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][1][2][3]}, with auxins and GAs being the crucial promoting hormones of fruit initiation ^{[4][6][9][10]}. MADS-box transcription factors have also emerged as one of the players recruited for the regulation of fruit set ^{[11][1][2][3]}.

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) **Referencies** 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 to the asymptotic from the store of the e3 ubiquitin ligase to the test of test of the test of test A Besting an Antiverse at the torseon sering month presence 1912 and reading a contract of the torseon technic and the contract of the torseon technic and tec severilaanstien an of sitter and the advertige of the several seve gegradatismath, Aux Llas, Mep consolation with the one who and the advertised of the state of th Merenansking Availability of the section of the sec

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12, 327-329 2.2. Gibberellins (GAs)

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Sugidessetellings Interview and a 2008 for a sociated with an an and the side of the side catapatic 1952/1952/mes, such as GA 2-oxidase [6]. The overexpression of citrus GA biosynthetic gene GA 20-oxidase 1 (GA20ox1) in tomato induced parthenocarpic fruit growth linked to an increased content of GA₄ ^[23]. The flowers of 8. Azzi, L.; Deluche, C.; Gévaudant, F.; Frangne, N.; Delmas, F.; Hernould, M.; Chevalier, C. Fruit growth-related genes in GA20ox1-overexpressing plants displayed alterations in pistil development with a long style protruding from the flower, tomato. J. Exp. Bot. 2015, 66, 1075–1086. thus preventing self-pollination at the stigma surface ^[23]. Silencing of the genes encoding for the GA inactivating enzyme, 8.A200xHBLISE TO \$200XIE SATENTIN PERHATION CONSTRUCTION OF THE ADDRESS TO ACCUMULATION OF

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repressor, a DELLA protein ^[25] The release of DELLA repression in tomato obtained by RNA silencing, allowed 11. Amponah-Dwamena, C.; Morris, B.A.; Sutherland, P.; Veit, B.; Yao, J.-L. Down-Regulation of TM29, a tomato parthenocarpic fruit growth ^[25] Parthenocarpic DELLA-silenced fruit were smaller than wild-type had an elongated SEPALLATA homotog, causes parthenocarpic fruit development and floral reversion. Plant Physiol. 2002, 130, 605– morphology and a reduction in the pericarp cell number ^[25]. In fact, in SIDELLA-silenced parthenocarpic fruit, auxin-

regulated cell division (phase II) is bypassed, while cell expansion phase III is activated [25]. Considering that manipulation 12. Wang, H.: Schauer, N.; Usadel, B.: Frasse, P.: Zouine, M.: Hernould, M.: Latché, A.: Pech, J.C.: Fernie, A.R.: of GA signaling leads to formation of parthenocarpic fruit elongated in shape and smaller than seeded fruit, whereas Bouzayena, M. Regulatory features underlying pollination-dependent and-independent tomato fruit set revealed by parthenocarpic fruit obtained by altering IAA signaling is generally similar in size and shape to seeded fruit ^{2012/128}, auxin transcript and primary metabolite profiling. Plant Cell 2009, 21, 1428–1452.

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15.8 other Hormones (Cytokinins, Brassinosteroids, Ethylene, and Abscisic acid) transcription in meiotic anthers of heat-tolerant and heat-sensitive tomato plants. BMC Genom. 2011, 12, 384,

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Nd *: not defined.

From all the studies described in the review, the involvement of MADS-box transcription factors in the regulation of fruit set and development appears to be evident, even if it is very difficult to place the information present in the literature in a clear picture. Seedlessness has been reported to occur both as a consequence of either suppression (AGL6, TM8, TM29, TAP3, SIGLO1, and SIGLO2) or ectopic overexpression (AGL11, TAG1, and TAGL1) of MADS-box genes. In the first case, the activity of the gene would directly or indirectly be linked either to the repression of fruit growth prior to fertilization or to maintenance of ovule or pollen viability. In the case of ectopic overexpression, parthenocarpy could represent a pleiotropic effect that highlights the need for strict spatial localization of MADS-box expression to avoid an untimely onset of ovary growth. It is interesting to note that in some cases, fruit seedlessness is accompanied by male sterility (TAG1,

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 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.