

REVIEW

Open Access



Micro-Tom tomato: from ornamental horticulture to fundamental research

Karla Gasparini¹, Yuri Gomes Figueiredo¹, Lucas Maia de Aquino¹, Cassia Nayana da Silva Vitorino¹, Dimas Mendes Ribeiro¹, Lázaro Eustáquio Pereira Peres² and Agustin Zsögön^{1*} 

Abstract

Model organisms have been instrumental in advancing discoveries in plant biology. Tomato (*Solanum lycopersicum*) is distinguished as a prominent model system due to its well-characterized genetics and economic significance as a crop. Micro-Tom (MT), an ornamental dwarf tomato variety, was adopted by the tomato research community as a model plant due to its short stature, fast life cycle, ease of genetic transformation, and ample genomic resources. Over the last 30 years, the use of MT has illuminated various facets of plant development, including the control of growth habit, glandular trichomes, leaf anatomy, and the formation of arbuscular mycorrhizal symbioses. We briefly summarize these contributions and point to further potential advances in the future.

Keywords Dwarfism, Model organism, Solanaceae

Introduction

Model organisms are a specific subgroup of species that have been standardized to serve as research objects (Ankeny and Leonelli 2011). Such model species have been the keystone of fundamental research in all areas of biology, and large research communities have been built around them. The selection and adoption of specific species to serve as models has frequently been serendipitous (Leonelli and Ankeny 2013), but they generally conform to a pattern that comprises common denominators such as *simplicity*, *prolificity*, and *brevity* (both in time and space). Conceptually, models are considered fundamental to translational science, as they function vicariously in generating knowledge that can subsequently be

extrapolated to other larger and more complex organisms of economic importance.

The first *bona fide* model organism was the fruit fly *Drosophila melanogaster*, and its establishment was driven by the rapid growth of experimental research during the 1910s (Kohler 1994). During the 1940s, the dawn of molecular biology necessitated a reductionist approach and fostered the use of microorganisms (bacteria and yeast). Prior to the advent of genomics, plants had been widely utilized as genetic and physiological model organisms, commencing with the forward genetics research of Gregor Mendel on peas (*Pisum sativum*) in 1865, followed by tissue culture techniques established initially in tobacco (*Nicotiana tabacum*) (Murashige and Skoog 1962), culminating in the pioneering genetic engineering achievements in petunia (*Petunia* spp.) (Herrera-Estrella et al. 1992).

The publication of the Arabidopsis genome was a landmark that bolstered its use as a model for reverse genetics (The Arabidopsis Genome Initiative 2000). The small size and short life cycle of Arabidopsis, in conjunction with the generation of large collections of insertional mutants (Alonso et al. 2003), facilitated the association of genes with their respective functions (O'Malley and Ecker

*Correspondence:

Agustin Zsögön
agustin.zsogon@ufv.br

¹ National Institute of Science and Technology on Plant Physiology Under Stress Conditions, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Viçosa, MG 36570-900, Brazil

² Laboratory of Hormonal Control of Plant Development, Departamento de Ciências Biológicas, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, CP 09, Piracicaba, SP 13418-900, Brazil

2010). Until the advent of next-generation sequencing (NGS), efforts to sequence full genomes of plants were hampered by financial, labor, and time constraints. Technical breakthroughs in the early 2000s, when NGS platforms such as Roche 454 and Illumina were introduced, significantly increased sequencing output, increasing concomitantly the number of available genomes (Sun et al. 2022). This has led to the multiplication and diversification of plant model species and the expansion of the scope of genetic analyses to dissect phenomena intractable in *Arabidopsis*. Such traits and processes include the development and maturation of fleshy fruits, the impact of sympodial flowering on growth habit, compound leaf architecture, glandular trichome formation, and mycorrhizal symbioses. As a model plant, tomato (*Solanum lycopersicum*) has been a critical contributor to generating new knowledge related to these areas of plant biology.

Tomato as a genetic model species

Tomato is a crop of global significance, distinguished by two distinct production variants: fresh consumption and processing varieties (Robbins et al. 2011). In addition, it has a series of attributes that render it an outstanding biological model for plant biology. The plants are self-pollinating and self-compatible, enabling the establishment of true-breeding lines and the use of introgression as a breeding and research tool (Eshed and Zamir 1995). Tomatoes are also cross-compatible with a group of wild relatives endemic to the Andes region in South America (Gibson and Moyle 2020). They can thus be utilized to access natural genetic variation (Alonso-Blanco and Koornneef 2000). Furthermore, tomato has a comparatively small genome size (950 Mb) (Tomato Genome Consortium 2012), extensive and well-curated germplasm resources (<https://tgrc.ucdavis.edu/>), and comprehensive genomic sequences (<https://solgenomics.net/>). It also exhibits high genomic synteny with other Solanaceae species (Peters et al. 2012) and demonstrates high genetic transformation efficiency across various protocols and tissue explants used (Van Eck 2018), making it a versatile subject for various plant research fields.

Micro-Tom: a model cultivar

One of the limitations of traditional tomato genotypes in comparison to other plant models, such as *Arabidopsis*, *Medicago truncatula*, or *Brachypodium distachyon*, is its large plant size and relatively long life cycle, primarily due to the time required for fruit ripening to harvest viable seeds. The Micro-Tom (MT) tomato cultivar, on the other hand, is a miniature tomato genotype initially developed for ornamental purposes. (Scott and Harbaugh 1989). It has short stature, determinate growth habit, and a fast life cycle (Campos et al. 2010). Its dwarf

phenotype is caused by two main recessive mutations, *dwarf* (*d*) and *miniature* (*mnt*), of which only the former has been molecularly characterized (Bishop et al. 1999). The wild-type D enzyme catalyzes a key step (C-6 oxidation) in brassinosteroid biosynthesis. This reduction in brassinosteroid biosynthesis leads to dwarfism, enabling the cultivation of plants in small pots and large numbers (Pino-Nunes et al. 2009). In addition to the *d* mutation, MT is characterized by a determinate growth habit, as it harbors a mutant allele of the *SELF PRUNING* (*SP*) gene (Pnueli et al. 1998; Marti et al. 2006). Despite these mutations in MT, the plant has served as an effective model for investigating plant hormone interactions, as illustrated by the interaction between *SP* and auxin (Silva et al. 2018) and by the introgression of additional mutations in brassinosteroid biosynthesis or signaling pathway genes leading to phenotypes with more severe dwarfism (Fig. 1).

Another advantage of MT is its high in vitro regeneration rate and genetic transformation efficacy (Lima et al. 2004). A plethora of MT transformation protocols using *Agrobacterium* has been published, demonstrating its versatility and high efficiency in transgenic explant generation (Dan et al. 2006; Sun et al. 2006; Pino et al. 2010; Cruz-Mendivil et al. 2011; Guo et al. 2012; Chetty et al. 2013; Khuong et al. 2013; Shikata and Ezura 2016; Kaplanoglu et al. 2022; Tóth et al. 2022; Jeong et al. 2024). Likewise, genomics tools have been developed for MT, encompassing a genome-wide analysis of SNPs and InDels in comparison to the reference cultivar Heinz 1706 (Kobayashi et al. 2014), transcriptomic data repositories (Bae et al. 2021; Goytia Bertero et al. 2021; Lubis et al. 2023) and, most recently, a near-complete assembly of its nuclear genome (Shirasawa and Ariizumi 2024).

The beneficial attributes of MT, coupled with its potential for biotechnological manipulation, have led to the establishment of a large research community and an ever-growing number of peer-reviewed publications and citations (Fig. 2). Key characteristics that differentiate MT (and other tomato cultivars) from *Arabidopsis* include: sympodial growth habit, heterobaric leaves, the presence of glandular trichomes and the establishment of arbuscular mycorrhizal symbioses in the roots. We next provide a brief overview of the contributions that have accrued from the use of MT to gain a deeper understanding of these topics in plant biology.

Molecular regulation of plant growth habit

Plant architecture is a key trait influencing productivity and agronomic management (Zsögön and Peres 2018). Plant architecture is defined by the growth habit, shaped by the combination and alternation of determinate and indeterminate meristems. In a determinate

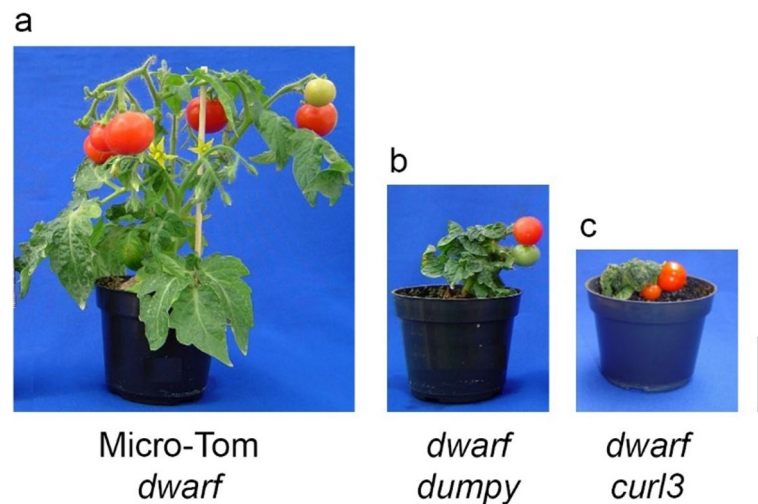


Fig. 1 The Micro-Tom (MT) tomato cultivar is deficient in brassinosteroids (BR) due to the *dwarf* mutation (a). However, double mutants with *dumpy* (b) and *curl3* (c), corresponding to BR biosynthesis and BR receptor genes, respectively, reveal that MT has a functional BR pathway and can be utilized to dissect hormone functions. Scale bar = 5 cm

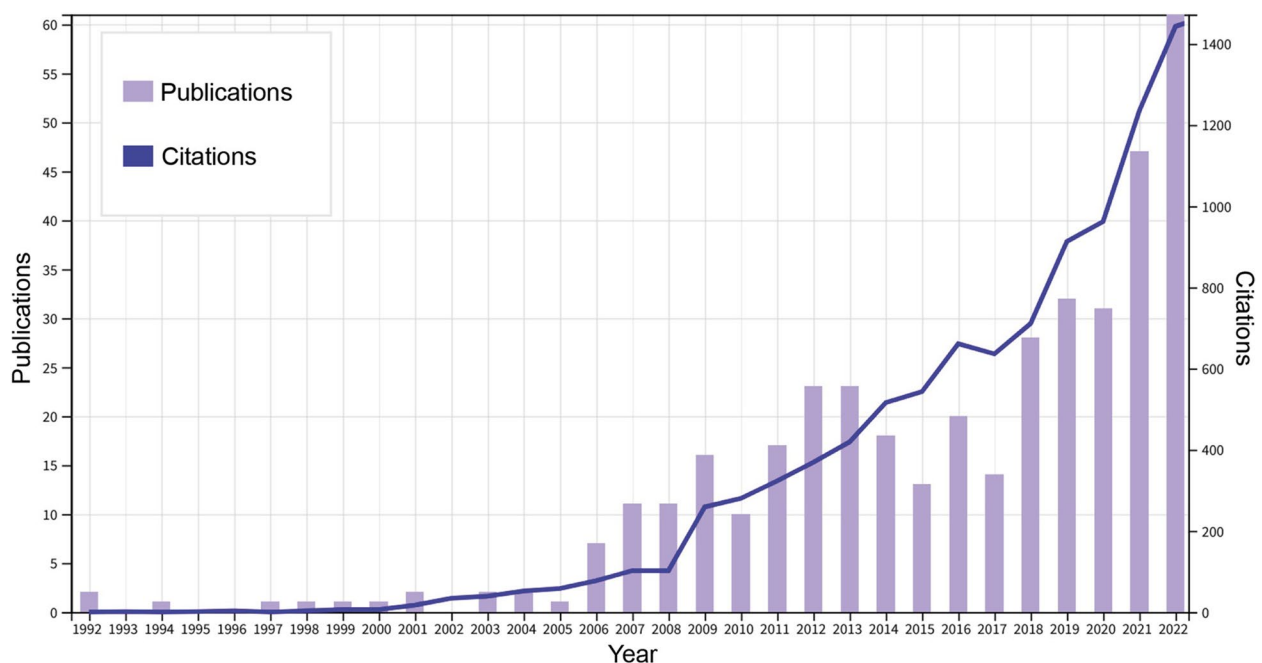


Fig. 2 Number of Micro-Tom publications and citations over a 30-year period from 1992 (the first year with a registered citation) to 2022 (the last year with a full record). Source: Web of Science

apical meristem, the stem cell niche is eventually expended toward the differentiation of a terminal structure, such as a flower or an inflorescence. Conversely, in indeterminate genotypes, the persistence of the stem cell niche in the apical meristem results in repetitive vegetative growth (Périlleux et al. 2019). Additionally, plant growth habits are classified as either monopodial

or sympodial. In genetic models such as *Arabidopsis* and *Antirrhinum*, growth is monopodial, with the indeterminate apical meristem producing a sequence of leaves until a photoperiodic signal transforms it into a floral meristem, generating an inflorescence (Reinhardt and Kuhlemeier 2002). This results in two distinct plant growth stages: vegetative and reproductive. In contrast,

Solanaceae species exhibit alternate vegetative and reproductive phases, forming modular units called sympodia, whose repetition characterizes sympodial growth (Périlleux et al. 2014; Vicente et al. 2015).

Wild tomatoes are perennial plants with indeterminate growth, but the domesticated tomato is commonly cultivated as an annual plant (Nakazato et al. 2010). A recessive mutation that spontaneously emerged in 1914 in Florida, in the *SELF PRUNING* (*SP*) gene, resulted in plants (*sp/sp*) with determinate growth (Yeager 1927). The mutation also leads to compact stature and greater uniformity in fruit ripening and was instrumental in allowing mechanical harvesting in field-grown tomatoes (Rick 1978). Subsequent studies have shown that *SP* is a member of a large and highly conserved gene family, *CETS*, named after its founding members *CENTRORADIALIS*, *TERMINAL FLOWER 1*, and *SP*, also including the “florigen” gene *SINGLE FLOWER TRUSS* (*SFT*), whose Arabidopsis ortholog is *FLOWERING LOCUS T* (*FT*) (Lifschitz and Eshed 2006). The *SFT* gene produces a non-autonomous flowering signal that is transported from the leaf to the vegetative apex of the shoot, prompting its conversion into a reproductive apex (Molinero-Rosales et al. 2004; Shalit et al. 2009).

Tomato plants heterozygous for the mutant *sft* allele, causing *SFT* gene loss of function, produce more inflorescences, flowers, and larger fruits, resulting in a 60% increase in productivity compared to control plants (Krieger et al. 2010; Vicente et al. 2015). While the *sft* mutant allele causes late flowering, the *SP* gene is associated with determinate growth. *SP* and *SFT* interactions influence the growth habit (determinate, semi-determinate, and indeterminate) and the transition to the flowering stage, depending on the relative expression of these genes in the meristem. In this context, Vicente et al. (2015) demonstrated that allelic variants of *SP* and *SFT*, not only impact the growth habit, but also affect fruit productivity and total soluble solids, which are traits influenced by source-sink relationships (Vicente et al. 2015). Furthermore, overexpression of the *SFT* gene (*SFT-ox*) in transgenic plants led to early flowering and reduced water use efficiency (WUE) due to higher stomatal conductance and thinner leaf laminae (Robledo et al. 2020).

The *SELF-PRUNING 3C* (*SP3C*) gene, a paralog of the *SP* gene, was studied by Moreira et al. (2022a) in CRISPR/Cas9 loss-of-function and 35S-overexpression MT lines. Plants overexpressing the *SP3C* gene exhibited delayed seed germination and flowering, more branched root systems, and delayed wilting under soil water deficit. In contrast, loss-of-function mutants displayed accelerated seed germination and flowering, longer roots, and greater drought susceptibility. The expression of *SP3C*

was mostly confined in roots, thus suggesting it could play a key role in connecting water availability and developmental transitions such as seed germination and flowering (Moreira et al. 2022a).

While MT is a *sp/sp* mutant (Marti et al. 2006), the targeted introgression of the wild-type allele allowed the creation of an MT line with an indeterminate growth habit (Carvalho et al. 2011). In an intriguing study, Silva et al. (2018) used MT-*SP* to investigate the interaction between *SP* and *DIAGEOTROPICA* (*DGT*) genes and their influence on polar auxin transport (PAT) and, consequently, tomato plant growth. The authors demonstrated that free auxin levels and auxin-regulated gene expression patterns were altered in *sp* mutants. Furthermore, the *diageotropica* (*dgt*) mutation, which impacts a gene coding for cyclophilin A protein, appeared to have epistatic interactions with *sp*. This suggests that the *SP* gene influences tomato growth habit, at least in part, by modulating auxin transport and responsiveness (Silva et al. 2018). Recent work has shown that gene editing of the *SP* and *DWARF* genes rapidly produces miniature plants suitable for industrial applications (Nagamine and Ezura 2024).

Genetic dissection of glandular trichome development

In Arabidopsis, significant advances have been made to unveil the molecular control of unicellular and non-glandular trichome development. However, this underscored the necessity for an alternative model for researching multicellular and glandular trichomes in plants, which are absent in Arabidopsis. Tomatoes exhibit considerable diversity in trichome morphology and functionality, possessing four glandular trichome types (I, IV, VI, and VII) and three non-glandular types (II, III, and V) (Luckwill 1943; Glas et al. 2012). The availability of numerous wild tomato species with sequenced genomes and unique trichome traits (e.g., *S. habrochaites* exhibits a greater glandular cavity in type VI trichomes, and *S. pennellii* has a higher density of type IV trichomes) has been key in uncovering the pathways regulating trichome development, particularly glandular trichomes, and their metabolic pathways (Bergau et al. 2015; Xu et al. 2018; Therezan et al. 2021; Vendemiatti et al. 2022).

Gene introgressions from wild relatives remain a powerful tool for basic and applied research in tomato. For example, the use of introgression lines is highly effective for QTL localization, gene identification, and identification of gene-by-gene and gene-by-environment interactions (Alseekh et al. 2013). Although some inter- and intra-specific incompatibility issues exist in tomato wild relatives (Mutschler and Liedl 1994), successful cross-breeding between species has been achieved (Chetelat 2016). This has enabled the introgression and

identification of genomic regions associated with trichomes development and metabolism in tomato plants (Therezan et al. 2021; Vendemiatti et al. 2022, 2024; Gasparini et al. 2023). The use of MT as the recurrent parent has been fundamental to the successful introgression of loci underlying trichome-related traits and their subsequent genetic dissection. MT introgression lines, named MT-*Get* (MT×*S. galapagense*) and MT-*Sst2* (MT×*S. habrochaites*), have unraveled the genetic determinants controlling the development and metabolism of type IV and VI glandular trichomes, respectively (Therezan et al. 2021; Vendemiatti et al. 2022, 2024).

Although the diversity in trichome types and densities among tomato plants and their wild relatives is essential for the identification of trichome-related genes, the epistatic effects of the genetic background can complicate these studies. Thus, using MT as a single cultivar is advantageous, especially for comparative studies. For example, analysis of monogenic trichome mutations (*Lanata*—*La*, *hairs absent*—*h*, and *Woolly*—*Wo*) all introgressed into MT has provided strong evidence that the *La* mutation is associated with increased leaf gas exchange and reduced leaf temperature, which are desirable traits in breeding programs (Gasparini et al. 2021). Moreover, the generation of transgenics in an MT background is straightforward and convenient (Pino et al. 2010). Genetic transformation of MT has been successfully employed to unravel trichome developmental pathways, metabolite production, and gland formation in tomato plants (Chang et al. 2021, 2024; Yang et al. 2021). The reporter genes GUS (β -glucuronidase) and YFP (yellow fluorescent protein), fused with promoter of the gene encoding the enzyme acyltransferase (AT2), allowed for tracking glandular cell development in type I and IV glandular trichomes in transformed MT plants (Chang et al. 2021). Recently, the pathway that modulates the spatiotemporal formation of trichome glands was elucidated using transgenics in various tomato cultivars, including MT, by altering the expression of *gland cell repressor* (*GRC*) genes (Chang et al. 2024).

Despite certain differences in glandular trichome metabolism between tomato species, MT transformation has helped identify the role of genes involved in terpene biosynthesis, such as the *SCL3* gene (a scarecrow-like subfamily transcription factor) (Yang et al. 2021). The ease of use of MT for reproducibility and validation of results from other species using MT plants is an additional advantage. A case in point is the characterization of the *h* phenotype (Gasparini et al. 2023). Wild tomato species (*S. pimpinellifolium*) with a disruption of the *H* gene exhibited the same phenotype as MT-*h* plants, specifically a decreased density of long trichomes and an increased density of type VI trichomes (Gasparini et al.

2023). This correlation of phenotypes exemplifies the robustness of MT as a model for studying trichomes, potentially facilitating advancements in research and the generation of consistent data.

Genetic basis of homobaric and heterobaric leaves

A rich array of diverse structures can be observed in the leaf arrangements of plants. These arrangements are fundamental for the organism's development in adverse environmental conditions. Leaves have a hydraulic design that optimizes water transport, facilitating environmental acclimatization and influencing the ecological distribution of plant species (Nicotra et al. 2011). The venation pattern contributes to the performance regarding water transport and distribution (Sack et al. 2012; Sack and Scoffoni 2013). Bundle sheath extensions (BSEs) consist of a column of parenchyma and sclerenchyma cells that connect the veins to the epidermis in the leaves of numerous species (Buckley et al. 2011). The hydraulic integration of the leaf blade is enhanced by the presence of BSEs, which reduce the resistance to water flow between veins and stomata (Zwieniecki et al. 2007). Leaves with BSEs are considered *heterobaric*, whereas those without BSEs are *homobaric* (Terashima 1992).

In tomato plants, leaves are classified as heterobaric (Thompson et al. 2007). Little is known about the genetic control of BSE formation, although a potential adaptive role is suggested by the clear ecological bias in the distribution of heterobaric and homobaric species (Kenzo et al. 2007). The monogenic *obscuravenosa* (*obv*) mutant (Jones et al. 2007), was characterized as homobaric using a near-isogenic introgression line in an MT background (Zsögön et al. 2015). The *obv* mutation has been incorporated into numerous tomato cultivars (Jones et al. 2007), suggesting that it may offer specific benefits in tomato breeding. The introgression of *obv* into MT paved the way for the fine-mapping and identification of the responsible gene, a C₂H₂ Zn-finger transcription factor (Moreira et al. 2022b). Interestingly, the homobaric phenotype of *AUXIN RESPONSE FACTOR 4* (*ARF4*) knockdown (*via* RNAi) and knockout (*via* CRISPR/Cas9) lines in MT (Bouzroud et al. 2020) contributed to placing *OBV* in an auxin signaling-related pathway (Moreira et al. 2022b). Further work will contribute to producing a more complete picture of this new auxin signaling module that controls BSE development.

Hormonal control of the arbuscular mycorrhizal symbiosis

Arbuscular mycorrhizal fungi (AMF) colonize the roots of certain angiosperms, resulting in a symbiotic relationship in which nutrients are exchanged between the plants and AMFs (Duan et al. 2024). In particular, inorganic phosphate (Pi) is the primary currency in

this interaction, with plants possessing a mechanism that promotes symbiosis under conditions of low Pi availability (Ezawa and Saito 2018). In addition, the fungal mycelium enhances access to previously inaccessible resources due to root absorption area expansion. However, species of some angiosperm families do not form mycorrhizal associations, amongst them various Proteaceae, Chenopodiaceae, and Brassicaceae family members, and certain Fabaceae and Cactaceae genera (Wang et al. 2021). The genetic coordination between the symbiotic partners is not well understood, and *Arabidopsis* is not a suitable model species, as it does not form mycorrhiza (Fernández et al. 2019).

It has long been established that phytohormones regulate AMF formation; however, the molecular specifics of this regulation remain elusive (Barker and Tagu 2000). The utilization of MT mutants constitutes an effective approach to elucidate such mechanisms (Shaul-Keinan et al. 2002; Rillig et al. 2008). One of the first studies comparing different hormone mutants for AM formation was conducted in a collection of near-isogenic lines in an MT background (Zsögön et al. 2008). The ethylene overproducing mutant *epinastic* was found to suppress hyphal penetration to the roots and reduce colonization. A subsequent study found that the ABA-deficient mutant *notabilis* interferes with the development of AMF symbiosis, even when using an ethylene inhibitor (Fracetto et al. 2013, 2017). Further work using MT genetic variants will provide more insight into the hormonal control of AMF formation and suggest approaches to its optimization.

Conclusions

Plant biology has been prolific and dynamic in the development of biological model organisms, as recently illustrated by a machine-learning-assisted analysis of the research trends over the last five decades (Shiu and Lehti-Shiu 2024). The top five genera with published records in the last 50 years are, in decreasing order, *Arabidopsis*, *Oryza*, *Nicotiana*, *Triticum*, and *Glycine* (Shiu and Lehti-Shiu 2024). The advent of the genomics era has ushered in a diversification and decentralization of research efforts, with experimental work increasingly conducted directly on species of interest. Thus, the tomato has emerged as a key player in both fundamental and applied research, as both a convenient genetic model and a cash crop. The adoption of the miniature cultivar MT has further expanded the repertoire of tools available for studying tomato genetics. It will continue to provide significant value for research, as we have attempted to demonstrate in this brief overview.

Acknowledgements

We thank the Graduate Program in Plant Physiology at UFV for unwavering support. We apologize to colleagues whose work could not be cited owing to space limitations.

Authors' contributions

KG, YGF, LMdA, CNDsV, DMR, LEPP and AZ drafted and revised the work, and approved the submitted version.

Funding

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) [Grant 406455/2022–8]; Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) [RED00060-23; APQ-01942–22 and BPD-00823–22]; and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil).

Data availability

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 1 October 2024 Revised: 3 December 2024 Accepted: 9 January 2025

Published: 15 March 2025

References

- Alonso JM, Stepanova AN, Leisse TJ, Kim CJ, Chen H, Shinn P, et al. Genome-wide insertional mutagenesis of *Arabidopsis thaliana*. *Science*. 2003;301:653–7. <https://doi.org/10.1126/science.1086391>.
- Alonso-Blanco C, Koornneef M. Naturally occurring variation in *Arabidopsis*: an underexploited resource for plant genetics. *Trends Plant Sci*. 2000;5:22–9. [https://doi.org/10.1016/S1360-1385\(99\)01510-1](https://doi.org/10.1016/S1360-1385(99)01510-1).
- Alseikh S, Ofner I, Pleban T, Tripodi P, Di Dato F, Cammareri M, et al. Resolution by recombination: breaking up *Solanum pennellii* introgressions. *Trends Plant Sci*. 2013;18:536–8. <https://doi.org/10.1016/j.tplants.2013.08.003>.
- Ankeny RA, Leonelli S. What's so special about model organisms? *Stud Hist Philos Sci*. 2011;42:313–23. <https://doi.org/10.1016/j.shpsa.2010.11.039>.
- Arabidopsis Genome Initiative. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature*. 2000;408:796–815. <https://doi.org/10.1038/35048692>.
- Bae SH, Park J, Park SJ, Han J, Oh JH. Transcriptome data for tissue-specific genes in four reproductive organs at three developmental stages of micro-tom tomato. *Data Brief*. 2021;34: 106715. <https://doi.org/10.1016/j.dib.2021.106715>.
- Barker SJ, Tagu D. The roles of auxins and cytokinins in mycorrhizal symbioses. *J Plant Growth Regul*. 2000;19:144–54. <https://doi.org/10.1007/s003440000021>.
- Bergau N, Bennewitz S, Syrowatka F, Hause G, Tissier A. The development of type VI glandular trichomes in the cultivated tomato *Solanum lycopersicum* and a related wild species *S. habrochaites*. *BMC Plant Biol*. 2015;15:289. <https://doi.org/10.1186/s12870-015-0678-z>.
- Bishop GJ, Nomura T, Yokota T, Harrison K, Noguchi T, Fujioka S, et al. The tomato DWARF enzyme catalyses C-6 oxidation in brassinosteroid biosynthesis. *Proc Natl Acad Sci U S A*. 1999;96:1761–6. <https://doi.org/10.1073/pnas.96.4.1761>.
- Bouzroud S, Gasparini K, Hu G, Barbosa MAM, Rosa BL, Fahr M, et al. Down regulation and loss of Auxin Response Factor 4 function using CRISPR/Cas9 alters plant growth, stomatal function and improves tomato tolerance to

- salinity and osmotic stress. *Genes* (Basel). 2020;11:272. <https://doi.org/10.3390/genes11030272>.
- Buckley TN, Sack L, Gilbert ME. The role of bundle sheath extensions and life form in stomatal responses to leaf water status. *Plant Physiol.* 2011;156:962–73. <https://doi.org/10.1104/pp.111.175638>.
- Campos ML, Carvalho RF, Benedito VA, Peres LEP. Small and remarkable. The Micro-Tom model system as a tool to discover novel hormonal functions and interactions. *Plant Signal Behav.* 2010;5:267–70. <https://doi.org/10.4161/psb.5.3.10622>.
- Carvalho RF, Campos ML, Pino LE, Crestana SL, Zsögön A, Lima JE, et al. Convergence of developmental mutants into a single tomato model system: 'Micro-Tom' as an effective toolkit for plant development research. *Plant Methods.* 2011;7:18. <https://doi.org/10.1186/1746-4811-7-18>.
- Chang J, Wu S, You T, Wang J, Sun B, Xu B, et al. Spatiotemporal formation of glands in plants is modulated by MYB-like transcription factors. *Nat Commun.* 2024;15:2303. <https://doi.org/10.1038/s41467-024-46683-0>.
- Chang J, Yang J, Wang J, Wu S. Comprehensive observation of trichome development in Micro-tom tomato. *Vegetable Research.* 2021;1:6. <https://doi.org/10.48130/VR-2021-0006>.
- Chetelat RT. Overcoming sterility and unilateral incompatibility of *Solanum lycopersicum* × *S. sitiens* hybrids. *Euphytica.* 2016;207:319–30. <https://doi.org/10.1007/s10681-015-1543-8>.
- Chetty VJ, Ceballos N, Garcia D, Narváez-Vásquez J, Lopez W, Orozco-Cárdenas ML. Evaluation of four *Agrobacterium tumefaciens* strains for the genetic transformation of tomato (*Solanum lycopersicum* L.) cultivar Micro-Tom. *Plant Cell Rep.* 2013;32:239–47. <https://doi.org/10.1007/s00299-012-1358-1>.
- Cruz-Mendivil A, Rivera-Lopez J, German-Baez LJ, Lopez-Meyer M, Hernandez-Verdugo S, Lopez-Valenzuela JA, et al. A simple and efficient protocol for plant regeneration and genetic transformation of tomato cv. micro-tom from leaf explants. *HortScience.* 2011;46:1655–60. <https://doi.org/10.21273/HORTSCI.46.12.1655>.
- Dan Y, Yan H, Muniyikwa T, Dong J, Zhang Y, Armstrong CL. MicroTom—a high-throughput model transformation system for functional genomics. *Plant Cell Rep.* 2006;25:432–41. <https://doi.org/10.1007/s00299-005-0084-3>.
- Duan S, Feng G, Limpens E, Bonfante P, Xie X, Zhang L. Cross-kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus–bacterium continuum. *Nat Rev Microbiol.* 2024;22:773–90. <https://doi.org/10.1038/s41579-024-01073-7>.
- Eshed Y, Zamir D. An introgression line population of *lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield-associated QTL. *Genetics.* 1995;141:1147–62. <https://doi.org/10.1093/genetics/141.3.1147>.
- Ezawa T, Saito K. How do arbuscular mycorrhizal fungi handle phosphate? New insight into fine-tuning of phosphate metabolism. *New Phytol.* 2018;220:1116–21. <https://doi.org/10.1111/nph.15187>.
- Fernández I, Cosme M, Stringlis IA, Yu K, de Jonge R, van Wees SM, et al. Molecular dialogue between arbuscular mycorrhizal fungi and the nonhost plant *Arabidopsis thaliana* switches from initial detection to antagonism. *New Phytol.* 2019;223:867–81. <https://doi.org/10.1111/nph.15798>.
- Fracetto GGM, Peres LEP, Mehdy MC, Lambais MR. Tomato ethylene mutants exhibit differences in arbuscular mycorrhiza development and levels of plant defense-related transcripts. *Symbiosis.* 2013;60:155–67. <https://doi.org/10.1007/s13199-013-0251-1>.
- Fracetto GGM, Peres LEP, Lambais MR. Gene expression analyses in tomato near isogenic lines provide evidence for ethylene and abscisic acid biosynthesis fine-tuning during arbuscular mycorrhiza development. *Arch Microbiol.* 2017;199:787–98. <https://doi.org/10.1007/s00203-017-1354-5>.
- Gasparini K, da Silva MF, Costa LC, Martins SCV, Ribeiro DM, Peres LEP, et al. The Lanata trichome mutation increases stomatal conductance and reduces leaf temperature in tomato. *J Plant Physiol.* 2021;260: 153413. <https://doi.org/10.1016/j.jplph.2021.153413>.
- Gasparini K, Gasparini J, Therezan R, Vicente MH, Sakamoto T, Figueira A, et al. Natural genetic variation in the HAIRS ABSENT (H) gene increases type-VI glandular trichomes in both wild and domesticated tomatoes. *J Plant Physiol.* 2023;280: 153859. <https://doi.org/10.1016/j.jplph.2022.153859>.
- Gibson MJS, Moyle LC. Regional differences in the abiotic environment contribute to genomic divergence within a wild tomato species. *Mol Ecol.* 2020;29:2204–17. <https://doi.org/10.1111/mec.15477>.
- Glas JJ, Schimmel BCJ, Alba JM, Escobar-Bravo R, Schuurink RC, Kant MR. Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. *Int J Mol Sci.* 2012;13:17077–103. <https://doi.org/10.3390/ijms131217077>.
- Goytia Bertero V, Pratta GR, Arce DP. Independent transcriptomic and proteomic networks reveal common differentially expressed chaperone and interactor genes during tomato cv. Micro-Tom Fruit Ripening Plant Gene. 2021;28: 100346. <https://doi.org/10.1016/j.plgene.2021.100346>.
- Guo M, Zhang YL, Meng ZJ, Jiang J. Optimization of factors affecting *Agrobacterium*-mediated transformation of Micro-Tom tomatoes. *Genet Mol Res.* 2012;11:661–71. <https://doi.org/10.4238/2012.March.16.4>.
- Herrera-Estrella L, Depicker A, Van Montagu M, Schell J. Expression of chimeric genes transferred into plant cells using a Ti-plasmid-derived vector. *Biotechnology.* 1992;24:377–81.
- Jeong YY, Noh YS, Kim SW, Seo PJ. Efficient regeneration of protoplasts from *Solanum lycopersicum* cultivar Micro-Tom. *Biol Methods Protoc.* 2024;9:bpae008. <https://doi.org/10.1093/biomethods/bpae008>.
- Jones CM, Rick CM, Adams D, Jernstedt J, Chetelat RT. Genealogy and fine mapping of *Obscuravenosa*, a gene affecting the distribution of chloroplasts in leaf veins and evidence of selection during breeding of tomatoes (*Lycopersicon esculentum*; Solanaceae). *Am J Bot.* 2007;94:935–47. <https://doi.org/10.3732/ajb.94.6.935>.
- Kaplanoglu E, Kolotilin I, Menassa R, Donly C. Plastid transformation of micro-tom tomato with a hemipteran double-stranded RNA results in RNA interference in multiple insect species. *Int J Mol Sci.* 2022;23:3918. <https://doi.org/10.3390/ijms23073918>.
- Kenzo T, Ichie T, Watanabe Y, Hiromi T. Ecological distribution of homobaric and heterobaric leaves in tree species of malaysian lowland tropical rain-forest. *Am J Bot.* 2007;94:764–75. <https://doi.org/10.3732/ajb.94.5.764>.
- Khuong TT, Crété P, Robaglia C, Caffari S. Optimisation of tomato micro-tom regeneration and selection on glufosinate/basta and dependency of gene silencing on transgene copy number. *Plant Cell Rep.* 2013;32:1441–54. <https://doi.org/10.1007/s00299-013-1456-8>.
- Kobayashi M, Nagasaki H, Garcia V, Just D, Bres C, Mauxion JP, et al. Genome-wide analysis of intraspecific DNA polymorphism in 'Micro-Tom', a model cultivar of tomato (*Solanum lycopersicum*). *Plant Cell Physiol.* 2014;55:445–54. <https://doi.org/10.1093/pccp/pct181>.
- Kohler RE. *Lords of the Fly: Drosophila Genetics and the Experimental Life.* Chicago: University of Chicago Press; 1994.
- Krieger U, Lippman ZB, Zamir D. The flowering gene SINGLE FLOWER TRUSS drives heterosis for yield in tomato. *Nat Genet.* 2010;42:459–63. <https://doi.org/10.1038/ng.550>.
- Leonelli S, Ankeny RA. What makes a model organism? *Endeavour.* 2013;37:209–12. <https://doi.org/10.1016/j.endeavour.2013.06.001>.
- Lifschitz E, Eshed Y. Universal florigenic signals triggered by FT homologues regulate growth and flowering cycles in perennial day-neutral tomato. *J Exp Bot.* 2006;57:3405–14. <https://doi.org/10.1093/jxb/erl106>.
- Lima JE, Carvalho RF, Neto AT, Figueira A, Peres LEP. Micro-Msk: a tomato genotype with miniature size, short life cycle, and improved in vitro shoot regeneration. *Plant Sci.* 2004;167:753–7. <https://doi.org/10.1016/j.plantsci.2004.05.023>.
- Lubis WMY, Adrian M, Jadid N, Widiastuti A, Ezura H, Mubarak S, et al. Transcriptome dataset from *Solanum lycopersicum* L. cv. Micro-Tom; wild type and two mutants of INDOLE-ACETIC-ACID (SIIA9) using long-reads sequencing oxford nanopore technologies. *BMC Res Notes.* 2023;16:40. <https://doi.org/10.1186/s13104-023-06306-1>.
- Luckwill LC. *The genus lycopersicon: an historical, biological and taxonomic survey of the wild and cultivated tomatoes.* Aberdeen: Aberdeen University Press; 1943.
- Marti E, Gisbert C, Bishop GJ, Dixon MS, Garcia-Martinez JL. Genetic and physiological characterization of tomato cv. Micro-Tom. *J Exp Bot.* 2006;57:2037–47. <https://doi.org/10.1093/jxb/erj154>.
- Molinero-Rosales N, Latorre A, Jamilena M, Lozano R. SINGLE FLOWER TRUSS regulates the transition and maintenance of flowering in tomato. *Planta.* 2004;218:427–34. <https://doi.org/10.1007/s00425-003-1109-1>.
- Moreira JDR, Rosa BL, Lira BS, Lima JE, Correia LNF, Otoni WC, et al. Auxin-driven ecophysiological diversification of leaves in domesticated tomato. *Plant Physiol.* 2022a;190:113–26. <https://doi.org/10.1093/plphys/kiac251>.
- Moreira JDR, Quiñones A, Lira BS, Robledo JM, Curtin SJ, Vicente MH, et al. SELF PRUNING 3C is a flowering repressor that modulates seed germination, root architecture, and drought responses. (*R Melzer, Ed.*) *J Exp Bot.* 2022b;73:6226–40. <https://doi.org/10.1093/jxb/erac265>.

- Murashige T, Skoog F. A revised medium for rapid growth and bio assays with tobacco tissue cultures. *Physiol Plant*. 1962;15:473–97. <https://doi.org/10.1111/j.1399-3054.1962.tb08052.x>.
- Mutschler MA, Liedl BE. Interspecific crossing barriers in *Lycopersicon* and their relationship to self-incompatibility. In: Williams EG, Clarke AE, Knox RB, editors. Genetic control of self-incompatibility and reproductive development in flowering plants. Dordrecht:Springer;1994.p.164–88. https://doi.org/10.1007/978-94-017-1669-7_9.
- Nagamine A, Ezura H. Genome editing of DWARF and SELF-PRUNING rapidly confers traits suitable for plant factories while retaining useful traits in tomato. *Breed Sci*. 2024;74:59–72. <https://doi.org/10.1270/jsbbs.23063>.
- Nakazato T, Warren DL, Moyle LC. Ecological and geographic modes of species divergence in wild tomatoes. *Am J Bot*. 2010;97:680–93. <https://doi.org/10.3732/ajb.0900216>.
- Nicotra AB, Leigh A, Boyce CK, Jones CS, Niklas KJ, Royer DL, et al. The evolution and functional significance of leaf shape in the angiosperms. *Funct Plant Biol*. 2011;38:535–52.
- O'Malley RC, Ecker JR. Linking genotype to phenotype using the Arabidopsis unimutant collection. *Plant J*. 2010;61:928–40. <https://doi.org/10.1111/j.1365-313X.2010.04119.x>.
- Périlleux C, Lobet G, Tocquin P. Inflorescence development in tomato: gene functions within a zigzag model. *Front Plant Sci*. 2014;5:121. <https://doi.org/10.3389/fpls.2014.00121>.
- Périlleux C, Bouché F, Randoux M, Orman-Ligeza B. Turning meristems into fortresses. *Trends Plant Sci*. 2019;24:431–42. <https://doi.org/10.1016/j.tplants.2019.02.004>.
- Peters SA, Bargsten JW, Szinay D, van de Belt J, Visser RGF, Bai Y, et al. Structural homology in the Solanaceae: analysis of genomic regions in support of synteny studies in tomato, potato and pepper. *Plant J*. 2012;71:602–14. <https://doi.org/10.1111/j.1365-313X.2012.05012.x>.
- Pino LE, Lombardi-Crestana S, Azevedo MS, Scotton DC, Borgo L, Quecini V, et al. The Rg1 allele as a valuable tool for genetic transformation of the tomato 'Micro-Tom' model system. *Plant Methods*. 2010;6:23. <https://doi.org/10.1186/1746-4811-6-23>.
- Pino LE, Tullmann Neto A, Zsögön A, Piotto FA, Bernardi WF, Peres LEP, et al. Induced mutagenesis and natural genetic variation in tomato 'Micro-Tom'. *Acta Horticulturae*. 2009;821:63–72. <https://doi.org/10.17660/ActaHortic.2009.821.5>.
- Pnueli L, Carmel-Goren L, Hareven D, Gutfinger T, Alvarez J, Ganai M, et al. The SELF-PRUNING gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of CEN and TFL1. *Development*. 1998;125:1979–89. <https://doi.org/10.1242/dev.125.11.1979>.
- Reinhardt D, Kuhlemeier C. Plant architecture. *EMBO Rep*. 2002;3:846–51. <https://doi.org/10.1093/embo-reports/kvf177>.
- Rick CM. The tomato. *Sci Am*. 1978;239:76–87. <https://doi.org/10.1038/scientificamerican0878-76>.
- Rillig MC, Ramsey PW, Gannon JE, Mummey DL, Gadkar V, Kapulnik Y. Suitability of mycorrhiza-defective mutant/wildtype plant pairs (*Solanum lycopersicum* L. cv Micro-Tom) to address questions in mycorrhizal soil ecology. *Plant Soil*. 2008;308:267–75. <https://doi.org/10.1007/s11104-008-9629-x>.
- Robbins MD, Sim SC, Yang W, Van Deynze A, van der Knaap E, Joobeur T, et al. Mapping and linkage disequilibrium analysis with a genome-wide collection of SNPs that detect polymorphism in cultivated tomato. *J Exp Bot*. 2011;62:1831–45. <https://doi.org/10.1093/jxb/erq367>.
- Robledo JM, Medeiros D, Vicente MH, Azevedo AA, Thompson AJ, Peres LEP, et al. Control of water-use efficiency by florigen. *Plant Cell Environ*. 2020;43:76–86. <https://doi.org/10.1111/pce.13664>.
- Sack L, Scoffoni C. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytol*. 2013;198:983–1000. <https://doi.org/10.1111/nph.12253>.
- Sack L, Scoffoni C, McKown AD, Frole K, Rawls M, Havran JC, et al. Developmentally based scaling of leaf venation architecture explains global ecological patterns. *Nat Commun*. 2012;3:837. <https://doi.org/10.1038/ncomms1835>.
- Scott JW, Harbaugh BK. Micro-Tom – a miniature dwarf tomato. *Agricultural And Food Sciences*. 1989.
- Shalit A, Rozman A, Goldshmidt A, Alvarez JP, Bowman JL, Eshed Y, et al. The flowering hormone florigen functions as a general systemic regulator of growth and termination. *Proc Natl Acad Sci U S A*. 2009;106:8392–7. <https://doi.org/10.1073/pnas.0810810106>.
- Shaul-Keinan O, Gadkar V, Ginzberg I, Grünzweig JM, Chet I, Elad Y, et al. Hormone concentrations in tobacco roots change during arbuscular mycorrhizal colonization with *Glomus intraradices*. *New Phytol*. 2002;154:501–7. <https://doi.org/10.1046/j.1469-8137.2002.00388.x>.
- Shikata M, Ezura H. Micro-tom tomato as an alternative plant model system: mutant collection and efficient transformation. *Methods Mol Biol*. 2016;1363:47–55. https://doi.org/10.1007/978-1-4939-3115-6_5.
- Shirasawa K, Ariizumi T. Near-complete genome assembly of tomato (*Solanum lycopersicum*) cultivar Micro-Tom. *Plant Biotechnol*. 2024;41:367–74. <https://doi.org/10.5511/plantbiotechnology.24.0522a>.
- Shiu SH, Lehti-Shiu MD. Assessing the evolution of research topics in a biological field using plant science as an example. *PLoS Biol*. 2024;22: e3002612. <https://doi.org/10.1371/journal.pbio.3002612>.
- Silva WB, Vicente MH, Robledo JM, Reartes DS, Ferrari RC, Bianchetti R, et al. SELF-PRUNING acts synergistically with DIAGEOTROPICA to guide auxin responses and proper growth form. *Plant Physiol*. 2018;176:2904–16. <https://doi.org/10.1104/pp.18.00038>.
- Sun HJ, Uchii S, Watanabe S, Ezura H. A highly efficient transformation protocol for Micro-Tom, a model cultivar for tomato functional genomics. *Plant Cell Physiol*. 2006;47:426–31. <https://doi.org/10.1093/pcp/pci251>.
- Sun Y, Shang L, Zhu QH, Fan L, Guo L. Twenty years of plant genome sequencing: achievements and challenges. *Trends Plant Sci*. 2022;27:391–401. <https://doi.org/10.1016/j.tplants.2021.10.006>.
- Terashima I. Anatomy of nonuniform leaf photosynthesis. *Photosynth Res*. 1992;31:195–212. <https://doi.org/10.1007/BF00035537>.
- Therezan R, Kortbeek R, Vendemiatti E, Legarra S, de Alencar SM, Schuurink RC, et al. Introgression of the sesquiterpene biosynthesis from *Solanum habrochaites* to cultivated tomato offers insights into trichome morphology and arthropod resistance. *Planta*. 2021;254:11. <https://doi.org/10.1007/s00425-021-03651-y>.
- Thompson AJ, Andrews J, Mulholland BJ, McKee JM, Hilton HW, Horridge JS, et al. Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. *Plant Physiol*. 2007;143:1905–17. <https://doi.org/10.1104/pp.106.093559>.
- Tomato Genome Consortium. The tomato genome sequence provides insights into fleshy fruit evolution. *Nature*. 2012;485:635–41. <https://doi.org/10.1038/nature11119>.
- Tóth M, Tóth ZG, Fekete S, Szabó Z, Tóth Z. Improved and highly efficient agrobacterium rhizogenes-mediated genetic transformation protocol: efficient tools for functional analysis of root-specific resistance genes for *Solanum lycopersicum* cv. Micro-Tom Sustainability. 2022;14:6525. <https://doi.org/10.3390/su14116525>.
- Van Eck J. Genome editing and plant transformation of solanaceous food crops. *Curr Opin Biotechnol*. 2018;49:35–41. <https://doi.org/10.1016/j.copbio.2017.07.012>.
- Vendemiatti E, Therezan R, Vicente MH, Pinto MS, Bergau N, Yang L, et al. The genetic complexity of type-IV trichome development reveals the steps towards an insect-resistant tomato. *Plants (Basel)*. 2022;11:1309. <https://doi.org/10.3390/plants11101309>.
- Vendemiatti E, Hernández-De Lira IO, Snijders R, Torne-Srivastava T, Therezan R, Simioni Prants G, et al. Woolly mutation with the Get02 locus overcomes the polygenic nature of trichome-based pest resistance in tomato. *Plant Physiol*. 2024;195:911–23. <https://doi.org/10.1093/plphys/kiae128>.
- Vicente MH, Zsögön A, de Sá AFL, Ribeiro RV, Peres LEP. Semi-determinate growth habit adjusts the vegetative-to-reproductive balance and increases productivity and water-use efficiency in tomato (*Solanum lycopersicum*). *J Plant Physiol*. 2015;177:11–9. <https://doi.org/10.1016/j.jplph.2015.01.003>.
- Wang Y, He X, Yu F. Non-host plants: Are they mycorrhizal networks players? *Plant Divers*. 2021;44:127–34. <https://doi.org/10.1016/j.pld.2021.06.005>.
- Xu J, van Herwijnen ZO, Dräger DB, Sui C, Haring MA, Schuurink RC. SIMYC1 regulates type VI glandular trichome formation and terpene biosynthesis in tomato glandular cells. *Plant Cell*. 2018;30:2988–3005. <https://doi.org/10.1105/tpc.18.00571>.
- Yang C, Marillonnet S, Tissier A. The scarecrow-like transcription factor SISL3 regulates volatile terpene biosynthesis and glandular trichome size in tomato (*Solanum lycopersicum*). *Plant J*. 2021;107:1102–18. <https://doi.org/10.1111/tbj.15371>.

- Yeager AF. Determinate growth in the tomato. *J Hered.* 1927;18:263–5. <https://doi.org/10.1093/oxfordjournals.jhered.a102869>.
- Zsögön A, Lambais MR, Benedito VA, de Oliveira Figueira AV, Peres LEP. Reduced arbuscular mycorrhizal colonization in tomato ethylene mutants. *Sci Agric.* 2008;65:259–67. <https://doi.org/10.1590/S0103-90162008000300006>.
- Zsögön A, Alves Negrini AC, Peres LEP, Nguyen HT, Ball MC. A mutation that eliminates bundle sheath extensions reduces leaf hydraulic conductance, stomatal conductance and assimilation rates in tomato (*Solanum lycopersicum*). *New Phytol.* 2015;205:618–26. <https://doi.org/10.1111/nph.13084>.
- Zsögön A, Peres LEP. Molecular control of plant shoot architecture. *Plant Cell.* 2018;30:tpc.118.tt1218. <https://doi.org/10.1105/tpc.118.tt1218>.
- Zwieniecki MA, Brodribb TJ, Holbrook NM. Hydraulic design of leaves: insights from rehydration kinetics. *Plant, Cell & Environment.* 2007;30:910–21. <https://doi.org/10.1111/j.1365-3040.2007.001681.x>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.