

Tomato Fruit Set and Parthenocarpy

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Fruit set is the earliest phase of fruit growth and represents the onset of ovary growth after successful fertilization. Environmental conditions can negatively affect fruit set and final productivity. In parthenocarpy, fruit formation is less affected by environmental factors because it occurs in the absence of pollination and fertilization, making parthenocarpy a highly desired agronomic trait. Elucidating the genetic program controlling parthenocarpy, and more generally fruit set, may have important implications in agriculture, considering the need for crops to be adaptable to climate changes. Several phytohormones play an important role in the transition from flower to fruit. Further complexity emerges from functional analysis of floral homeotic genes. Some homeotic MADS-box genes are implicated in fruit growth and development, displaying an expression pattern commonly observed for ovary growth repressors.

Keywords: Fruit Set ; Tomato ; Hormonal Regulation ; MADS-box

1. Introduction

Tomato is one of the most important crops worldwide cultivated for the nutritional value of its fruit, which is a source of health-promoting compounds such as vitamins, carotenoids, phenolic compounds, and small peptides [1]. Furthermore, tomato has been adopted as an experimental model for studying fleshy fruit growth, development, and ripening. Botanically, the tomato fruit that originates from the ovary, the expanded basal portion of the pistil, is a berry composed of pericarp derived from the ovary wall, the placenta, and the pulp containing seeds [2]. Shortly before flower anthesis, the growth of the unpollinated ovary is actively blocked by developmental repressors and cell division temporarily stops. The control on ovary quiescence in tomato and Arabidopsis is exerted at least in part by negative factors derived from the communication between the anthers and the ovary [3][4]. After successful completion of pollination and ovule fertilization, the coordinated action of growth signals acts in relieving the ovary growth repression [5][6]. The switch from the static condition of the unpollinated ovary to that of rapidly growing fruit after fertilization is called the fruit set phase, after which fruit growth occurs by cell division and cell expansion, until reaching the ripening stage. Auxins, gibberellins (GAs), cytokinins (CKs), abscisic acid (ABA), ethylene, and brassinosteroids (BRs) have been implicated in controlling different stages of fruit growth [1][7][8], with auxins and GAs being the crucial promoting hormones of fruit initiation [4][9][10]. MADS-box transcription factors have also emerged as one of the players recruited for the regulation of fruit set [11][12][13].

Fruit set is a very critical phase because it is more sensitive to endogenous and exogenous signals than later stages of growth [14]. Insufficient supply of nutrients, such as the phloem-imported sucrose, and adverse environmental conditions, such as drought or excessive/low temperatures, may impair the reproductive process, leading to the abortion of either flowers, seeds, or fruit with dramatic implications for fruit productivity [14][15]. The induction of parthenocarpy, which is the formation of seedless fruit in the absence of pollination and fertilization [3], could help prevent problems linked to low fruit yield under unfavorable conditions [9][16]. Parthenocarpy is generally the consequence of precocious activation of molecular events occurring normally upon pollination and fertilization. Some species or varieties (e.g., genetic mutants or plants with altered ploidy) have a natural capacity to produce parthenocarpic fruit [17][16]. In addition, parthenocarpy can be artificially obtained by applying synthetic growth factors to unpollinated ovaries or by genetic engineering [9].

2. Hormonal Regulation of Fruit Set

2.1. Auxins

Immediately after pollination and fertilization, auxin content (with indole-3-acetic acid—IAA—the major active auxin) increases within the ovary, activating the auxin signaling pathway that initiates fruit set. Auxin is perceived by its receptor, the TRANSPORT INHIBITOR RESPONSE 1 (TIR1), which is the F-box protein component of the E3 ubiquitin ligase complex, called SKP1/CUL1/F-box complex (SCF^{TIR1}). Auxin acts as a "molecular glue", stabilizing interaction between AtTIR1 and its target proteins AUXIN/INDOLE-3-ACETIC ACID (Aux/IAAs), thus promoting ubiquitination and degradation of the Aux/IAAs through SCF^{TIR1} and the proteasome [19][20][21]. In this way, free AUX/IAA-AUXIN-RESPONSE FACTORS

References

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(ARF) in an analysis of the tomato fruit growth response to temperature. Overexpression of fruit IAR1 in relation to cell division, cell expansion and cell differentiation, including AgRP, and the overexpression of SIT1R1 would promote the degradation of Aux/IAA repressors with the subsequent destabilization of the AUX/IAA-ARF inhibitory complex [22]. Members of the AUX/IAA and ARF transcription factors have been demonstrated to play a role in fruit set.

The review describes in detail the studies. The role of auxin and gibberellin in tomato fruit set. J. Exp. Bot. 2009, 60, 1523–1532. This hormone, in the case of auxin, A. Molecular dissection of the role of auxin in fruit initiation. Trends Plant Sci. 2007, 12, 327–329.

2.2. Gibberellins (GAs)

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9. Bandolfini, T. Seedless Fruit production by hormonal regulation of fruit set. *Nutrients* 2009, 1, 168–177. GA 2-oxidase (GA2ox), which in tomato constitute a small multigene family of five members, caused an accumulation of

10. active GA in the ovary and parthenocarpic fruit development [24]. As observed for auxin signaling, it was demonstrated that the GA signal transduction pathway is blocked in the ovary before fertilization by the presence of a transcriptional

11. repressor, a DELLA protein [25]. The release of DELLA repression in tomato, obtained by RNA silencing, allowed parthenocarpic fruit growth [25].

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13. has been recognized as an early signal acting upstream from GA responses in fruit initiation [5]. The crosstalk between auxin and GA signaling components in fruit set regulation has recently been demonstrated. It was reported that

14. SIARF7/SIIAA9 and SEPALLATA1 interact with both SIIAA9 and SIDELLA through distinct protein regions. SIDELLA and SIARF7/SIIAA9 act additively in the regulation of ovary/fruit growth-related genes [29].

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The role of these hormones in fruit set has been discussed in the review and their action has been schematically illustrated in the figure (Figure 1).

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27. The tomato AUX/IAA transcription factor IAA9 is involved in fruit development and leaf morphogenesis. *Plant Cell* 2005, 17, 2609–2622. determining the identity of the organs in the four concentric whorls of the flower: sepal, petal, stamen,

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TAGL1, AGL11, TAP3, TM29, SIGLO1, and SIGLO2). It is known that early anther ablation can favour parthenocarpy, thus relieving the ovary growth repression probably by increasing GA concentration [34]. Another possible explanation is that the defective pollen fails to fertilize ovules but still produces some signals that induce fruit initiation. On the other hand, when parthenocarpy is obligatory, as in the case of TM29 downregulation, parthenocarpic trait is most likely linked to alteration in the female organ rather than pollen defects. The most interesting case of MADS-box-related parthenocarpy is that of AGL6 whose suppression results in facultative parthenocarpy, as the transgenic plants produce seeded fruit when pollinated and seedless fruit under unfavorable conditions. Both pollen and ovules are viable and no pleiotropic effects on reproductive or vegetative development, except parthenocarpy, are observed in the mutated plants [39]. The AGL6 mutation suggests that some MADS-box genes might have undergone sub functionalization, thus conserving only the activity as ovary growth regulator, while their function in flower organ identity would have been lost. It would be interesting to deepen the research of MADS-box genes in fruit set, identifying downstream targets and elucidating the relationship between hormone signaling and MADS-box activity. The observation that some elements of the genetic network controlling the formation of flower organs and gametogenesis might also be involved in the successive phases of fruit formation and growth, supports the idea that the two developmental programs are tightly connected.