NOTE / NOTE

Inflorescence development in two tomato species

N. Welty, C. Radovich, T. Meulia, and E. van der Knaap

Abstract: The inflorescence of tomato has been characterized as either a cyme or raceme. Cymose inflorescences are determinate, whereas racemose inflorescences are indeterminate. In this study, we addressed the discrepancy in inflorescence architecture by analyzing the morphology of a wild relative of tomato *Solanum pimpinellifolium* L. and four domesticated *Solanum lycopersicum* L. lines. Careful observation of developing inflorescences of both species showed a bifurcation of the meristem into a determinate floral and an indeterminate inflorescence meristem. Interestingly, higher fruit carpel number was associated with delayed floral development, which might give the impression of determinate growth in some of the lines. Nevertheless, our results demonstrated that tomato inflorescences are indeterminate in nature regardless of the line studied. Floral buds were formed concomitantly with the development of the inflorescence meristem and not on the flanks of the peduncle, a characteristic of racemose growth. Thus, tomato inflorescences should be classified as a cyme with the note that the inflorescence meristem does not terminate into a flower and, in fact, maintains indeterminacy. In addition, *S. pimpinellifolium* produced many more flowers in a highly regular manner when compared with the cultivated types. This demonstrated the usefulness of wild relatives of tomato as a tool to further understand flower and fruit development in this crop species.

Key words: inflorescence, tomato, cyme, raceme, meristem, bifurcation.

Résumé : On a caractérisé l'inflorescence de la tomate comme une cyme ou un racème. Les inflorescences en cyme sont déterminées, alors que les inflorescences en racème sont indéterminées. Les auteurs examinent ici la divergence de l'architecture florale en analysant la morphologie d'un congénère sauvage de la tomate, le *Solanum pimpinellifolium* L., et quatre lignées domestiquées du *Solanum lycopersicum* L. Une observation soignée du développement des inflorescences, chez les deux espèces, révèle une bifurcation du méristème en un méristème floral déterminé et un méristème indéterminé de l'inflorescence. Il faut noter qu'un nombre plus élevé de carpelles est associé à un délai du développement floral, ce qui pourrait donner l'impression d'une croissance déterminée, chez certaines lignées. Cependant, les résultats démontrent que les inflorescences sont déterminées en nature, indépendamment de la lignée étudiée. Les bourgeons floraux se forment de façon concomitante au développement du méristème de l'inflorescence, et non sur le flanc du pédoncule, une caractéristique de la croissance en racème. Ainsi, les inflorescences de tomate devraient être classifiées comme une cyme, en notant que le méristème de l'inflorescence ne se termine pas par une fleur et, en fait, maintient son indétermination. De plus, le *S. pimpinellifolium* produit beaucoup plus de fleurs de façon régulière que ne le font les types cultivés. Ceci démontre l'utilité des congénères sauvages de la tomate comme moyen de mieux comprendre le développement et la croissance de cette espèce cultivée.

Mots clés : inflorescence, tomate, cyme, racème, méristèmes, bifurcation.

[Traduit par la Rédaction]

Introduction

The inflorescence of species in the *Solanaceae* family has been generally classified as a cyme. Typically, cymose inflorescences are defined by determinate growth in which the inflorescence meristem terminates into a floral bud, followed by the next floral meristem forming on the flank of the previous flower. The helicoid cyme produces floral buds on a single side of the peduncle, whereas the scorpioid cyme produces floral buds alternately on opposing sides of the peduncle. Unlike a cyme, a raceme inflorescence does not terminate into a flower, rather, the inflorescence meristem remains indeterminate, and floral meristems are produced in a monopodial manner on the flank of the inflorescence meristem (Fig. 1).

The earliest study that described tomato inflorescences as cymose was based on observation by unaided eye (Cooper 1927). Other studies indicated that environment and (or) genotype played an important role in determining either

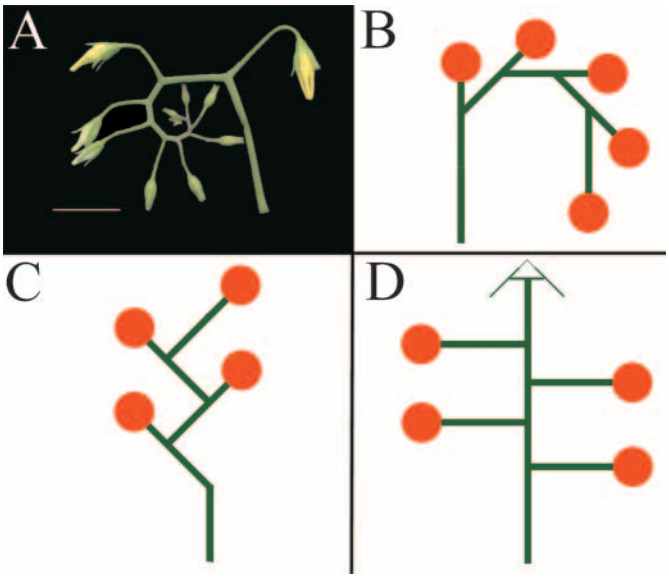
Received 30 November 2006. Published on the NRC Research Press Web site at http://canjbot.nrc.ca on 16 March 2007.

N. Welty, C. Radovich, and E. van der Knaap.[1] Horticulture and Crop Sciences, The Ohio State University – Ohio Agricultural Research and Development Center (OARDC), Wooster OH 44691, USA.
T. Meulia. Molecular and Cellular Imaging Center, The Ohio State University – Ohio Agricultural Research and Development Center (OARDC), Wooster OH 44691, USA.

[1]Corresponding author (e-mail: vanderknaap.1@osu.edu).

 doi:10.1139/B06-154

Fig. 1. Inflorescence structures. (A) An inflorescence of *Solanum pimpinellifolium* LA1589. (B) Helicoid cyme. (C) Scorpioid cyme. (D) Raceme. Scale bar = 1 cm.



cymose or racemose inflorescence structure (Went 1944). Using light microscopy techniques, Sawhney and Greyson (1972) concluded that the inflorescence apex formed the first flower, while the next flower initiated as a protuberance from the base of the previous flower with succeeding flowers forming in a similar manner thus producing a cyme. This study was followed by a scanning electron microscopic analysis of inflorescence development after which similar conclusions were reached (Chandra Sekhar and Sawhney 1984). However, the conclusion of cymose development of the tomato inflorescence was challenged by Allen and Sussex (1996). Their description of inflorescence development indicated that growth proceeded via apparent bifurcations of the inflorescence meristem. These results implied that the tomato inflorescence was indeterminate rather than determinate in nature, hence more similar to a raceme (Allen and Sussex 1996). Previously, Ecole (1974) concluded that a narrow band of differentiated cells divided the prefloral stem cell region into a flower and a meristematic region consistent with the observations made by Allen and Sussex (1996). Despite the conflicting conclusions, the issue was not resolved, and many researchers still considered tomato inflorescence growth as cymose, in which the inflorescence meristem terminated in a floral bud.

In our laboratory, tomato flower and fruit development is studied as part of a larger project focused on fruit morphology. Most of our efforts are centered on a particular accession of a close wild relative of tomato, *Solanum pimpinellifolium* L., LA1589. This red-fruited species produces inflorescences with an average of 20 flowers, giving the impression of an indeterminate reproductive structure. In addition to the differing conclusions on cultivated tomato inflorescence development as mentioned above, others classified the inflorescence of *S. pimpinellifolium* as a raceme, whereas cultivated types were classified as either raceme or branched racemose-cyme types (Hayward 1938). This led to the hypothesis that tomato inflorescence structure is different between tomato species. To shed light on tomato inflorescence architecture and to address whether cultivated tomato displays an altered inflorescence compared with wild relatives, we investigated the early stages of inflorescence development of several *Solanum lycopersicum* L. lines and LA1589. In addition, we determined flower opening, carpel number, and fruit mass of each line to further correlate these earliest stages of inflorescence development with flower and fruit characteristics.

Materials and methods

Plant materials

Accession LA1589 (*Solanum pimpinellifolium* L.) was used in this study as the reference wild tomato species. *Solanum lycopersicum* L. lines were selected based on their use in previous studies: LA0854 (Allen and Sussex 1996); Marglobe, LA0502 (Went 1944); Vantage, LA3905 (similar to the variety used by Sawhney and Greyson 1972); Pearson, LA0012 (Chandra Sekhar and Sawhney 1984). LA0854 seed lot is heterozygous for the *falsiflora* mutation, which, when homozygous, fails to produce flowers. Thus, floral development was analyzed in heterozygous or homozygous wild-type lines. These seed stocks were obtained from the C.M. Rick Tomato Genetics Resource Center, Davis, California. Plants were randomized and grown in the greenhouse twice (June–August 2005 and March–May 2006) in 1-gallon containers (1 gal (Imp.) = 4.546 L) under the following conditions: night 20–22 °C (±3.3 °C) and day 27–29 °C (±3.3 °C) with supplemental lighting from 0600 to 2200 h during cloudy conditions (less than 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$).

Scanning electron microscopy

LA1589 shoots were harvested 12, 14, 17, or 19 d after sowing. The proximal visible leaves were removed prior to fixation of the remaining apex. A similar procedure performed on seedlings of *S. lycopersicum* lines failed to yield developing inflorescences because of delayed floral transition and irregular pattern of floral development in these lines. Instead, inflorescences were collected from new lateral shoots carrying two visible leaves. The inflorescence samples were vacuum infiltrated and fixed in 2% glutaraldehyde, 4% paraformaldehyde, 0.05% Triton-X in 0.1 $mol \cdot L^{-1}$ potassium phosphate buffer at pH 7.0 for 2 h at room temperature and then overnight at 4 °C. After three washes with potassium phosphate buffer, samples were dehydrated through a graded ethanol series, critical point dried, mounted on aluminum stubs, and sputter-coated with platinum. When necessary, buds were further dissected after platinum coating. Samples were viewed, and images were recorded using a Hitachi S-3500 N scanning electron microscope under high vacuum. Three to eight inflorescences harvested from the plants grown in 2005 were analyzed per genotype.

Phenotypic analyses

Number of flowers per inflorescence, and fruit carpel number and mass were collected from the two experiments. Flowers were hand-pollinated to ensure uniform fruit set. Flower opening was determined as follows: inflorescences with unopened flowers were tagged, and flower opening was monitored daily for each flower on a given inflores-

cence. From this, the number of days between consecutive flower openings was counted and termed "days between anthesis" (DBA). The DBA count was repeated on several inflorescences per plant. Branched inflorescences or inflorescences that showed vegetative reversion were discarded from the analysis. Fruit that exhibited blossom end rot were excluded from the mass measurements.

Statistical analysis

Data for number of flowers per inflorescence, fruit carpel number and mass, and DBA were analyzed using an ANOVA model that included genotype, experiment, and genotype × experiment interaction as sources of variation using the SAS system 9.1 (SAS institute Inc., Cary, North Carolina) GLM procedure. The proportion of variance explained for each term in the model was estimated using the VARCOMP procedure. Significance was ascertained from p values calculated from type III sums of squares with degrees of freedom estimated using the Satterthwaite approximation to correct for differences in sample sizes. Mean separations were determined using a t test only after a significant ANOVA.

Results

Our objective was to examine and compare the early stages of inflorescence development in the wild species *S. pimpinellifolium* accession LA1589 and several accessions of cultivated tomato. The *S. lycopersicum* lines used in this comparative analysis were also used in previous studies: LA0854 by Allen and Sussex (1996), Marglobe by Went (1944), Vantage, which is very similar to the variety used by Sawhney and Greyson (1972), and Pearson by Chandra Sekhar and Sawhney (1984).

An overview of an LA1589 inflorescence is depicted in Fig. 1A. This inflorescence resembled the structure of a scorpioid cyme (Fig. 1C). The other major cyme structure is represented by the helicoid cyme shown in Fig. 1B. Raceme structure, in which the floral buds develop at the flanks of the inflorescence meristem, is depicted in Fig. 1D. LA1589 inflorescences with developing fruit resembled a racemose structure. Based on observations by the unaided eye however, it is difficult to conclusively classify the inflorescence as either cymose or racemose. Therefore, we conducted scanning electron microscopy analysis to further investigate the formation of the inflorescence and floral meristems. The transition to flowering occurred with the termination of the shoot meristem into an inflorescence meristem (if) (Figs. 2A, 2B). Vegetative growth continued with the formation of the sympodial unit (su) in the axil of the proximal leaf. The youngest floral bud is indicated with a "1" in Figs. 2B, 2C, 2D, and the next youngest is indicated with a "2". Whereas the vegetative meristem clearly terminated into the inflorescence meristem, the inflorescence meristem did not appear to terminate into the floral meristem. Instead, the inflorescence meristem of LA1589 bifurcated, giving rise to the floral meristem (arrow, Figs. 2C, 2D). These bifurcations took place at an angle perpendicular to the previous bifurcation. The round inflorescence meristem maintained its indeterminate growth pattern, while the floral meristem flattened and developed into a flower. Slightly older inflorescences of LA1589 with four to five floral buds are shown in Figs. 2E and 2F, respectively. In LA1589, individual inflorescences continued to produce many more flowers.

Inflorescence structure of four cultivated *S. lycopersicum* lines is depicted in Fig. 3. The floral buds of wild-type LA0854 are shown with the fifth youngest in the upper right corner (Fig. 3A). A close-up view of the inflorescence meristem showed that the second youngest bud was separated by a clear crease from the inflorescence meristem (Fig. 3B). Perpendicular to this crease, another crease was developing separating the inflorescence meristem from the youngest bud by bifurcation (arrow, Fig. 3B). The development of the inflorescence of tomato line Marglobe was similar to that of LA0854 (Figs. 3A, 3C). The second youngest bud (upper left corner in Fig. 3D) was clearly separated by a crease from the inflorescence meristem, which just started to bifurcate again (arrow, Fig. 3D). The line Vantage showed similar inflorescence morphology to LA0854 and Marglobe (Figs. 3A, 3C, 3,E). When examining the inflorescence structure of Vantage in detail, a crease could be distinguished (arrow, Fig. 3F) in addition to a newer but less visible crease (arrowhead, Fig. 3F). Lastly, in Pearson, floral development appeared irregular (Figs. 3G, 3H). The oldest flower bud of Pearson (4) is much larger than the second oldest bud positioned to its right (3) when compared with the size of consecutive buds of the other lines (Figs. 3A, 3C, 3E, 3G). This implied that in Pearson, floral formation did not occur at regular time intervals and was less predictable than the other lines. In addition, it was difficult to discern the bifurcating inflorescence meristem in the Pearson line (arrow, Fig. 3H); however, this may be due to the limited number of flowers formed on its inflorescences restricting the opportunity to observe this stage of floral development. Nevertheless, the inflorescence meristem of Pearson was still visible and did not terminate in a floral bud (Fig. 3H). In summary, when comparing inflorescence structure of *S. lycopersicum* lines with LA1589, development of floral and inflorescence meristems appeared to be similar between the domesticated lines and the wild relative. In all cases, we were able to detect a bifurcating inflorescence meristem giving rise to a new floral bud. Thus, we concluded that inflorescence structure was the same in both *S. lycopersicum* and *S. pimpinellifolium* and resulted from an apparent bifurcation of the meristem, which gave rise to a floral meristem while continuing the inflorescence meristem in an indeterminate fashion.

To determine whether the lines differed in other floral and fruit developmental parameters, we examined the number of flowers per inflorescence, carpel number, fruit mass, and days between anthesis (DBA, Table 1). LA1589 displayed the largest number of flowers per inflorescence followed by LA0854. Conversely, LA1589 carried the smallest fruit followed by LA0854. Furthermore, number of flowers per inflorescence was inversely associated to carpel number and to a lesser extent fruit size (Table 1). In addition to carpel number, other factors also influence fruit size. For example, Pearson carried fruit comprising approximately 10 carpels that weighed 150 g on average, whereas Marglobe carried fruit comprising only 4 carpels that weighed nearly the same as Pearson. With respect to the time between consecu-

Fig. 2. Floral transition and inflorescence development of *Solanum pimpinellifolium* LA1589. (A) The shoot meristem terminates into an inflorescence meristem. The sympodial unit, which will continue vegetatively before terminating into an inflorescence meristem, has emerged in the axil of the youngest leaf. (B) Inflorescence showing a stage-1 bud (1). (C) Slightly older inflorescence displaying the youngest floral bud (1) and second youngest bud (2). The arrow points to the bifurcation. (D) The same inflorescence as in C viewed from a different angle. (E, F) Overview of an inflorescence with four and five floral buds, respectively. Scale bar = 50 μm. if, inflorescence meristem; su, sympodial unit; 1, youngest floral bud; 2, second youngest floral bud, and so on.

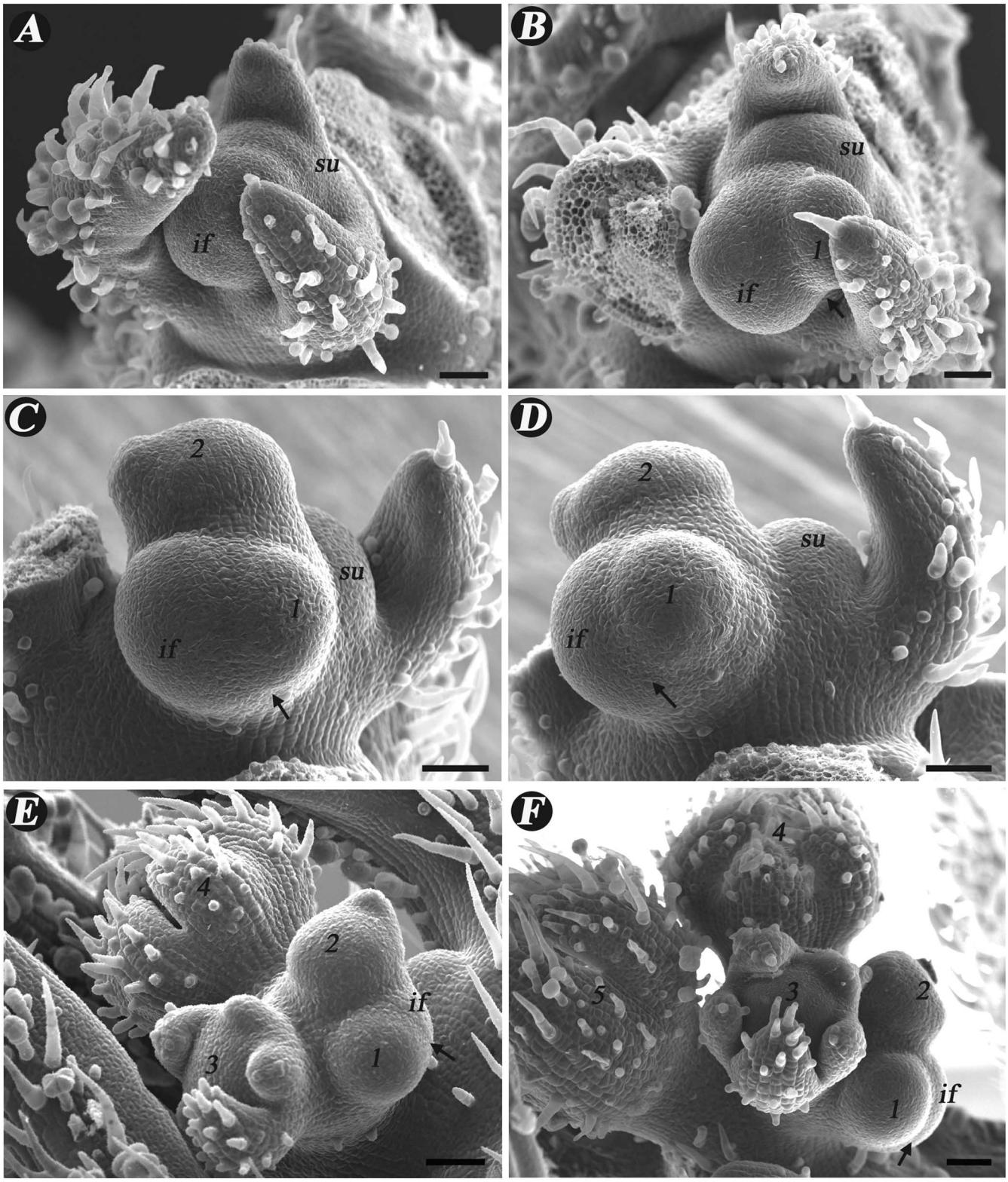


Fig. 3. Inflorescence development of *Solanum lycopersicum* lines: (A and B) LA0854; (C and D) Marglobe; (E and F) Vantage; (G and H) Pearson. Scale bar = 100 μm in A, C, E, G; scale bar = 50 μ m in B, D, F, H. Identical inflorescences are presented in the paired images at lower (A, C, E, G) and higher (B, D, F, H) magnification. Arrows point to the bifurcation. if, inflorescence meristem; 1, youngest floral bud; 2, second youngest floral bud, and so on.

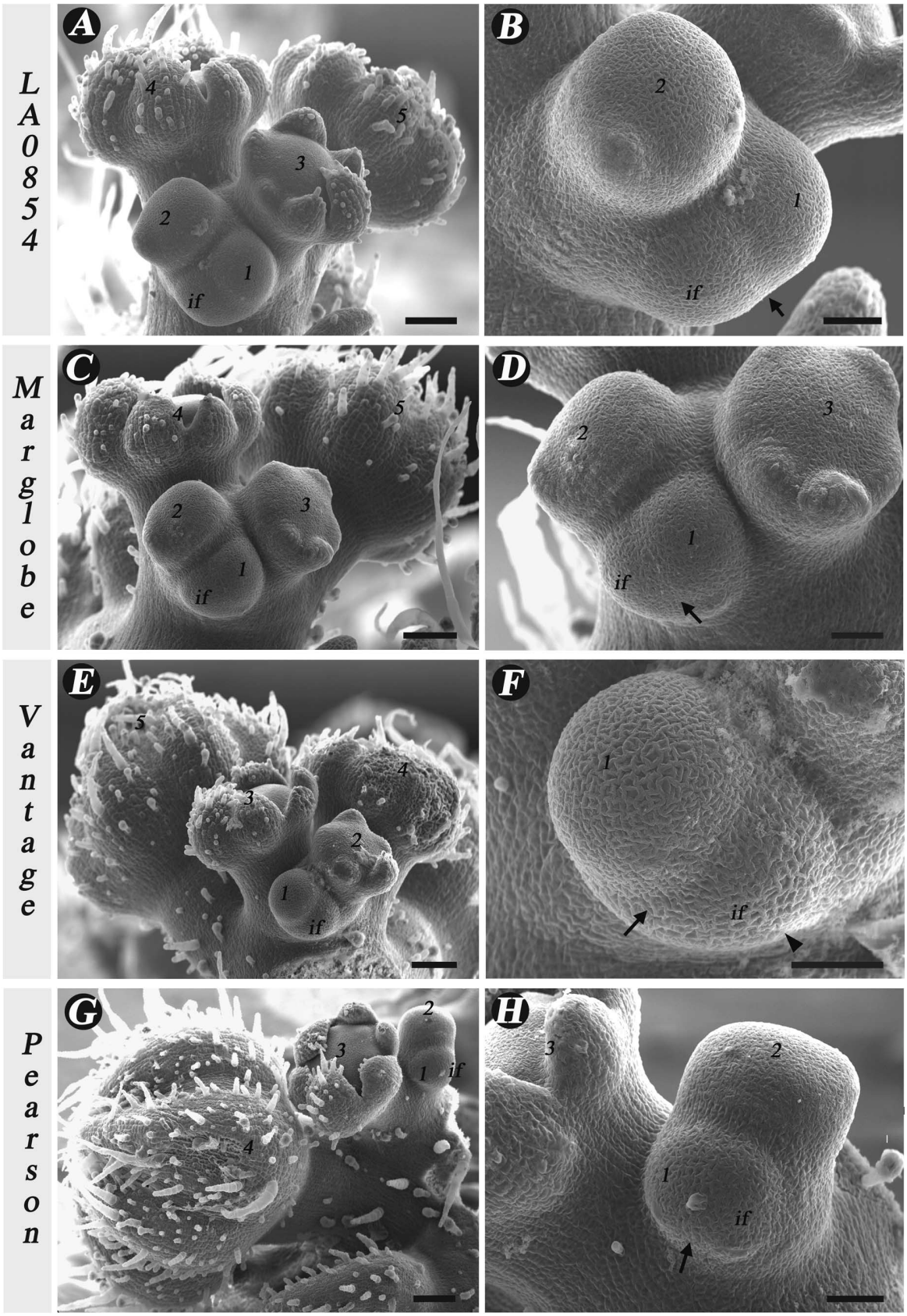


Table 1. Floral and fruit characteristics of *Solanum pimpinellifolium* LA1589 and *Solanum lycopersicum* lines.

	LA1589	LA0854	Marglobe	Vantage	Pearson
Flowers per inflorescence	19.7a	7.1b	5.7c	4.1d	2.8e
Carpel number	2a	2.1a	4.2b	5b	9.5c
Fruit mass (g)	1.1a	87b	166c	124d	150cd
DBA	0.91a	1.5b	1.4b	1.4b	2.6c

Note: Values followed by the same letter are not significantly differents. DBA, "days between anthesis" of consecutive flowers beginning with the second oldest flower on a given inflorescence.

tive flower opening, which we used as an indirect measure of the timing of floral bud development, the wild relative LA1589 showed values of 0.91 d between anthesis (DBA, Table 1). This number meant that out of 100 flowers, 91 opened 1 d after the previous flower opened, whereas 9 flowers opened within 24 h of one another. Thus for a given inflorescence of LA1589, flower opening of consecutive buds occurred at close to 24 h intervals. Flower opening in the domesticated lines was delayed compared with the wild relative LA1589 (Table 1). The lines LA0854, Marglobe, and Vantage displayed DBA values between 1.4 and 1.5, which was not significantly different between these three lines but was different from LA1589 (Table 1). Pearson displayed a DBA value of 2.6, which was significantly different from LA1589, LA0854, Marglobe, and Vantage. In addition, as carpel number increased, so did the DBA value, which implied that floral development on an inflorescence was delayed in lines carrying highly loculed fruit (Table 1).

Discussion

Tomato reproductive development initiates with the termination of the primary shoot meristem into an inflorescence. Our observations show that following termination of the vegetative shoot meristem, reproductive development ensues via apparent consecutive bifurcations of the inflorescence meristem, thus producing a floral meristem while maintaining the inflorescence meristem. This bifurcation process is seen in all the lines we investigated. Therefore, we conclude that inflorescence and floral meristem development is similar between a wild relative and cultivated lines of tomato. Moreover, our results indicate that an increase in fruit carpel number, and to a lesser extend decrease in number of flowers per inflorescence and increase in fruit mass, is associated with a decrease in DBA, that is, delayed floral development. For example the line Pearson, carrying the highest loculed fruit of the lines studied, displays the longest time between consecutive flower openings (Table 1). The significance of correlations of DBA and the floral and fruit characteristics was not determined because of the relatively limited number of lines analyzed. However, the results indicate that the inflorescence architecture of cultivated tomato may give the appearance of cymose and determinate growth because of the delay of floral outgrowth and fewer flowers formed. Despite the appearance of the inflorescence terminating in a flower in cultivated tomato, our data support the notion that tomato inflorescence meristem does not terminate but instead bifurcates.

Our description of tomato inflorescence and floral formation is in agreement with that of Ecole (1974), Allen and Sussex (1996), and recently Quinet et al. (2006). Instead, some researchers consider the tomato inflorescence terminates into a flower after which the inflorescence continues on the flank of the flower, hence resulting in a determinate structure (Sawhney and Greyson 1972; Chandra Sekhar and Sawhney 1984; Pnueli et al. 1998; Brukhin et al. 2003; Molinero-Rosales et al. 2004). A description of developing inflorescences of a plant with cymose structure, *Echeveria derenbergii*, is presented by Green (1988). In this study, the division of the inflorescence of *E. derenbergii* is described, which results in a crease or cleft separating the cyclic inflorescence meristem from the terminal floral meristem. It concludes that *E. derenbergii* displays an unusual cymose inflorescence compared with other members of the *Crassulaceae* family, and that the cymose character may come from the rapid over-topping of the inflorescence meristem by new flowers rather than by intermittant origin of new meristems (Green 1988). Tomato inflorescences also exhibit a similar growth pattern as *E. derenbergii* inflorescences without apparently resulting from the termination of the inflorescence meristem. Allen and Sussex (1996) conclude that, based on previous literature, it is not completely clear how to label the division pattern of the tomato inflorescence. However, Weberling (1989) points out that in addition to the distinction of cymose and racemose growth, inflorescences can also be classified as determinate (terminating in a flower) as well as indeterminate (producing lateral flowers), and even racemes and cymes can be classified as either determinate or indeterminate. While not many studies offer the same detailed insights into inflorescence and floral formation as presented herein, recent in-depth studies have illuminated the variation in inflorescence architecture, many of which cannot easily be classified into determinate cymose and indeterminate racemose structures. For example, species of the *Vitaceae* family showed variability and plasticity in vegetative and reproductive structures between three species of *Cyphostemma* (Wilson et al. 2006). Whereas inflorescence development results in termination of the main shoot into an inflorescence in two species, the third species displays inflorescences that arise as a primordium equal to or larger than the size of the shoot apical meristem (Wilson et al. 2006). After formation of several inflorescences using up more and more of the remaining shoot meristem, the shoot terminates or occasionally reverts back to vegetative growth (Wilson et al. 2006). Inflorescence development is similar between the three species, in that inflorescences bifurcate into bracts and branches, and eventually terminate into flowers comprising a complex cyme (Wilson et al. 2006). Racemose plants, on the other hand, have been found to carry terminal flower-like structures also (Sokoloff et al. 2006).

Thus, the results from these studies support the notion that cymose and racemose structures are not strictly the result of determinate and indeterminate growth processes, respectively. Since the tomato inflorescence doesn't appear to terminate in a floral meristem, one would conclude that it does not meet the common definition of a cymose inflorescence. On the other hand, a racemose inflorescence results in development of flowers on the flank of the inflorescence meristem, which is not observed either. For that reason, it would be confusing to classify tomato inflorescence as a raceme despite its indeterminate nature. It is conceivable that the general understanding of what constitutes a cymose or racemose inflorescence would need to be adjusted to reflect the bifurcating and cycling inflorescence meristem, as is seen in tomato and *Echeveria*. Therefore, we propose that tomato inflorescences should to be classified as a cyme with the understanding that the inflorescence meristem does not terminate into a flower but instead maintains indeterminacy.

Additional insights into the early stages of tomato inflorescence development will likely come from further developmental and molecular studies into the genes and loci controlling inflorescence and floral initiation. Mutations in the *jointless* (*j*), *blind* (*bl*), *anantha* (*an*), *falsiflora* (*fa*), *single flower truss* (*sft*), *self-pruning* (*sp*), *compound inflorescence* (*s*), and *uniflora* (*uf*) loci all affect inflorescence and floral meristem development by either blocking the transition, reverting to vegetative growth, or controlling the number of flowers per inflorescence (Allen and Sussex 1996; Dielen et al. 1998; Molinero-Rosales et al. 1999, 2004; Schmitz et al. 2002; Lifschitz et al. 2006; Quinet et al. 2006; Szymkowiak and Irish 2006). In addition, these mutations are often pleiotropic, in that they control other aspects of development such as flowering time and formation of an abscission zone on pedicels. Further insights into inflorescence formation in the *Solanaceae* family may also come from a relative of tomato, *Petunia* and the *extrapetals* (*exp*), *hermit* (*her*), and *evergreen* (*evg*) loci (Souer et al. 1998; Angenent et al. 2005).

While our studies are aimed to address a discrepancy in the literature concerning tomato inflorescence and floral development, the research also highlights the usefulness of the wild relative of tomato, LA1589, for detailed flower and fruit developmental analyses. The abundance of flowers and inflorescences and predictability of their development is an extremely useful tool to further our understanding of growth and development in this important plant species.

Acknowledgements

We thank Dr. D.M. Francis and Dr. J.C. Jang for critically reading the manuscript, Dr. R. Lamb for helpful discussions, J. Moyseenko and L. Duncan for plant care, and D. Fulton for assistance at the scanning electron microscope. This research was supported by the National Science Foundation (DBI-0227541). Salaries and research support were also provided by State and Federal Funds appropriated to the Ohio Agricultural Research and Development Center, the Ohio State University.

References

Allen, K.D., and Sussex, I.M. 1996. *Falsiflora* and *anantha* control early stages of floral meristem development in tomato (*Lycopersicum esculentum* Mill.). Planta, **200**: 254–264.

Angenent, G.C., Stuurman, J., Snowden, K.C., and Koes, R. 2005. Use of *Petunia* to unravel plant meristem function. Trends Plant Sci. **10**: 243–250. doi:10.1016/j.tplants.2005.03.004. PMID:15882657.

Brukhin, V., Hernould, M., Gonzalez, N., Chevalier, C., and Mouras, A. 2003. Flower development schedule in tomato *Lycopersicon esculentum* cv. Sweet cherry. Sex. Plant Reprod. **15**: 311–320.

Chandra Sekhar, K.N., and Sawhney, V.K. 1984. A scanning electron microscope study of the development and surface features of floral organs of tomato (*Lycopersicum esculentum*). Can. J. Bot. **62**: 2403–2413.

Cooper, D.C. 1927. Anatomy and development of tomato flower. Bot. Gaz. **83**: 399–411. doi:10.1086/333747.

Dielen, V., Marc, D., and Kinet, J.M. 1998. Flowering in the *uniflora* mutant of tomato (*Lycopersicon esculentum* Mill.): description of the reproductive structure and manipulation of flowering time. Plant Growth Regul. **25**: 149–157. doi:10.1023/A:1006094318083.

Ecole, D. 1974. Fonctionnement sympodial chez deuz *Solanacees* du genre *Lycopersicum.* Rev. Cytol. Biol. Veg. **37**: 127–160.

Green, P. 1988. A theory for inflorescence development and flower formation based on morphological and biophysical analysis of *Echeveria.* Planta, **175**: 153–169. doi:10.1007/BF00392424.

Hayward, H.E. 1938. The structure of economic plants. The Macmillen Company, New York.

Lifschitz, E., Eviatar, T., Rozman, A., Shalit, A., Goldshmidt, A., Amsellem, Z., Alvarez, J.P., and Eshed, Y. 2006. The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. Proc. Natl. Acad. Sci. U.S.A. **103**: 6398–6403. doi:10.1073/pnas.0601620103. PMID:16606827.

Molinero-Rosales, N., Jamilena, M., Zurita, S., Gomez, P., Capel, J., and Lozano, R. 1999. *FALSIFLORA*, the tomato orthologue of *FLORICAULA* and *LEAFY*, controls flowering time and floral meristem identity. Plant J. **20**: 685–693. doi:10.1046/j.1365-313X.1999.00641.x. PMID:10652140.

Molinero-Rosales, N., Latorre, A., Jamilena, M., and Lozano, R. 2004. SINGLE FLOWER TRUSS regulates the transition and maintenance of flowering in tomato. Planta, **218**: 427–434. doi:10.1007/s00425-003-1109-1. PMID:14504922.

Pnueli, L., Carmel-Goren, L., Hareven, D., Gutfinger, T., Alvarez, J., Ganal, M., Zamire, D., and 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.

Quinet, M., Dubois, C., Goffin, M.C., Chao, J., Dielen, V., Batoko, H., Boutry, M., and Kinet, J.M. 2006. Characterization of tomato (*Solanum lycopersicum* L.) mutants affected in their flowering time and in the morphogenesis of their reproductive structure. J. Exp. Bot. **57**: 1381–1390. doi:10.1093/jxb/erj117. PMID:16547125.

Sawhney, V.K., and Greyson, R.I. 1972. On the initiation of the inflorescence and floral organs in tomato (*Lycopersicon esculentum*). Can. J. Bot. **50**: 1493–1495.

Schmitz, G., Tillmann, E., Carriero, F., Fiore, C., Cellini, F., and Theres, K. 2002. The tomato *Blind* gene encodes a MYB transcription factor that controls the formation of lateral meristems. Proc. Natl. Acad. Sci. U.S.A. **99**: 1064–1069. doi:10.1073/pnas.022516199. PMID:11805344.

Sokoloff, D., Rudall, P.J., and Remizowa, M. 2006. Flower-like

terminal structures in racemose inflorescences: a tool in morphogenetic and evolutionary research. J. Exp. Bot. **57**: 3517–3530. doi:10.1093/jxb/erl126. PMID:17005921.

Souer, E., van der Krol, A., Kloos, D., Spelt, C., Bliek, M., Mol, J., and Koes, R. 1998. Genetic control of branching pattern and floral identity during *Petunia* inflorescence development. Development, **125**: 733–742. PMID:9435293.

Szymkowiak, E.J., and Irish, E.E. 2006. *JOINTLESS* suppresses sympodial identity in inflorescence meristems of tomato. Planta, **223**: 646–658. doi:10.1007/s00425-005-0115-x. PMID:16200409.

Weberling, F. 1989. Morphology of flowers and inflorescences. Cambridge University Press, Cambridge.

Went, F.W. 1944. Morphological observations on the tomato plant. Bull. Torrey. Bot. Club, **71**: 77–92. doi:10.2307/2481487.

Wilson, T.C., Gerrath, J.M., and Posluszny, U. 2006. Morphological and anatomical development in the Vitaceae. III. Comparative development of three *Cyphostemma* (Vitaceae) species reveals important vegetative and reproductive differences among the species. Can. J. Bot. **84**: 702–716. doi:10.1139/B06-017.