolla also with a short supporting tube terminated in 5-6 petal lobes; (3) a whorl of 5-6 stamens attached to the corolla by short enlarged filaments that bear elongated anthers which are laterally coalesced to form a hollow cone and (4) a central gynoecium which consists of 2 to several carpels with a long style terminating in a rather flattened stigma and is enclosed within the encircling androecium (Cooper 1927; Sawhney and Greyson 1973a).

Flower morphogenesis

After initiation of the floral meristem, the 4 floral whorls arise successively in the following order: calix, corolla, androecium, and gynoecium. Sepals appear in a helical sequence while the pattern of initiation is simultaneous for petals, stamens and carpels (Chandra Sekhar and Sawhney 1984). After initiation, the sepal and petal, that arise as separate organs, fuse in the basal region by "zonal growth". The cohesion of anthers to form the staminal tube occurs later in development and is achieved by the interlocking of epidermal hairs present on their lateral and adaxial surfaces. Carpel primordia are produced at the periphery of the remaining meristem and fuse laterally, early during their development.

CONTROL OF FLOWERING TIME

In a strict sense, the vegetative phase is usually short in tomato since, in most cultivars, floral transition of the initial segment occurs when the third leaf is expanding. This is within three weeks of cotyledon expansion (Hurd and Cooper 1970).

Flowering time of the initial segment

Flowering time of the initial segment, as measured by the number of leaves produced before the conversion of the vegetative SAM into a reproductive structure, is rather stable in various environmental conditions (Kinet and Peet 1997). Usually, the first inflorescence differentiates after initiation of 6-12 leaves, a number which is under genetic control. The major effect upon the extent of the vegetative growth is attributable to the light energy integral, i.e. the accumulation of photosynthetic active radiations (PAR), to which plants are exposed within a 24-h cycle (Kinet and Peet 1997). High irradiance reduces the number of leaves below the first inflorescence and stimulates the rate of leaf initiation, resulting in earlier flowering as measured by the number of days from sowing to macroscopic appearance of the reproductive structure or first anthesis (Calvert 1959; Kinet 1977a). This effect of high light, along with the finding that continuous removal of young leaves results in earlier flowering, suggests that floral transition is stimulated by increasing assimilate availability. It has been indeed postulated that vegetative growth and reproductive development strongly compete for available assimilates in tomato (de Zeeuw 1954; Kinet 1977b). In insufficient light conditions, this competition never benefits generative development, suggesting a priority of vegetative growth. Stimulation of flowering by increasing assimilate availability is also suggested by the observation that altering starch/sucrose-partitioning by increasing the capacity for sucrose synthesis in transgenic tomatoes results in a reduced time to 50% flowering (Micallef *et al.*1995).

When the daily light energy integral, is kept constant, flowering is advanced in short days (Binchy and Morgan 1970; Kinet 1977a). However, as typical growing conditions of tomatoes in temperate regions are long days, this species is classified as day-neutral plant that flowers autonomously: its conversion from vegetative to reproductive development is normally regulated by a developmental program rather than by environmental cues and the plant flowers with time, provided the environmental conditions allow growth.

The potential role of photoreceptors in the regulation of the flowering time of tomato did not receive much attention, probably because the plant is essentially not dependent on daylength for flowering. Recently however, the manipulation of the blue light photoreceptor *CRYPTOCHROME 2* (*CRY2*) was reported to strongly influence flowering time in tomato. Its overexpression increases the number of days to first anthesis under both short and long days without affecting the number of leaves below the first inflorescence (Giliberto *et al*. 2005). This retardation in flowering time is unexpected since in *A. thaliana*, *CRY2* overexpressors flower earlier than the wild type under short days but not long days (Guo *et al*. 1998). Further work is required to explain this finding.

Flowering time is also affected by temperature: lowering temperature during early plant growth reduces the number of leaves preceding floral initiation but slows down the leaf initiation rate (Calvert 1959) so that the number of days to flowering is not necessarily less. Tomato seeds cannot be vernalized (Calvert 1957; Wittwer and Teubner 1957).

In contrast to *Arabidopsis thaliana*, there are only a limited number of tomato mutants that have been reported to be affected in flowering time. Two main explanations could account for such a discrepancy between the two species. First, tomato has been far less investigated than *A. thaliana* with respect to flowering time. Second, domestication that, most probably, considered mainly fruit traits, may have unwittingly eliminated potential mechanisms controlling flowering time in order to extend the environmental conditions under which tomato is able to flower. Tomato mutants affected in their flowering time are also most usually late flowering, a situation that, once again, could be due to the domestication process that frequently resulted in shortening life cycles (Evans 1993). The precocious floral transition of the initial segment of tomato probably makes easier the occurrence of late flowering than early flowering mutants. Four early flowering mutants have however been recorded in an isogenic 'mutation library' developed by Menda *et al*. (2004), but none of them was precisely characterised.

Up to date, no pathway controlling flowering time in tomato has been clearly identified. *FALSIFLORA* (*FA*), *SINGLE FLOWER TRUSS* (*SFT*) and, in a lesser extent, *JOINTLESS* (*J*) and *BLIND* (*BL*) could act as regulatory components of a promotion autonomous pathway.

The *sft* and *fa* mutations produce a late flowering phenotype in both long-day and short-day conditions and the combination of both mutations completely block the transition to flowering (Molinero-Rosales *et al*. 1999, 2004). The *FA* gene is the orthologue of the *A. thaliana LEAFY* (*LFY*) and *Anthirrinum majus FLORICAULA* (*FLO*) genes; all three genes are acting as floral identity genes (see following section). As *fa*, the *lfy* mutant shows a late flowering phenotype (Blazquez *et al*. 1997) but it is not the case for *flo* (Coen *et al*. 1990).

The flowering delay in the *j* mutant, is slight and usually not statistically significant as compared to the wild-type; it is however consistently recorded in all conditions (Emery and Munger 1967; Philouze 1978; Quinet *et al*. 2006b). The *J* gene was shown to belong to the extensive family of MADS box genes in the same clade as the *A. thaliana SHORT VEGETATIVE PHASE* (*SVP*) gene, a floral transition repressor (Hartmann *et al*. 2000; Mao *et al*. 2000; Brill and Watson 2004).

Defects due to the *bl* mutation are multiple affecting both vegetative and reproductive development (Schmitz *et al*. 2002), including a slightly delayed flowering (Quinet *et al*. 2006a).

An environmentally regulated pathway for the control of floral transition in tomato, implicating the promoter genes *UNIFLORA* (*UF*) and *COMPOUND INFLORESCENCE* (*S*), would also exist. Mutations in these genes that have not been sequenced so far, delay flowering especially in winter (Dielen *et al*. 1998; Quinet *et al*. 2006b).

In *uf*, an adequate supply of sugars to the meristem could constitute the essential signal since flowering is advanced by a high daily light energy integral and by continuous excision of growing leaves which compete for nutrients with the flowering process. Interestingly, Dielen *et al*. (2004) observed that the *uf* mutant develops strong lateral shoots at node levels grossly corresponding with the level where the wild type cultivar initiates its first reproductive structure under the same growing conditions (**Fig. 6**). Release of apical dominance is considered to be an early event associated with floral evocation (Bernier *et al*. 1981), and it thus appears that the *uf* plants undergo a partial evocation at

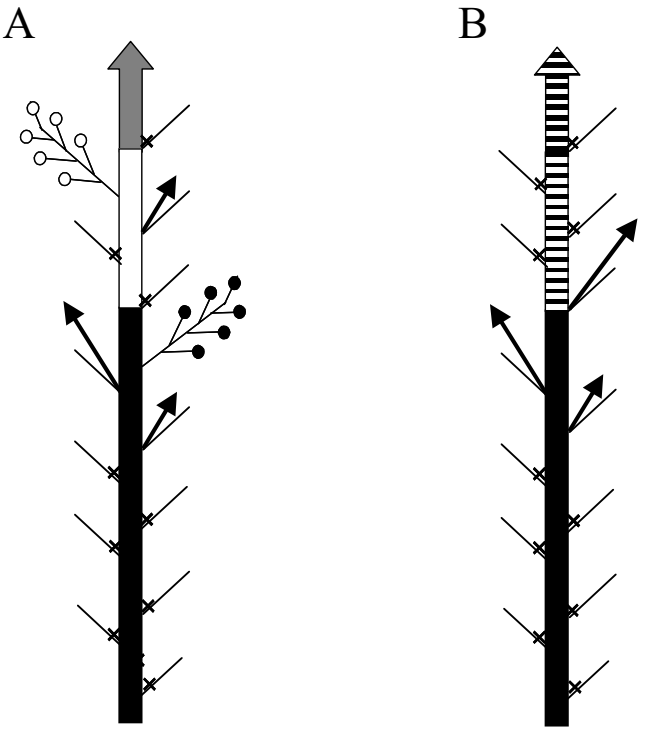

Fig. 6 Develoment of strong axillary shoots remoted from reproductive structure in *uniflora*. (**A**) Flowering in the tomato wild type. (**B**) Development of strong axillary shoots in the *uniflora* mutant at the level where the wild type initiates its first inflorescence. The initial segment initiated by the SAM is in black. In the wild type, the successive sympodial segments initiated by the successive sympodial meristems are alternatively in white and grey. In the *uniflora* mutant, the vegetative segment after the partial evocation is lined white and black (circle, flower; central column, main shoot; line, leaf; arrow, developed axillary shoot; cross, inhibited axillary bud).

approximately the same time as the wild type, but that they are unable to complete the process. This phenotype is indicative of the occurrence of processes upstream of *UF* that direct the SAM of the initial segment into reproductive growth. These processes could be triggered by the *SFT* gene that was shown recently to have a primary role in the regulation of the floral transition in tomato (Lifschitz *et al*. 2006; Lifschitz and Eshed 2006). *SFT* has been identified as the orthologue of the *FT* gene of *Arabidopsis thaliana* which is a major integrator of the pathways to flowering. *SFT* generates a graft-transmissible signal which complement the defects in *sft* plants as long as the graft union with a donor over-expressing *SFT* under the constitutive 35S promoter is maintained. After removal of the donor, all mutant *sft* features reappear in the receptor. The *SFT* signal also substitutes for the high light requirement of *uf*. Indeed, *uf 35S:SFT* plants flower precociously, after 3-5 leaves, even in poor light conditions which suppress flowering of the mutant and grafts with *35S:SFT* donors induce very early flowering of *uf* receptors. Once again, as in the case of *sft* grafts, the graft union has to be maintained to rescue the *uf* mutant phenotype indicating that it is the graft-transmissible signal generated by the *35S:SFT* transgenic plants which promotes flowering in *uf*. *SFT* also induces early flowering in a day-neutral tobacco Samsun and substitutes for the photoperiodic signal in the short day plant tobacco Maryland Mammoth and in the long day plant *Arabidopsis thaliana* (Lifschitz *et al*. 2006).

Other genes may control the flowering time in tomato. A constitutive expression of the *A. thaliana APETALA1* (*AP1*) gene, another floral meristem identity gene, in tomato reduces the flowering time: transgenic tomato plants undergo floral transition after the production of 6 vegetative nodes as compared to 11 nodes for the wild type plant, suggesting that the *AP1* tomato homologue can promote flowering (Ellul *et al*. 2004). The tomato *AP1* orthologue is thought to be *LeMADS-MC* (Vrebalov *et al*. 2002) but the first description of the *macrocalyx* (*mc*) tomato mutant which is affected in this gene mentions only reproductive structure defects (Rick and Butler 1956). Similarly, transgenic plants expressing *LeMADS-MC* antisense RNA were just reported to produce indeterminate inflorescences with large sepals and no allusion was made to their flowering time (Vrebalov *et al*. 2002).

Genetic interactions in flowering time regulation have been investigated using double and sometimes triple mutants. The *uf:bl*, *uf:sp*, *j:uf*, and *s:uf* double mutants are late flowering (Quinet *et al*. 2006a). Flowering time in *uf:bl* and *uf:sp* is intermediate between their two parents, which means that it is in advance as compared to the *uf* simple mutant. This result is puzzling since the *bl* and *sp* mutations alone are either delaying or not affecting the flowering time of the initial segment as compared to the wild-type. Both mutations however activate the flowering of the sympodial segments, which could suggest that when flowering, the meristem of the double mutants is in a condition reminiscent of that of a sympodial meristem (see below). Both *j:uf* and *s:uf* double mutants flowered later than the *uf* parent. The slight and consistent delay in *j* flowering time in comparison to the wild type may apparently be cumulated with the delaying effect of the *uf* mutation. In the *s:uf* double mutant, flowering was particularly delayed, being observed before the 40th leaf, in a very small proportion of plants when growing conditions were highly favourable and failing to occur under low light. This difficulty to undergo floral transition could be due to the fact that two critical processes that take place in sequence, namely the inflorescence meristem and the floral meristem specifications (see below), are impaired, increasing the chance of flowering inhibition during each successive sympodial phase. Molinero-Rosales *et al*. (2004) and Lifschitz and Eshed (2006) reported that the *sft:fa* and *sft:uf* double mutants are non flowering in their experimental conditions, suggesting that the genes affected in these mutants are not acting in a same sequence.

In double mutants, mutated in *UF*, strong lateral shoots develop in a few nodes well before flowering occurrence, a typical trait of the *uf* mutant (see above), and with a slight delay, in term of node number, as compared to the single *uf* mutant (**Table 1**). This confirms that the genes combined with *uf* marginally influence the timing of events that actually initiate the floral transition of the initial segment. After its partial evocation, the *uf* SAM is returning to a vegetative functioning and apical dominance is re-established as axillary outgrowth is inhibited at upper nodes (**Fig. 6**; Dielen *et al*. 2004). Apparently, from that time point, the different genes associated with *uf* in double mutants are strongly interacting to regulate flowering time (**Table 1**). Hence, it could be possible that in the *uf* mutant and the double mutants, after the partial evocation, the plants are in a condition comparable to that of the wild type during its sympodial growth, which results in the regular alternation of vegetative and reproductive phases (Dielen *et al*. 2004). This condition is not alike the one of plants during their initial growth from germination to floral transition of initial segment since, as demonstrated by Pnueli *et al*. (1998, see below), flowering time of the sympodial and of the initial segments of tomato is not regulated in the same way. In the *uf* mutant and the double mutants, genes affecting the flowering time of the sympodial segments could thus be activated after the first partial floral evocation, a process which could be reiterated, even if the plants had not initiated flowers.

Although *SP* has been reported not to be involved in the regulation of floral transition of the initial segment (Pnueli *et al*. 1998), it has been observed that the *sp* mutation promotes this transition, in peculiar genetic backgrounds, partially rescuing flowering of the non-flowering double mutants *sft fa* and *sft uf* in triple mutant combinations (Lifschitz and Eshed 2006). However, in the absence of a precise description of the plants, it is not possible to know whether

Table 1 Number of nodes to first reproductive structure and to first strong axillary shoot in the simple *uf* mutant and in double mutants mutated in *uf* and either in *s*, *bl*, *sp* or *j*.

Genotype	Number of nodes to first reproductive structure[1]	Number of nodes to first strong axillary shoot[1]	Differences between mean numbers of nodes to first reproductive structure and to first strong axillary shoot
uf	28.9 ± 4.14	10.1 ± 1.5a	18.8
uf:s	-	11.5 ± 1.5b	>28.5
uf	18.9 ± 1.4 a	10.5 ± 0.7a	8.4
uf:bl	16.3 ± 1.9b	10.6 ± 1.1a	5.7
uf	18.4 ± 1.1a	10.3 ± 0.6a	8.1
uf:sp	15.5 ± 1.6b	11.0 ± 2.4a	4.5
uf	19.0 ± 5.2a	10.3 ± 0.5a	8.7
uf:j	26.2 ± 2.1b	12.2 ± 1.2b	14.0

- = no plants flowered before the initiation of the 40th leaf.
[1] values followed by the same letter in a column for a same comparison are not statistically different at the 5% level

Table 2 Tomato genes regulating morphogenesis of reproductive structures in tomato and their homologue in *Arabidopsis*.

Function	Tomato		*Arabidopsis*
Inflorescence development			
Inflorescence meristem identity gene	*UF*	*UNIFLORA*	
	BL = TO	*BLIND = TOROSA*	
Floral meristem identity gene	*S*	*COMPOUND INFLORESCENCE*	
	AN	*ANANTHA*	
	FA	*FALSIFLORA*	*LEAFY*
Inflorescence identity maintenance	*J*	*JOINTLESS*	
	SFT	*SINGLE FLOWER TRUSS*	*FLOWERING LOCUS T*
	LeMADS-MC	*LeMADS-MC*	*APETALA1*
Flower development			
Class A genes	*LeMADS-MC*	*LeMADS-MC*	*APETALA1*
Class B genes	*SL = CS*	*STAMENLESS = COROLLALESS*	
	GPI	*GREEN PISTILLATE*	
	TM6 = TGR6	*TOMATO MADS BOX GENE 6*	*APETALA3*
	LeAP3	*Lycopersicum esculentum AP3*	*APETALA3*
Class C genes	*TAG1*	*TOMATO AGAMOUS1*	*AGAMOUS*
Class E genes	*TM5 = TGR5*	*TOMATO MADS BOX GENE 5*	*SEPALLATA3*
	TM29	*TOMATO MADS BOX GENE 29*	*SEPALLATA*
Others	*TM4 = TGR4*	*TOMATO MADS BOX GENE 4*	*FRUITFULL*
	LS	*LATERAL SUPPRESSOR*	
Floral organ fusion	*SF*	*SOLANIFOLIA*	

the meristem that flowered previously passed through a partial evocation in which case it could be in a condition different from its initial vegetative state.

Flowering time of the sympodial segments

Before undergoing floral transition, the sympodial units most usually produce 3 leaves although this number may be modulated by environmental conditions, being increased under low light daily integrals, or by genotype. The vegetative-reproductive switch of the different sympodial segments is controlled by *SP* which has to be down-regulated with each successive internode of each sympodial segment to permit transition to flowering after three internodes. Constitutive expression of *SP* increases the number of leaves and thus delays floral transition of sympodial segments (Pnueli *et al*. 1998).

Other genes, including *FA*, *BL*, *S*, *J* and *UF* also affect flowering of sympodial meristems (Molinero-Rosales *et al*. 1999; Schmitz *et al*. 2002; Quinet 2005). *bl* mutants show a tendency to terminate shoot growth after formation of an inflorescence (Schmitz *et al*. 2002) while the other four genes have an effect opposite to *SP*, since, when mutated, more leaves are produced in the sympodial segments. According to Emery and Munger (1970) and Philouze (1978) the *j* mutation partly masks the *sp* character suggesting that *J* acts upstream from *SP*.

Although being critical in the control of floral transition of the initial segment, *SFT* appears to have a limited influence on flowering in sympodial segments. The sympodial growth pattern is indeed maintained in transgenic plants overexpressing *SFT* under the constitutive 35S promoter, with two or three leaves per segment, depending on the *35S:SFT* plant, i.e. on the strength of the transgene (Lifschitz *et al*. 2006).

Lifschitz and Eshed (2006) postulate that the *SFT* to *SP* balance could be a major determinant in the control of floral transition of both initial and sympodial tomato segments. They hypothesise that *SFT* is increasingly up-regulated in the initial segment relative to *SP* while *SP* only becomes expressed at high levels in the axillary and sympodial buds. This would explain that the initial SAM is indifferent to the *sp* mutation but highly sensitive to *SFT* and that the sympodial segments hardly react to increased levels of *SFT*, but are sensitive to a reduction in *SP*. How *SP* function nullifies after three leaves in the sympodial segments remains however unknown and interactions with additional factors must be involved. A role for *FA*, *S*, *UF* or *J* could be considered.

CONTROL OF REPRODUCTIVE MORPHOGENESIS

An influence of the environment and of hormonal factors on the structure of the tomato inflorescence and of the flower, although limited, has been reported in a few studies. Major effects are on inflorescence branching and number of floral organs, especially the number of stamens and carpels is increased under low temperature (Sawhney 1983; Lozano *et al*. 1998). The number of locules in the ovary is also enhanced by GA_3 (Sawhney and Greyson 1973b).

The genes regulating the morphogenesis of the tomato reproductive structure may be divided into 3 categories (**Table 2**), respectively (1) specifying and/or maintaining the identity of the inflorescence meristem, (2) specifying the identity of the floral meristem and (3) specifying the identity of the floral organs. Many genes of the first 2 categories also affect flowering time and have already been presented in the preceding sections.

Inflorescence meristem identity and/or maintenance genes

SFT and *UF* are among the genes that control the identity of the tomato inflorescence meristem. The morphology of the reproductive structure of the *sft* mutant is highly variable and strongly affected by environmental conditions (Quinet *et al*. 2006b). Solitary flowers are more frequent in winter, when light conditions are poor. In contrast, the reproductive structure of *uf* is remarkably stable. Throughout the years we have not found a single treatment capable of modifying the single-flower phenotype of this mutant. This altered developmental pattern indicates that an inflorescence meristem is not functioning and that both *SFT* and *UF* are implicated in the regulation of the inflorescence meristem identity.

SFT is also involved, along with the *J*, *LeMADS-MC* and *BL* genes, in the maintenance of this identity, preventing reversion to a vegetative identity or early termination of the inflorescence. In summer conditions, the *sft* mutant produces indeed simple or branched inflorescences, with variable numbers of leaves, which revert to sympodial growth. The reproductive structure of the *j* mutant contains flowers and leaves (Rick and Butler 1956; Philouze 1978; Quinet *et al*. 2006b). A first leaf is initiated usually after the production of two flowers, and then the inflorescence produces some flowers and leaves alternately before reverting to a sympodial growth. Axillary meristems are always found at the axil of the leaves and the leaf-axillary meristem complex frequently develops in the place occupied by a flower in the wild-type 'zigzag' inflorescence conformation. Apparently, the inflorescence meristem of the *j* mutant progressively returned to a vegetative functioning, acquiring a vegetative identity by sectors until its total conversion into a vegetative meristem (Quinet *et al*. 2006b). The inflorescence axis of the *mc* mutant and of plants expressing the antisense of *LeMADS-MC* is indeterminate (Rick and Butler, 1956; Vrebalov *et al*. 2002) while in *bl*, inflorescences are highly reduced, producing only 1 to 4 flowers (Schmitz *et al*. 2002).

The *s:uf*, *uf:sp*, *uf:bl* and *j:uf* double mutants all initiate solitary normal fertile flowers, as the *uf* mutant, indicating that *UF* is epistatic to *S*, *SP*, *BL* and *J* in regulating morphogenesis of the reproductive structure of tomato. The reproductive structure of the *sft:uf* mutant has not been observed. However, when the *SFT* gene is overexpressed in a *uf* background, the reproductive structure of the transgenic plant is once again a solitary flower (Lifschitz *et al*. 2006; Lifschitz and Eshed 2006). This suggests that *UF* is also epistatic to *SFT* with respect to the type of the reproductive structure although the reverse was found for the regulation of the flowering time (see above). Dielen *et al*. (1998, 2004) postulated that *UF* is a pivotal gene with a dual role, regulating flowering time and inflorescence meristem identity (Dielen *et al*. 1998, 2004) That *UF* acts upstream of *J*, *BL* and *S* is consistent with the view that *J* and *BL* are involved in the maintenance of the inflorescence meristem identity and that *S* is a floral meristem identity gene (see below), hence all three acting necessarily downstream of a gene which regulates the production of an inflorescence meristem. The *SP* gene has been reported not to be implicated in the regulation of the reproductive structure development (Pnueli *et al*. 1998), thus accounting for the prevailing role of the *uf* mutation in the double mutant *uf:sp*. Several double mutants having *sp* as one of the parents have been described and, in agreement with the view that *SP* would not be involved in the morphogenesis of the reproductive structures, their phenotype is reminiscent of that of the non *sp* parent. (Pnueli *et al*. 1998; Schmitz *et al*. 2002; Molinero-Rosales *et al*. 2004).

The *j:bl-2* double mutant plants are highly determinate, terminating with a solitary flower as a result of the combined loss of inflorescence and sympodial meristems (Szymkowiak and Irish 2006). This additive phenotype indicates that *BL* and *J* are acting independently until the pathways in which they work converge at some point as suggested by the presence of large and leaf-like sepals in the double mutant's flower.

Floral meristem identity genes

The phenotypes of 3 mutants affected in a gene specifying the identity of the floral meristem, namely *COMPOUND INFLORESCENCE* (*S*), *FALSIFLORA* (*FA*) and *ANANTHA* (*AN*) have already been described in section III of this review, devoted to the 'inflorescence architecture'. They produce inflorescences either bearing numerous flowers due to a repeated branching of the reproductive structure, as in *s* (Quinet *et al*. 2006b), or vegetative inflorescences with leaves, in the case of *fa*, or without leaves as in *an* (Allen and Sussex 1996). Another mutant affected in floral meristem identity, namely *leafy inflorescence* (*lfi*), was shown to be allelic to *fa*. The *lfi* mutant shows a less strong phenotype than *fa* since in this mutant, some fleshy carpeloid leaves developed and were able to ripen to a red colour (Kato *et al*. 2005). As already reported, the *FA* tomato gene is the orthologue of the *A. thaliana LFY* gene (Molinero-Rosales *et al*. 1999), one of the most important floral meristem identity genes in this species. The *S* and *AN* tomato genes have not been cloned yet.

Phenotypes of different double mutants having *an* as one of the 2 parents have been described by Allen and Sussex (1996), Pnueli *et al*. (1998) and Szymkowiak and Irish (2006). They indicate that *fa* is completely epistatic to *an* which is consistent with the fact that *fa* appears to be blocked at an earlier stage than *an* (Allen and Sussex 1996).The inflorescence structure of the *an:j* and *bl:an* double mutants is strongly altered and not easily interpreted (Szymkowiak and Irish 2006). In both cases, floral development is inhibited and vegetative development is promoted: inflorescences composed of leaves and elongated internodes, bearing occasionally carpel-like structures, are produced. This phenotype could be indicative of synergistic interactions among the implicated genes.

Finally, a role for *SP* is not completely excluded since overexpression of *SP* in wild-type tomato and *sp* mutant plants resulted in a tendency for the transgenics to promote development of extra leaves in the inflorescences (Pnueli *et al*. 1998). On the same way, *an* and *an:sp* plants overexpressing *SP* have a phenotype similar to *an:j* or *fa* (Allen and Sussex 1996; Pnueli *et al*. 1998, 2001).

Floral organ identity genes

Some mutants, with organ transformations that fit the two-whorl combinatorial ABC model developed by Coen and Meyerowitz (1991) and Meyerowitz *et al*. (1991) for *A. thaliana* and *Antirrhinum majus*, have been identified in tomato. Most of them are B class genes, affected in the second and third whorls, with different degrees of sepaloid petals and carpelloid stamens. Two allelic series were represented among 8 stamenless mutants analysed by Nash *et al*. (1985). Unfortunately, the description of these mutants is frequently insufficient to relate them to those that were most investigated, namely *stamenless-2* (*sl-2*) (Sawhney and Greyson 1973a; Sawhney 1992), *stamenless* (*sl*) (Marc *et al*. 1994; Gomez *et al*. 1999), and *green pistillate* (*gpi*) (Rasmussen and Green 1993). *sl-2* and *sl* probably belong to the same allelic series, but the genetic interaction of *gpi* with other related mutants has not been analysed although the phenotypes of the *gpi* and *sl* flowers are strikingly similar. Flower alterations in *sl-2*, are less than in *sl* and *gpi*. Apparently only stamens are modified in *sl-2*. They are laterally free, twisted, shorter and paler than wild type stamens; they contain abnormal pollen and bear naked external ovules. In *sl* and *gpi*, both whorls two and three are profoundly modified: petals are transformed in sepals and stamens in carpels (**Fig. 5**). The transformed carpels, which may contain ovules (Marc *et al*. 1994), fuse with the central pistil in a unique gynoecium. In both *sl-2* and *sl*, the mutant phenotype is sen-

sitive to temperature and gibberellins, reverting to wild type after treatments at relatively low temperature or by gibberellic acid (Sawhney and Greyson 1973b; Sawhney 1983, 1992; Gomez *et al*. 1999).

Some tomato genes homologue to ABC genes of *A. thaliana* have been isolated. The *TOMATO MADS BOX GENE 6* (*TM6*) and *L. esculentum AP3* gene are homologues to the B class *APETALA3* gene (Pnueli *et al*. 1991; Rijpkema *et al*. 2006); *LeMADS-MC* is the putative orthologue of *AP1* (Vrebalov *et al*. 2002) and a homologue of the class C *AGAMOUS* gene of *A. thaliana* has been designated *TAG1* (Pnueli *et al*. 1994b). Much remains to be discovered about the precise function of these genes in tomato flower development. If phenotype of transgenic plants expressing *TAG1* antisense RNA is consistent with the role of a class C gene, mutations in *LeMADS-MC* cause homeotic conversion from sepals to leaf-like structures without affecting petals identity, which contrasts with the phenotype of the *ap1* mutant of *A. thaliana*, and the role of the dual *AP3/TM6* system remains unknown. *FALSIFLORA* was shown to positively regulate the expression of *TM6* and *TAG1* (Kato *et al*. 2005) suggesting that, as in *Arabidopsis thaliana*, the floral organ identity genes are induced by a meristem identity gene.

The ABC model has now become more complex and includes two additional classes of genes referred to as the D- and E-function genes. D genes characterized in petunia (Angenent *et al*. 1995) are necessary for determining ovule identity and E genes, the *SEPALLATA* (*SEP*) genes in *A. thaliana*, are required for B and C floral organ identity functions (Honma and Goto 2001). In tomato, D genes have not been identified so far while two E class genes that are orthologues of the *SEP* genes of *A. thaliana*: the *TOMATO MADS BOX GENE 5* (*TM5*) and *TOMATO MADS BOX GENE 29* (*TM29*) have been isolated (Pnueli *et al*. 1994a; Ampomah-Dwamena *et al*. 2002). They regulate the formation of the inner three whorls of the tomato flower. *TM5* is positively regulated by *FA* (Kato *et al*. 2005) and its transcripts accumulate in response to a low temperature treatment which enhance the number of stamens and carpels in the flower (Lozano *et al*. 1998).

Several other genes implicated in the differentiation of the floral organs have been identified, indicating that there is still a large field to investigate to understand flower morphogenesis in tomato. They will not be exhaustively reviewed and just the cases of the *LATERAL SUPPRESSOR* (*LS*) and *SOLANIFOLIA* (*SF*) genes will be quoted here as examples of the diversity of functions of genes implicated in the process. The *ls* mutation, so called because it suppresses certain axillary meristems, also suppresses petals (Schumacher *et al*. 1995) whereas the *SF* gene controls the fusion of floral organs in the flower. It has been investigated by Chandra Sekhar and Sawhney (1987, 1990) through a refined analysis of mutant plants.

CONCLUSION

Tomato is for a long time a model plant to investigate the physiological control of flowering in autonomously flowering species. The influences of environmental conditions and of internal signals, such as hormones or carbohydrates, received much attention. Recently, genetic and molecular studies allowed the identification of numerous genes implicated in the regulation of various aspects of tomato reproduction but there is still an important gap preventing the connection with the physiological work. An improved knowledge of how expression of the flowering genes is affected by environmental and internal signals and of how these genes interact during the flowering process is required.

Unravelling the mechanisms involved in the regulation of flowering time in tomato is complicated because the plant has a sympodial growth habit: it flowers repeatedly in successive plant segments and floral transition is not regulated in the same way in the initial and sympodial segments. Schemes intended to summarise the genetic control of flowering of tomato have to take into account this particular and challenging features.

There is a need for a unified vision of the structure and genesis of the inflorescence and flowers of tomato. In the absence of such an agreement, conflicting views concerning the role of the genes regulating the production of the reproductive structures may emerge. One example is provided by the *SFT* gene that, depending on the interpretation of the nature of the tomato inflorescence, is considered to control flower meristem (Lozano *et al*. 2000; Molinero-Rosales *et al*. 2004) or inflorescence meristem (Quinet *et al*. 2006b) identity. Available evidence strongly supports the view that the tomato inflorescence is a raceme.

Further development of reproductive structures to anthesis received much attention since the failure of the tomato plant to set fruit is a common problem. Both fundamental and applied studies investigated the causes of flower abortion before anthesis and of flower shedding after they open. Particular attention was paid to flower fertility and many mutations that affect microsporogenesis and cause male sterility have been investigated (Kaul 1991). Several reviews focussed on theses aspects that are out of the scope of the present paper and the interested readers are referred to these publications (Picken *et al*. 1985, 1986; Gorman and McCormick 1997; Kinet and Peet 1997).

ACKNOWLEDGEMENTS

The authors wish to thank the institutions which funded their work in Louvain-la-Neuve: the Fonds National de la Recherche (FNRS) of Belgium (Fonds de la Recherche Fondamentale et Collective, 2001-2004, 2004-2008) and the Université catholique de Louvain (Fonds Spécial de la Recherche, 1995-1999). MQ is grateful to the FNRS for the award of a research grant.

REFERENCES

Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikeda Y, Ichinoki H, Notaguchi M, Goto K, Araki T (2005) FD, a bzip protein mediating signals from the floral pathway integrator FT at the shoot apex. *Science* **309**, 1052-1056

Allen KD, Sussex IM (1996) *falsiflora* and *anantha* control early stages of floral meristem development in tomato (*Lycopersicon esculentum* Mill.). *Planta* **200**, 254-264

Ampomah-Dwamena C, Morris BA, Sutherland P, Veit B, Yao JL (2002) Down-regulation of *TM29*, a tomato *SEPALLATA* homologue, causes parthenocarpic fruit development and floral reversion. *Plant Physiology* **130**, 605-617

Angenent GC, Franken J, Busscher M, Vandijken A, Vanwent JL, Dons HJM, Vantunen AJ (1995) A novel class of MADS box genes is involved in ovule development in *Petunia*. *Plant Cell* **7**, 1568-1582

Bernier G, Kinet JM, Sachs RM (1981) *The Physiology of Flowering* (Vol 2), CRC Press, Boca Raton, FL, 274 pp

Binchy A, Morgan JV (1970) Influence of light intensity and photoperiod on inflorescence in tomatoes. *Irish Journal of Agricultural Research* **9**, 261-269

Blazquez MA, Soowal LN, Lee Y, Weigel D (1997) *LEAFY* expression and flower initiation in *Arabidopsis*. *Development* **124**, 3835-3844

Bonnand J (1961) Ontogénie de la cyme unipare scorpioïde de *Nicotiana glutinosa* L. *Comptes Rendus de l'Académie des Sciences* **252**, 1498-1500

Brill EM, Watson JM (2004) Ectopic expression of a *Eucalyptus grandis SVP* orthologue alters the flowering time of *Arabidopsis thaliana*. *Functional Plant Biology* **31**, 217-224

Calvert A (1957) The effect of the early environment on the development of flowering in the tomato. I. Temperature. *Journal of Horticultural Science* **32**, 9-17

Calvert A (1959) Effect of the early environment on the development of flowering in tomato II. light and temperature interactions. *Journal of Horticultural Science* **34**, 154-162

Calvert A (1965) Flower initiation and development in the tomato. *National Agricultural Advisor Service Quarterly Review* **70**, 79-88

Carmel-Goren L, Liu YS, Lifschitz E, Zamir D (2003) The *SELF PRUNING* gene family in tomato. *Plant Molecular Biology* **52**, 1215-1222

Chandra Sekhar KN, Sawhney VK (1984) A scanning electron microscope study of the development and surface features of floral organs of tomato (*Lycopersicon esculentum*). *Canadian Journal of Botany* **62**, 2403-2413

Chandra Sekhar KN, Sawhney VK (1987) Ontogenetic study of the fusion of floral organs in the normal and *"solanifolia"* mutant of tomato (*Lycopersicon esculentum*). *Canadian Journal of Botany* **65**, 215-221

Chandra Sekhar KN, Sawhney VK (1990) Regulation of the fusion of floral organs by temperature and gibberellic acid in the normal and *solanifolia* mu-

tant of tomato (*Lycopersicon esculentum*). *Canadian Journal of Botany* **68**, 713-718

Coen ES, Meyerowitz EM (1991) The war of the whorls genetic interaction controlling flower development. *Nature* **353**, 31-37

Coen ES, Romero JM, Doyle S, Elliott R, Murphy G, Carpenter R (1990) *FLORICAULA*: a homeotic gene required for flower development in *Antirrhinum majus*. *Cell* **63**, 1311-1322

Cooper DC (1927) Anatomy and development of tomato flower. *Botanical Gazette* **83**, 399-411

de Zeeuw D (1954) De invloed van het blad op de bloei. *Mededelingen van de Landbouwhogeschool te Wageningen* **54**, 1-44

Dielen V, Marc D, Kinet JM (1998) Flowering in the *uniflora* mutant of tomato (*Lycopersicon esculentum* Mill.): description of the reproductive structure and manipulation of flowering time. *Plant Growth Regulation* **25**, 149-157

Dielen V, Quinet M, Chao J, Batoko H, Havelange A, Kinet JM (2004) *UNIFLORA*, a pivotal gene that regulates floral transition and meristem identity in tomato (*Lycopersicon esculentum*). *New Phytologist* **161**, 393-400

Ecole D (1974) Fonctionnement sympodial chez deux Solanacées du genre *Lycopersicum*. *Revue de Cytologie et Biologie Végétales* **37**, 127-160

Ellul P, Angosto T, Garcia-Sorgo B, Garcia-Hurtado N, Martin-Trillo M, Salinas M, Moreno V, Lozano R, Martinez-Zapater JM (2004) Expression of *Arabidopsis APETALA1* in tomato reduces its vegetative cycle without affecting plant production. *Molecular Breeding* **13**, 155-163

Emery GC, Munger HM (1970) Alteration of growth and flowering in tomatoes by the *Jointless* genotype. *The Journal of Heredity* **61**, 51-53

Evans LT (1993) The physiology of flower induction paradigm lost and paradigm regained. *Australian Journal of Plant Physiology* **20**, 655-660

Giliberto G, Perrotta G, Pallara P, Weller JL, Fraser PD, Bramley PM, Fiore A, Tavazza M, Giuliano G (2005) Manipulation of the blue light photoreceptor Cryptochrome 2 in tomato affects vegetative development, flowering time, and fruit antioxidant content. *Plant Physiology* **137**, 199-208

Gomez P, Jamilena M, Capel J, Zurita S, Angosto T, Lozano R (1999) *Stamenless*, a tomato mutant with homeotic conversions in petals and stamens. *Planta* **209**, 172-179

Gorman SW, McCormick S (1997) Male sterility in tomato. *Critical Reviews in Plant Sciences* **16**, 31-53

Gorenflot R (1997) Biologie végétale In: Masson (Ed) *Plantes Supérieures: Appareil Reproducteur* (Vol II, 3rd Edn), Paris, France, 256 pp

Green PB (1988) A theory for inflorescence development and flower formation based on morphological and biophysical analysis in *Echeveria*. *Planta* **175**, 153-169

Guo H, Yang H, Mockler TC, Lin C (1998) Regulation of flowering time by *Arabidopsis* photoreceptors. *Science* **279** 1360-1360

Harlan JR (1992) *Crops and Man* (2nd Edn), American Society of Agronomy, Crop Science Society of America, Madison, Wisconsin, USA, 284 pp

Hartmann U, Hohmann S, Nettesheim K, Saedler H, Huijser P (2000) Molecular cloning of *SVP*: a negative regulator of the floral transition in *Arabidopsis*. *Plant Journal* **21**, 351-360

Honma T, Goto K (2001) Complexes of MADS-box proteins are sufficient to convert leaves into floral organs. *Nature* **409**, 525-529

Huang, T, Bohlenius H, Eriksson S, Parcy F, Nilsson O (2005) The mRNA of the *Arabidopsis* gene *FT* moves from leaf to shoot apex and induces flowering. *Science* **309**, 1694-1696

Hurd RG, Cooper AJ (1970) The effect of early low temperature treatment on the yield of single-inflorescence tomatoes. *Journal of Horticultural Science* **45**, 19-27

Kaul MLH (1991) Reproductive biology in tomato. In: Kalloo G (Ed) *Genetic Improvement of Tomato, Monographs on Theoretical and Applied Genetics* (Vol 14), Springer-Verlag, Berlin, Germany, pp 39-50

Kalloo G (1991) Introduction. In: Kalloo G (Ed) *Genetic Improvement of Tomato, Monographs on Theoretical and Applied Genetics* (Vol 14), Springer-Verlag, Berlin, Germany, pp 1-9

Kato K, Ohta K, Komata Y, Araki T, Kanahama K, Kanayama Y (2005) Morphological and molecular analyses of the tomato floral mutant *leafy inflorescence*, a new allele of *falsiflora*. *Plant Science* **169**, 131-138

Kinet JM (1977a) Effect of defoliation and growth substances on the development of the inflorescence in tomato. *Scientia Horticulturae* **6**, 27-35

Kinet JM (1977b) Effect of light conditions on the development of the inflorescence on tomato. *Scientia Horticulturae* **6**, 15-26

Kinet JM (1989) Environmental and chemical control of flower development. In: Lord E, Bernier G (Eds) *Plant Reproduction: From Floral Induction to Pollination*, American Society of Plants Physiologists Symposium Series (Vol I), Rokville, MD, pp 95-105

Kinet JM, Sachs RM, Bernier G (1985) *The Physiology of Flowering*, *The Development of Flowers* (Vol III), CRC Press, Boca Raton, FL, 274 pp

Kinet JM, Peet MM (1997) Tomato. In: Wien HC (Ed) *The Physiology of Vegetable Crops*, CAB International, Wallingford, pp 207-258

Kobayashi K, Kaya H, Goto K, Iwabuchi M, Araki T (1999) A pair of related genes with antagonistic roles in mediating flowering signals. *Science* **286**, 1960-1962

Lewis D (1953) Some factors affecting flower production in the tomato. *Journal of Horticultural Science* **28**, 207-220

Lifschitz E, Eviatar T, Rozman A, Shalit A, Goldshmidt A, Amsellem Z, Alvarez JP, Eshed Y (2006). The tomato FT ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. *Proceedings of the National Academy of Sciences USA* **103**, 6398-6403

Lifschitz E, Eshed Y (2006) Universal florigenic triggered by *FT* homologues regulate growth and flowering cycles in perennial day-neutral tomato. *Journal of Experimental Botany* **57**, 3405-3414

Lozano R, Angosto T, Gomez P, Payan C, Capel J, Huijser P, Salinas J, Martinez-Zapater JM (1998) Tomato flower abnormalities induced by low temperatures are associated with changes of expression of MADS-box genes. *Plant Physiology* **117**, 91-100

Lozano R, Angosto T, Capel J, Gomez P, Molinera-Rosales N, Zurita S, Jamilena M (2000) Floral transition and flower development in tomato: functional homology with *Arabidopsis*. *Flowering Newsletter* **30**, 26-33

Mao L, Begum D, Chuang HW, Budiman MA, Symkowiak EJ, Irish EE, Wing RA (2000) *Jointless* is a MADS-box gene controlling tomato flower abscission zone development. *Nature* **206**, 910-913

Marc D, Orban I, Kinet JM (1994) Phenotypic characterization of the recessive mutation *stamenless* (*sl*) in tomato (*Lycopersicon esculentum*). *Biologia Plantarum* **36** (Suppl.), S102

Menda N, Semel Y, Peled D, Eshed Y, Zamir D (2004) *In silico* screening of a satured mutation library of tomato. *Plant Journal* **38**, 861-872

Meyerowitz EM, Bowman JL, Brockman LL, Drews GN, Jack T, Sieburth LE, Weigel D (1991) A genetic and molecular model for flower development in *Arabidopsis thaliana*. *Development* **S1**, 157-167

Micallef BJ, Haskins KA, Vanderveer PJ, Roh KS, Shewmaker CK, Sharkey TD (1995) Altered photosynthesis, flowering, and fruiting in transgenic tomato plants that have an increased capacity for sucrose synthesis. *Planta* **196**, 327-334

Molinero-Rosales N, Jamilena M, Zurita S, Gomez P, Capel J, Lozano R (1999) *FALSIFLORA*, the tomato orthologue of *FLORICAULA* and *LEAFY*, controls flowering time and floral meristem identity. *The Plant Journal* **20**, 685-693

Molinero-Rosales N, Latorre A, Jamilena M, Lozano R (2004) *SINGLE FLOWER TRUSS* regulates the transition and maintenance of flowering in tomato. *Planta* **218**, 427-434

Müller D, Schmitz G, Theres K (2006) *Blind* homologous R2R3 Myb genes control the pattern of lateral meristem initiation in *Arabidopsis*. *Plant Cell* **18**, 586-597

Nash AF, Gardner RG, Henderson WR (1985) Evaluation of allelism and seed set of eight stamenless tomato mutants. *HortScience* **20**, 440-442

Peralta IE, Knapp SK, Spooner DM (2005) New species of wild tomatoes (*Solanum* section *Lycopersicon: Solanaceae*) from Northern Peru. *Systematic Botany* **30**, 424-434

Philouze J (1978) Comparaison des effets des gènes *J* et *J-2* conditionnant le caractère '*jointless*' chez la tomate et les relations d'épistasie entre *j* et *j-2* dans les lignées de même type variétal. *Annales d'Amélioration des Plantes* **28**, 431-445

Picken AJF, Hurd RG, Vince-Prue D (1985) *Lycopersicon esculentum*. In: Halevy AH (Ed) *CRC Handbook of Flowering* (Vol III), CRC Press, Boca Raton, FL, pp 330-346

Picken AJF, Grimmett M (1986) The effects of two fruit setting agents on the yield and quality of tomato fruit in glasshouses in winter. *Journal of Horticultural Science* **61**, 243-250

Pnueli L, Abu-Abeid M, Zamir D, Nacken W, Schwarzsommer Z, Lifschitz E (1991) The MADS box gene family in tomato: temporal expression during floral development, conserved secondary structures and homology with homeotic genes from *Antirrhinum* and *Arabidopsis*. *The Plant Journal* **1**, 255-266

Pnueli L, Carmel-Goren L, Hareven D, Gutfinger T, Alvarez J, Ganal M, Zamir D, Lifschitz E (1998) The *SELF-PRUNING* gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of *CEN* and *TFL1*. *Development* **125**, 1979-1989

Pnueli L, Gutfinger T, Hareven D, Ben-Naim O, Ron N, Adir N, Lifschitz E (2001) Tomato SP-interacting proteins define a conserved signaling system that regulates shoot architecture and flowering. *Plant Cell* **13**, 2687-2702

Pnueli L, Hareven D, Rounsley SD, Yanofsky MF (1994a) Isolation of the tomato *AGAMOUS* gene *TAG1* and analysis of its homeotic role in transgenic plants. *Plant Cell* **6**, 163-173

Pnueli L, Hareven D, Broday L, Hurwitz C (1994b) The TM5 MADS box gene mediates organ differentiation in the three inner whorls of tomato flowers. *Plant Cell* **6**, 175-186

Quinet M (2005) Genetical control of flowering in tomato (*Lycopersicon esculentum* Mill.): A case study of some key genes regulating flowering time and morphogenesis of reproductive structures. PhD Thesis, Université Catholique de Louvain, Belgium, 192 pp

Quinet M, Dielen V, Batoko H, Boutry M, Havelange A, Kinet JM (2006a) Genetic interactions in the control of flowering time and reproductive structure development in tomato (*Solanum lycopersicum*). *New Phytologist* **170**, 701-710

Quinet M, Dubois C, Goffin MC, Chao J, Dielen V, Batoko H, Boutry M, Kinet JM (2006b) Characterization of tomato (*Solanum lycopersicum* L.) mutants affected in their flowering time and in the morphogenesis of their

reproductive structure. *Journal of Experimental Botany* **57**, 1381-1390

Rasmussen N, Green PB (1993) Organogenesis in flowers of the homeotic *green pistillate* mutant of tomato (*Lycopersicon esculentum*). *American Journal of Botany* **80**, 805-813

Rick CM (1978) The tomato. *Science* **239**, 66-76

Rick CM, Butler L (1956) Cytogenetics of tomato. *Advanced Genetics* **8**, 847-857

Rijpkema AS, Royaert S, Zethof S, van der Weerden G, Gerats T, Vandenbussche M (2006) Analysis of the Petunia *TM6* MADS box gene reveals functional divergence within the *DEF/AP3* lineage. *Plant Cell* **18**, 1819-1832

Sawhney VK (1983) Temperature control of male sterility in a tomato mutant. *The Journal of Heredity* **74**, 51-54

Sawhney VK (1992) Floral mutants in tomato: development, physiology and evolutionary implications. *Canadian Journal of Botany* **70**, 701-707

Sawhney VK, Greyson RI (1972) On the initiation of the inflorescence and floral organs in tomato (*Lycopersicon esculentum*). *Canadian Journal of Botany* **50**, 1493-1495

Sawhney VK, Greyson RI (1973a) Morphogenesis of the *stamenless-2* mutant in tomato. I. comparative description of the flowers and ontogeny of stamens in the normal and mutant plants. *American Journal of Botany* **60**, 514-523

Sawhney VK, Greyson RI (1973b) Morphogenesis of the *stamenless-2* mutant in tomato. II. Modifications of sex organs in the mutant and normal flowers by plant hormones. *Canadian Journal of Botany* **51**, 2473-2479

Schmitz G, Tillmann E, Carriero F, Fiore C, Cellini F, Theres K (2002) The tomato *Blind* gene encodes a MYB transcription factor that controls the formation of lateral meristems. *Proceedings of the National Academy of Sciences USA* **99**, 1064-1069

Schumacher K, Ganal M, Theres K (1995) Genetic and physical mapping of the *LATERAL SUPPRESSOR* (*LS*) Locus in tomato. *Molecular and General Genetics* **246**, 761-766

Schumacher K, Schmitt T, Rossberg M, Schmitz C, Theres K (1999) The *Lateral suppressor* (*Ls*) gene of tomato encodes a new member of the VHIID protein family. *Proceedings of the National Academy of Sciences USA* **96**, 290-295

Szymkowiak EJ, Irish EE (1999) Interactions between *jointless* and wild-type tomato tissues during development of the pedicel abscission zone and the inflorescence meristem. *Plant Cell* **11**, 159-175

Szymkowiak EJ, Irish EE (2006) *JOINTLESS* suppresses sympodial identity in inflorescence meristems of tomato. *Planta* **223**, 646-658

Vrebalov J, Ruezinsky D, Padmanabhan V, White R, Medrano D, Drake R, Schuch W, Giovannoni J (2002) A MADS-box gene necessary for fruit ripening at the tomato ripening-inhibitor (Rin) locus. *Science* **296**, 343-346

Weberling F (1989) *Morphology of Flowers and Inflorescences*, Cambridge University Press, Cambridge, UK, 405 pp

Wittwer SH, Teubner FG (1957) The effects of temperature and nitrogen nutrition on flower formation in the tomato. *American Journal of Botany* **44**, 125-129