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Hormonal Regulation of Tomato Fruit Development: A Molecular Perspective

Alka Srivastava and Avtar K. Handa*

Department of Horticulture and Landscape Architecture, 625 Agricultural Mall Drive, Purdue University, West Lafayette, Indiana 47907-2010, USA

Abstract

Fruit development is a complex yet tightly regulated process. The developing fruit undergoes phases of cell division and expansion followed by numerous metabolic changes leading to ripening. Plant hormones are known to affect many aspects of fruit growth and development. In addition to the five classic hormones (auxins, gibberellins, cytokinins, abscisic acid and ethylene) a few other growth regulators that play roles in fruit development are now gaining recognition. Exogenous application of various hormones to different stages of developing fruits and endogenous quantifications have highlighted their importance during fruit development. Information acquired through biochemical, genetic and molecular studies is now beginning to reveal the possible mode of hormonal regulation of fruit development at molecular levels. In the present article, we have reviewed studies revealing hormonal control of fruit development using tomato as a model system with emphasis on molecular genetics.

Key words: Fruit development; *Lycopersicon esculentum*; Hormonal regulation, Auxins; Cytokinins, Gibberellins; Abscisic acid; Ethylene; Parthenocarpy

Introduction

Fruit development and ripening is a well-coordinated, temporally and spatially tightly regulated complex process involving the interplay of a number of biotic and abiotic factors. Plant hormones have long been known to regulate the development and ripening of fruits (Crane 1964, 1969; Nitsch 1970). The five classical hormones, namely, auxins, cytokinins, gibberellins (GAs), abscisic acid (ABA), and ethylene, are all known to modulate growth and development at various stages of the developing fruit (Ozga and Rienecke 2003). In addition, the roles of growth regulators such as polyamines (PAs), salicylic acid, jasmonic acid, and brassinosteroids on fruit development and ripening are beginning to be identified (Li and others 1992; Cohen 1999; Mehta and others 2002; Vardhini and Rao 2002; Sheng and others 2003).

Fruits serve as receptacles for the developing seeds, initially protecting them from destructive environmental and predatory elements, and later promoting their dispersal. To that end, fruits usually develop distinct characteristics such as bright colors, aroma, flavor, and succulence, as observed in such

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Corresponding author; e-mail: handa@hort.purdue.edu

fleshy fruits as tomato or wings of maple fruit. Despite their varied morphologies, fruits share common events and pathways in their life cycle that are crucial for their induction and development. The development of a fruit can be separated into phases that include pre-pollination, pollination, fertilization and fruit set, post-fruit set, ripening, and senescence stages. Pre-pollination development involves the floral and fruit primordia (ovary and ovule) initiation, with the ovary and the ovule undergoing development until pollination/fertilization. Successful pollination of the ovary and fertilization of the ovule warrant further development; failure in either of these two events results in their senescence. The successful fertilization of the ovule is followed by cell divisions and expansion resulting in the growth of the fruit (fruit set). Fruit may either undergo growth entirely by cell enlargement after the cell division phase, as in *Lycopersicon esculentum*, or some cell division may accompany cell enlargement throughout the period of fruit growth, as in *Lycopersicon pimpinellifolium* (Crane 1964). Fruit maturation is followed by ripening and ultimately senescence, which marks the switch in the fruit's function from protection of the developing seeds to their dispersal, and is accompanied by myriad changes in the biochemical and physiological aspects. Seeds, a rich source of many hormones (Crane 1969), are known to be essential for normal development of fruits; the size and shape of many fruits being determined by seed number and distribution. Fruits also act as mobilization centers for nutrients, with hormones possibly modulating the process (Brenner and Cheikh 1995). Plant hormones are essential for successful completion of each developmental stage and progression of the developing fruit into the next stage. However, despite extensive studies on the effects of hormones on plant growth and development over many years, the mode of their action at the molecular level in fruit development is not yet understood. Only in recent years have the molecular components involved in control of hormonal effects during fruit development begun to emerge. In this review, we have focused on recent advances in hormonal control of tomato (*Lycopersicon esculentum*) fruit development, with emphasis on molecular regulators.

Tomato, a fleshy climacteric fruit, has long-served as a model for fruit development and ripening studies. Extensive work in this fruit crop has resulted in the development of large populations of well-characterized mutants, which provide a system amenable to analyzing molecular aspects of fruit development and ripening, including the aspects of hormonal regulation (Table 1). Tomato fruit development has been broadly divided into four phases, with the growth and maturation of tomato fruit following a single sigmoidal growth curve (Figure 1A, 1C) (Crane 1964). Phase I represents floral development, pollination, fertilization, and fruit set. Phase II involves cell division that lasts for 7–14 days after pollination (Mapelli and others 1978). During this phase most of the fruit cells are established. However, fruit growth is slow, reaching only about 10% of the final fruit fresh weight (Figure 1C). Phase III primarily comprises cell expansion, which, depending on the genotype, continues for 3–5 weeks and is responsible for attainment of the maximum fruit size (Ho and Hewitt 1986). The final fruit size is dependent on the number of cells established in phase II (Ho 1996). It is also a function of the cell number within the ovary prior to fertilization, the number of successful fertilizations that occur in the ovary, and the extent of cell enlargement (Bohner and Bangerth 1988). Phase IV involves ripening, which is characterized by slow growth and intense metabolic changes. The life cycle of tomato fruit spans 40–70 days from fertilization to the ''red ripe'' stage. Many factors such as cultivar, position on the cluster, climactic conditions, and cultural practices influence the overall fruit development.

Hormonal Roles during Tomato Fruit Development

Early studies involving exogenous application of various hormones to developing fruit indicate their roles at different stages of fruit development (Crane 1964). However, the fact that the effects of exogenous application may not be a true representation of their cellular role has led to an examination of the endogenous levels of hormones during fruit development and ripening (Figure 1B). The abundance of certain hormones over others at specific stages of fruit development indicates a possible role for these hormones during that developmental stage. Exogenous application studies and endogenous quantifications have provided insights into the roles of hormones during tomato fruit development.

Exogenous application of gibberellins (GAs) at or near anthesis to the styles of tomato flowers induces cell enlargement in pre-formed normal ovaries and leads to parthenocarpic fruit development (Fos and others 2000). Application of GAs to unpollinated tomato flowers results in increased

Table 1. Hormone-Related Tomato Mutants Used for Fruit Development Studies

Mutant	Description	Hormonal deviations	Reference
pat	Parthenocarpy	GA metabolism pathway may be affected; Net spermine and spermidine accumulation during pre-anthesis floral development.	Mazzucato and others 1998; Antognoni and others 2002
pat-2	Parthenocarpy (Russian cv. Severianin)	High GA_{20} levels in the ovaries	Fos and others 2003
pat-3/4	Parthenocarpy (German line RP75/59)	Enhanced early 13-hydroxylation pathway of GA biosynthesis	Fos and others 2001
gib-1	GA deficient	GA biosynthetic pathway affected (lesion in *ent-copalyl diphosphate synthase*, *CPS*, gene)	Bensen and Zeevart 1990
gib-3	GA deficient	GA biosynthetic pathway affected (lesion in *ent-kaurene synthase*, *KS*, gene)	Bensen and Zeevart 1990
sitiens (*sitw*)	ABA deficient	ABA deficient	Groot and Karssen 1992; Liu and others 1996
rin	*ripening inhibitor*	Low ethylene production, impaired putrescine decline during ripening	Tigchelaar and others 1978
nor	*non-ripening*	Low ethylene production; peak ABA levels 50% that of normal fruit; peak in ABA level is delayed	Tigchelaar and others 1978
Nr	*Never ripe*	Insensitive to ethylene	Tigchelaar and others 1978
alc	*alcobaca*	Reduced ethylene, high PA contents	Dibble and others 1988
Cnr	*Colorless non-ripening*	Reduced ethylene	Thompson and others 1999
flc	*flacca*	Reduced ABA levels	Sharp and others 2000
not	*notabilis*	Reduced ABA levels	Burbidge and others 1999
d^x	*extreme dwarf*	Brassinosteroid deficient (biosynthesis mutant)	Bishop and others 1999
dpy	*dumpy*	Brassinosteroid insensitive (signaling mutant)	Koka and others 2000
cu3	*curl3*	Brassinosteroid insensitive (signaling mutant)	Koka and others 2000
dgt	*diageotropica*	Blocked rapid auxin reaction of tomato hypocotyls	Balbi and Lomax 2003; Coenen and others 2003

GA = gibberellin; ABA = abscisic acid; PA = polyamines.

auxin levels in tomato ovaries (Sastry and Muir 1963). It has been suggested that the GAs produced by the pollen may play a role in increasing auxin production in the ovary, which may serve as a signal for fruit set and further cell division (Gillaspy and others 1993). High GA levels have been detected in young, immature tomato fruits (Koornneef and others 1990). GA may play a role in anthesis and stimulate fruit and seed development (Rebers and others 1999). Bioassay studies have shown that the endogenous GA-like activities in normal seeded tomato plants follow a bimodal pattern (Figure 1B), with the levels peaking first from anthesis to about the 8th day and then from about the 15th day to ripening (Mapelli and others 1978; Sjut and Bangerth 1982). Gas chromatography-mass spectrometry (GC-MS) along with gas chromatography-selected ion monitoring (GC-SIM) studies show that the levels of GA_1 and GA_{20}, considered to be the most important GAs physiologically, are high in pericarp and seeds, with the GA_1 levels decreasing during development in pericarp whereas the seed GA levels increase with peaks between 15 and 30 days after pollination (Bohner and others 1988). The two peaks of gibberellin accumulation coincide with the cell division (phase II) and cell expansion phase (phase III) of tomato fruit development (Figure 1).

The presence of auxins in pollen, its production in the style and ovary accompanying pollen tube growth and fertilization, and resultant stimulation of ovary growth along with production of parthenocarpic fruits by exogenous application of auxins, strongly indicates a function for this hormone during fruit set (Crane 1964). Bioassay studies for auxins also reveal a bimodal pattern of activity (Figure 1B), with the peaks in activity occurring at about 10 days after anthesis and then again at about 30 days after anthesis in developing tomato fruits, suggesting roles for this hormone both at initiation

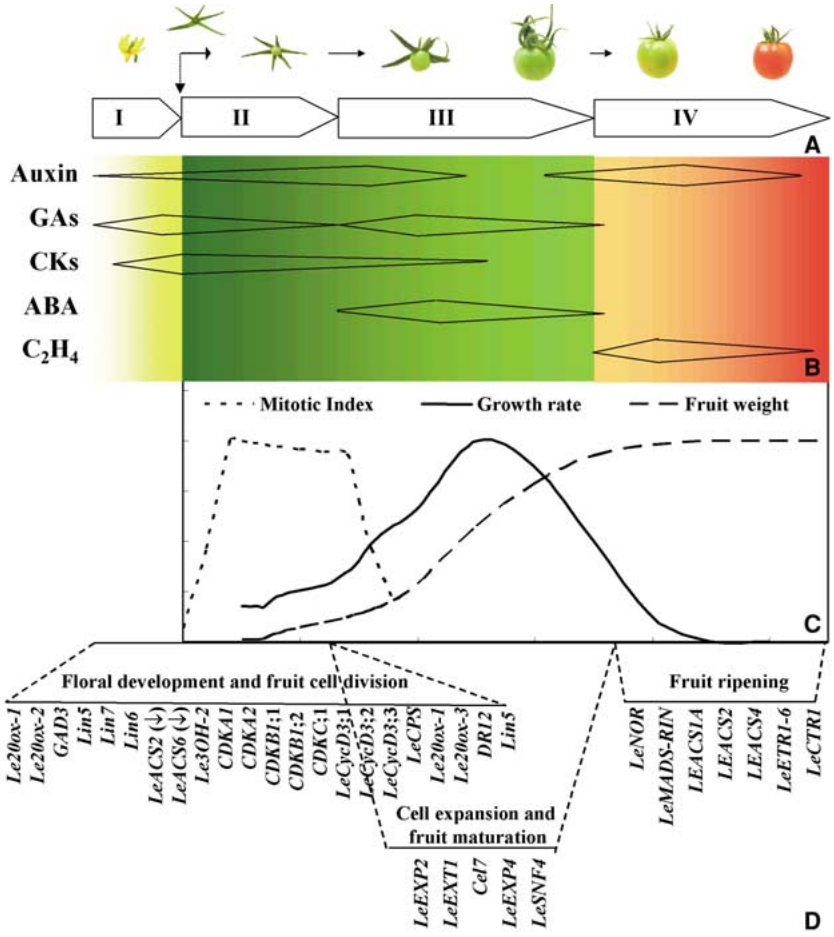

Figure 1. Hormonal regulation of tomato fruit development. Shown are various phases of tomato fruit development **(A)** and classical hormonal fluxes **(B)**. The hormonal fluxes were redrawn with approval from Gillaspy and others 1993 (copyright ©American Society for Plant Biologists). The phases represent: I, floral development and fruit set (broken arrow); II, cell division during early fruit development; III, cell expansion and fruit maturation, and IV, fruit ripening. Middle panel **(C)** depicts sigmoidal growth curve, mitotic index , and growth rate for tomato fruit (redrawn with approval from Cong and Tanksley 2002; copyright © National Academy of Sciences, USA; Abdel-Rahaman 1977). Some of the genes whose expression is associated with hormonal changes in developing fruit are also indicated. **(D)** The down-pointing arrow represents the downregulation of a gene.

of the cell expansion phase (phase III) and at the final embryo development phase (phase IV) (Abdel-Rahman 1977; Mapelli and others 1978; Gillaspy and others 1993). A more quantitative approach with GC-SIM-MS studies and radioimmunoassays has confirmed the occurrence of two auxin peaks during tomato fruit development, with the auxin levels in seeds also showing a constant increase in the first 30 days of fruit development (Bohner and Bangerth 1988; Buta and Spaulding 1994). Radio-immunoassays show high levels of cytokinins (Figure 1B) at 5 days after anthesis (Bohner and Bangerth 1988). The levels of cytokinin found in seeds in this study are higher than those in the pericarp. The correlation between cell number and cytokinin levels in young developing tomato fruits suggests a possible role for cytokinin in cell division (phase II). Bioassays also show a coincidence between cytokinin level and cell division activities in tomato fruit (Abdel-Rahman and others 1975; Mapelli 1981). Gas liquid chromatographic (GLC) studies reveal a dramatic decline in cytokinin levels during ripening, reaching the lowest level at the red ripe stage (Desai and Chism 1978), which suggests lesser roles for cytokinins during ripening. The mode of cell-division regulation exerted by cytokinins in the developing seeds of the fruits is not yet clear. It is hypothesized that cytokinins in the developing seed may control the synthesis of a positive regulator that may diffuse into surrounding cells that are developmentally regulated to divide (Gillaspy and others 1993).

Seeds play an important role in normal fruit development. Normal seed development within the tomato fruit is also dependent on developmental stages of the sheath and the locular tissues. ABA concentration and osmotic potential fluxes in these tissues appear to regulate seed desiccation and dormancy induction, which prevents precocious germination (Berry and Bewley 1991). Radioimmunoassays and GLC studies show detectable ABA levels at about 5 days after pollination, with the levels rising in both seed and pericarp until 30–50 days after pollination (Sjut and Bangerth 1982; Bohner and Bangerth 1988; Berry and Bewley 1991), with the peak level coinciding with the cell expansion phase (phase III).

Ethylene has been the most widely studied hormone because of its well-demonstrated ripening and senescence enhancing effects. Ethylene levels are high in the early stages of fruit set (phase I), decrease in later stages, and again increase at the onset of fruit ripening (Abdel-Rahman 1977; Lacheene and El-Beltagy 1986). This latter increase in ethylene levels is associated with the climacteric rise of respiration (phase IV). The need to control tomato fruit ripening process to increase the shelf life of fruit has led to a detailed but not yet complete understanding of its molecular role during fruit development and ripening (Giovannoni 2004; Klee 2004).

Molecular Perspective of Parthenocarpy and Hormone-Deficient Mutants

Parthenocarpy, the phenomenon of seedless fruit development, has provided abundant information about the involvement of hormones during early fruit development. Tomato shows facultative parthenocarpy; that is, seedless fruits may develop depending upon environmental stimuli (George and others 1984). Artificial parthenocarpy may be induced by exogenous application of hormones, especially auxins and GAs that mimic the effect of pollination, thereby resulting in parthenocarpic fruit (Gustafson 1936; Nitsch 1971). The genetics of a number of parthenocarpic lines in tomato have been described (George and others 1984; Fos and Nuez 1996; Mazzucato and others 1998; Fos and others 2000, 2001). Parthenocarpy in *pat* mutant is controlled by the recessive *pat* gene, whereas the *pat-2* gene controls facultative parthenocarpy in "Severianin" (George and others 1984). Parthenocarpy in the German line RP75/59 is controlled by *pat-3/pat-4* (Nuez and others 1986). The genes *pat*, *pat-2*, and *pat-3/pat-4* responsible for the three parthenocarpic lines in tomato are non-allelic (George and others 1984; Fos and others 2001).

Studies on parthenocarpic lines of various fruits suggest that these lines have increased endogenous hormone levels in the ovary, which promotes the development of fruits even in the absence of pollination or fertilization (George and others 1984). These studies have led to the acceptance of Nitsch's proposal (Nitsch 1970) of a minimum concentration requirement in the parthenocarpic ovary at anthesis before occurrence of pollination. In *pat* fruits, the endogenous levels of auxin-like substances have been found to be threefold higher than the normal lines at anthesis; levels of GA-like substances are four times higher during the first 8 days of growth, whereas those of cytokinin-like substances are 20 times lower than in the normal fruit (Mapelli and others 1978; Mapelli 1981).

Several GAs (GA_1, GA_8, GA_{19}, GA_{20}, GA_{29}, and GA_{44}) have been found in developing tomato fruits (Bohner and others 1988; Koshioka and others 1994). Quantification of GA levels in *pat-2* and *pat-3/pat-4* mutant lines reveal increased levels of GA_1, GA_{19}, GA_{20}, GA_{29}, and GA_{44} (which are members of the 13-hydroxylation pathway) in *pat-3/pat-4* ovaries, indicating that this pathway is enhanced in the latter parthenocarpic system. These changes are not seen in the *pat-2* system, indicating that the alteration of GA metabolism produced in the unpollinated ovaries of the *pat-3/pat-4* genetic system is different from that in the *pat-2* genetic system (Fos and others 2000, 2001). These studies are in agreement with earlier observation of increased levels of GA-like substances in *pat* fruits at the early stages of development (Mapelli and others 1978), and they further illustrate the importance of GAs in the control of fruit set and development. Studies with the GA-deficient mutants *gib-1* and *gib-2* have demonstrated the requirement of GAs for normal floral development and seed set (Groot and others 1987; Bensen and Zeevart 1990), and three flower-specific cDNAs (*tgas100*, *tgas105*, and *tgas118*) upregulated by GAs have been isolated from the GA-deficient *gib-1* mutant (van den Heuvel and others 2001, 2002). The deduced TGAS105 polypeptide shows homology to extensin-like proteins, whereas the TGAS100 polypeptide is similar to a stamen-specific gene from *Antirrhinum*. Transcript expression studies of three GA20 oxidase cDNA clones, namely, *Le20ox-1*, *-2*, and *-3*, show organ-specific patterns of mRNA accumulation. *Le20ox-1*, *-2*, *copalyl diphosphate synthase* (*LeCPS*), and *GA 3β-hydroxylase* (Le3OH-2) transcript accumulation occurs up until anthesis, with high levels of *Le3OH-2*

transcripts in open flowers, as compared to *Le20ox-1*, *-2*, and *LeCPS*. A post-anthesis increase in transcript levels of LeCPS and *Le20ox-1*, *-3* is observed, whereas the transcript levels of *Le3OH-2* decrease. These results reveal tight spatial and temporal regulation of GA biosynthesis during tomato flower bud development (Rebers and others 1999).

GAD3 (similar to non-metallo short-chain alcohol dehydrogenase) and *LeSPH1* (S protein homolog), two differentially expressed genes putatively involved in fruit set and early development, have been isolated from tomato *pat* mutant lines by differential display (Testa and others 2002). *LeSPH1* upregulation seems to be specific for the expression of parthenocarpic lines, as it is also found in ovaries of *pat-2* lines. Transcript levels of *GAD3* and *LeH2A-2* (similar to Histone H2A) increase in response to GA_3 treatment in wild-type ovaries but not in *pat* mutant lines, showing that both are GA-responsive genes in tomato (Jacobsen and Olszewski 1996; van den Heuvel and others 1999). The non-responsiveness of these genes to GA treatment in parthenocarpic lines could be due to saturated levels of GAs in parthenocarpic ovaries (Mapelli and others 1978; Fos and others 2000, 2001), further supporting the role of GAs in this mode of fruit development. Placenta-specific transcription of *GAD3* genes reflects the tissue specificity of this gene for rapidly dividing cells and supports the hypothesis that it plays an important role in early fruit development and, possibly, in parthenocarpic fruit development.

Unpollinated ovaries induced for parthenocarpic growth with 2,4-dichlorophenoxyacetic acid (2,4-D) show more rapid weight increase than with GA_3, indicating that auxins have a more important role than GAs in tomato fruit set and development (Bangerth 1981; Alabadi and others 1996). Furthermore, 2,4-D– or GA_3–induced parthenocarpic fruits show decreased arginase activity, indicating that a change in arginine metabolism is associated with early tomato fruit development. Also, a decrease in the levels of conjugated PAs post 2,4-D treatment of the unpollinated ovaries has led to the speculation that conjugated polyamines serve as a source of polyamines and related compounds involved in fruit growth by cell division, resulting in their depletion before growth by cell expansion. In the parthenocarpic *pat* ovaries, a net accumulation of PAs has been observed at pre-anthesis floral stages, whereas in the control plants the PA pattern did not change significantly during the developmental stages considered in the study (Antognoni and others 2002). These results are correlated to the typical rapid growth of the ovary at anthesis in parthenocarpic lines. These studies have correlated the levels of PAs with parthenocarpic tomato fruit development, indicating a possible role for this growth regulator in inducing parthenocarpy. Fos and others (2003) have demonstrated partial parthenocarpic growth in tomato on application of putrescine, spermidine, and spermine to unpollinated wild-type ovaries, confirming the role of PAs in parthenocarpic fruit set. They have also shown that parthenocarpic growth in the *pat-2* genetic system relies on PAs and requires both arginine decarboxylase (ADC) and ornithine decarboxylase (ODC) pathways, and that *pat-2* activates PA biosynthesis through the ODC pathway, leading to elevated free spermine content in unpollinated ovaries.

A detailed light and electron microscopic study of male and female organ development in tomato *pat* mutant lines has led to the suggestion that parthenocarpy may be an induced secondary effect of a mutated gene whose primary function is to regulate floral organ development (Mazzucato and others 1998). In addition to aberrant male and female organs, defective ovules, and parthenocarpic fruits, *pat* mutants also exhibit defective pollen–pistil interactions that obstruct seed set (Mazzucato and others 2003). An association between patterns of modulation of certain proteins and the phenotypic expression of genetically controlled parthenocarpy has been shown in studies where a 62-kDa protein shows a sharp decline in seeded fruits, while remaining elevated in *pat-2* parthenocarpic fruits (Barg and others 1990). In another study, comparisons of *in vitro* translation products of two different parthenocarpic lines (*pat-2* and *pat-3*/*pat-4*) and normal tomato flower at bud, anthesis, pre-, and post-anthesis stages revealed a dramatic increase in a 30-kDa polypeptide at the pre-anthesis and anthesis stages in parthenocarpic lines (Fos and Nuez 1996). More work is needed to understand the function of these proteins in parthenocarpic fruit development. Studies with tomato parthenocarpic and mutant lines are making it increasingly clear that auxins, GAs, and PAs are important players in fruit set and early development of tomato fruits.

Molecular Components of Fruit Development

Following successful fruit set, a phase of rapid cell division establishes the total cell population of the final fruit (Figure 1A). Depending on the species, the cell expansion phase (phase III) may follow or accompany the cell division phase in tomato. Auxins, GAs, and cytokinins, found at high con-

centrations during pollination/fertilization and early fruit development, have been implicated in the cell division and expansion phase of the fruit (Abdel Rahman 1977; Mapelli and others 1978; Bohner and Bangerth 1988), with the hormones affecting many other components. In the following section, we have compiled the studies revealing various molecular components that are affected by hormones during tomato fruit development. Fruit ripening and seed dormancy, largely affected by ethylene and ABA, respectively, are addressed in a separate section.

Auxin Response Factors

Auxin is known to induce the expression of several gene families, including the *SAUR* (*s*mall *a*uxin *u*pregulated *R*NA), *GH3*, and *Aux/IAA* genes (Guilfoyle and others 1998). The *Aux/IAA* genes constitute a family of early auxin response genes (Abel and Theologis 1996) that encode for proteins containing nuclear localization signals with short half-lives (Abel and others 1994; Oeller and Theologis 1995). *Aux/IAA* family members are capable of forming homo- and heterodimers with DNA-binding auxin response factors, supporting their role as regulators of auxin responses (Reed 2001). Auxin-resistant *dgt* (*diageotropica*) tomato mutant lines homozygous for any of the three independent alleles ($dgt^{1\text{-}1}$, $dgt^{1\text{-}2}$, and dgt^{dp}) show similar plieotropic phenotypes, which include reduced apical dominance and gravitropic response, hyponastic leaves, retarded vascular development, high levels of anthocyanin and chlorophyll, and lack of lateral roots (Zobel 1972). The *dgt* mutation affects size, weight, and internal anatomy of the fruit, with fruit weight, number of locules, and seeds per fruit significantly reduced in the mutant as compared to the wild-type lines (Balbi and Lomax 2003). As the overall auxin metabolism and transport in *dgt* mutants is not affected and the auxin responsiveness is only partially abolished (Muday and others 1995; Rice and Lomax 2000), it has been proposed that the *dgt* lesion disrupts a specific step during early auxin signal transduction (Nebenfuhr and others 2000). Expression studies for members of the *AUX/IAA* family (*LeIAA1-11*) in mutant and wild-type control fruits show higher expression for *LeIAA2* and *LeIAA8* in the *dgt* mutant at early developmental stages of the fruit, indicating that in wild-type fruit, the intact *Dgt* gene product may serve as a negative regulator (Balbi and Lomax 2003). Furthermore, altered expression of members of the *LeACS* gene family (*LeACS6* and *LeACS7*) in the early stages of fruit development in *dgt* mutants also indicates a significant role for ethylene biosynthesis in early fruit development. In a separate study, transcript accumulation for several *Aux/IAA*-like (*DR1*, *DR3 DR4*, and *DR8*) genes in tomato was found to be differentially regulated by ethylene (Jones and others 2002).

DR12, an auxin response factor (ARF), encodes for a protein that exhibits nuclear localization, in accordance with its putative function as a transcriptional regulator (Jones and others 2002). *DR12* transcript accumulation is ethylene dependent, with its highest accumulation in early red fruit. Phenotypes displayed by *DR12* inhibited or overexpressed transgenic plants indicate that the *DR12* encoded protein is important in seed development, seedling growth, and fruit cell division, processes where auxin is expected to play a role. *DR12* inhibited lines show upwardly curled leaves, dramatically increased chlorophyll content in the fruit resulting in a dark green unripe fruit, increased hypocotyl lengths, and blotchy fruit ripening. These varied phenotypes are indicative of different hormonal effects, with the curling of leaves and increased hypocotyl lengths indicating auxin responses, whereas the blotchy fruit ripening is similar to the phenotype observed in the *ipt* transformed cytokinin enhanced tomato lines (Martineau and others 1994). These observations implicate *DR12* in physiological processes where both auxin and ethylene have been shown to play roles and further indicate that *DR12* may be involved in modulating the responses of other hormones.

Cell Division and Cyclins

At the molecular level, cyclin-dependent protein kinases (CDK) are involved in regulation of cell division processes in eukaryotes such as yeast (Forsburg and Nurse 1991) and animals (Norbury and Nurse 1992). Cyclin binding to CDK is necessary for protein kinase activity and target specificity determination (Morgan 1995; Nigg 1995). Among over 60 cyclin cDNA clones isolated from plants (Renaudin and others 1996), many are related to the animal A- and B- type cyclins, which are involved in progression through G2 and for mitosis; additionally, type-A is essential for S-phase. The transcripts for Lyces;*CDKA1* and Lyces;*CDKA2*, that encode for tomato homologs of CDK $p34^{cdc2}$ and the corresponding CDKA proteins predominantly accumulate between anthesis and 5 days after anthesis in tomato fruit (Joubès and others 1999). The CDK activity seems to be post-translationally regulated at both temporal and spatial levels during early tomato fruit

development. Lyces;*CDKC*;1, a tomato C type cyclin, is preferentially expressed in actively dividing cells of the fruit and shows slight modulation by sugars or hormones, whereas the expression of CDKA (Lyces;*CDKA*;1) and CDKB (Lyces;*CDKB1*;1 and Lyces;*CDKB2*;1), which are also associated with meristematic tissues, is either induced by or strictly dependent on sugar availability (Joubès and others 1999, 2001). Three tomato *D3* cyclins (Le*CycD3*;1, Le*CycD3*;2, and Le*CycD3*;3) show upregulation in ovaries after pollination/fertilization, with the transcript levels reaching a peak at 3 days after anthesis (Kvarnheden and others 2000). As the levels of GAs and cytokinins are known to peak at the time of fertilization, the authors in this study speculate that the cyclin genes may be involved in transducing the hormonal signals leading to fruit growth by cell divisions.

Invertases and Sugar Trafficking

In tomato, extracellular invertase isoenzymes are encoded by a gene family comprising of at least four members: *Lin5*, *Lin6*, *Lin7*, and *Lin8* (Godt and Roistch 1997). The expression of *Lin5* is specific to reproductive organs and fruit (Godt and Roitsch 1997), and it is higher during early fruit development (Preols and others 2003). In addition, a 1.6-kb promoter fragment of *Lin5* shows hormone (GA, AUX, and ABA) inducibilty. *Lin7* expression, on the other hand, is restricted to anther and pollen grains (Godt and Roitsch 1997; Proels and others 2003) and suggests an important function in supplying carbohydrates to these flower organs. *Lin6* is expressed under conditions that require a high carbohydrate supply such as seedling roots, flower buds, and *Agrobacterium* induced tumors. Transcripts show a sink tissue-specific distribution, and the concentration is elevated by stress-related stimuli, cytokinin, and in response to the induction of heterotrophic metabolism (Godt and Roitsch 1997). The induction of these extracellular invertase genes by various hormones during flower and fruit development indicates their hormonal regulation and also the fact that they may be important in maintaining a carbohydrate supply during the active growth and development phases of these organs. Further work should elucidate the molecular basis for the hormonal induction of these genes and their contributions to flower and fruit development.

Cytokinins are generally associated with increasing sink strength and delaying senescence (Brenner and Cheikh 1995; Roitsch and Ehneß 2000; Balibrea Lara and others 2004). Tomato *2A11:ipt* transgenic lines producing high cytokinin in the fruit show blotchy ripening, with regions of green and red tissues in the same fruit (Martineau and others 1994). The authors argue that this phenotype in the transgenic lines implicates cytokinin involvement in blocking various cellular differentiation and gene expression pathways associated with fruit ripening. In a different study, increased cytokinin levels in tomato lines transformed with the *ipt* gene expressed predominantly in the ovary tissues are associated with higher total solids and improved sugar:acid ratio, and with a reduction in average fruit size (Martineau and others 1995). The increased cytokinin levels improve fruit set, possibly by enhancing the ovary/young fruit sink strength, thereby leading to higher total solids in the fruit. However, competition for photosynthates among the greater number of fruits in these transgenic lines may have a limiting effect on the fruit size.

The ASR (abscisic acid, stress, and ripening) proteins induced by ABA, stress, and ripening, were first described in tomato (Iusem and others 1993; Amitai-Zeigerson and others 1994; Rossi and Iusem, 1994). The ASR proteins resemble eukaryotic nonhistone chromosomal proteins (Iusem and others 1993) and might act as downstream components of a common signal transduction pathway involved in responses of plant cells to environmental factors (Maskin and others 2001) The sugar-induced VuMSA, a grape ASR, homolog, shows strongly enhanced expression in the presence of ABA, thus providing molecular evidence for ABA-sugar cross talk in fruit development and ripening (Cakir and others 2003). Although reverse transcriptase polymerase chain reaction (RT-PCR) studies in three developmental stages of tomato have failed to detect any differences in the expression of *Asr* genes (Maskin and others 2001), microarray data sets generated from a broader developmental time scale reveal a decrease in the expression of these genes over time (Carrai and others 2004). In contrast to a grape *Asr* gene, which shows positive correlation with a plasma membrane hexose transporter, the tomato *Asr* genes are negatively correlated with hexose transporter homologs (Carrari and others 2004). Further knowledge about the functional interactions between all proposed players in the presence of ABA and sucrose is required to elucidate the possible physiological significance of ASR as regulators of sugar trafficking in fruits.

The **s**ucrose **n**on-**f**ermenting 1 (*SNF1*)-related kinase (SnRK1) complex has been implicated in both sugar and ABA sensing (Himmelbach and others 2003; Lunn and MacRae 2003). The SnRK1 complex is thought to be the central component of

the sugar sensing and response mechanism and was first identified in yeast (Halford and Hardie 1998, 2000, 2003). Expression studies of tomato cDNAs corresponding to the kinase (*LeSNF1*), regulatory (*LeSNF4*), and localization (*LeSIP1* and *LeGAL83*) subunits of the SnRK1 complex during seed development reveal that *LeSNF4* expression is influenced by ABA and GA levels (Bradford and others 2003). The authors further suggest that, during seed maturation, binding of LeSNF4 to LeSNF1/LeGAL83 (or other SIP proteins) alters the kinase activity of the complex, thereby promoting metabolic pathways involved in the accumulation or maintenance of storage reserves and blocking those involved in the mobilization or utilization of stored reserves. After inhibition, expression of *LeSNF4* is reduced in seeds that are not dormant or stimulated by GA, which potentially alters LeSNF1 kinase activity to de-repress genes encoding enzymes required for reserve mobilization and metabolism (Bradford and others 2003). This study provides insight into the possible mechanism of sugar and hormonal regulation of seed maturation and germination.

Expansins and Other Cell Wall Components

Fruit development stages provide an excellent model system for the study of cell wall dynamics, including wall assembly, restructuring, and disassembly, as well as the role that hormones may play during this process. Expansins are proteins that induce extension in isolated plant cell walls *in vitro* and have been proposed to disrupt noncovalent interactions between hemicellulose and cellulose microfibrils (Rose and others 1997). LeEXP1, a tomato expansin protein, has been detected at the ripening stage of the fruit and is regulated by ethylene (Rose and others 1997, 2000). Both expanding and ripening fruit contain expansin proteins and possess expansin-like activities, suggesting that the basic mechanism of action of ripening-related and expansion-related expansins is likely to be similar. However, immunological differences between expansion-related and ripening-related expansin isoforms hint at functional and biochemical variability (Rose and others 2000). *LeExp2*, another expansin gene, isolated from auxin-treated, etiolated tomato hypocotyl along with genes encoding for xyloglucan endotransglycolase (*LeEXT1*) and endo-1, 4-β-glucanase (*Cel7*), two enzymes responsible for cellulose-xyloglucan framework reorganization, showed auxin regulation (Catala and others 1997, 2000). All three genes, namely *LeEXP2*, *LeEXT1*, and *Cel7*, show higher expression during the cell expansion phase of fruit development, with temporal differences in their peaks and stability prior to onset of ripening (Catala and others 2000). *LeEXP4*, an expansin gene, and *LeXET4*, a xyloglucan endotransglycosylase isolated from GA-deficient *gib1* mutant lines, are expressed specifically in the endosperm cap of seed, flowers, and expanding fruits and micropylar endosperm cap tissue (Chen and Bradford 2000; Chen and others 2002). In addition, the expression of these genes is dependent on application of GA in the *gib-1* mutant, which indicates a hormonal regulation of these genes.

Tomato LeAGP-1 represents a major arabinogalactan-protein (AGP) that is localized to the plasma membrane via a glycosylphosphatidylinositol (GPI) anchor and is suggested to play roles in cellular signaling and matrix remodeling (Sun and others 2004). The phenotype of GFP-LeAGP-1 overexpressing transgenic plants is similar to that of cytokinin-overproducing plants, displaying significantly shorter plants that are highly branched and produce more flower buds, most of which, however, do not mature, resulting in less fruit production and smaller than normal seeds (Sun and others 2004). Examination of hormonal effects on these transgenics reveals that cytokinins upregulate LeAGP-1 mRNA expression, whereas auxins and ABA inhibit LeAGP-1 mRNA expression. These results indicate that GPI-anchored LeAGP-1 most likely functions in plant growth and development in concert with auxin/cytokinin signaling.

Rab GTPases are a class of proteins found on vesicles affecting cellular transport of proteins and other large molecules (Sanderfoot and Raikhel 1999). Each type of Rab is associated with a specific type of vesicle and probably plays a role in ensuring correct fusion (Takai and others 2001). *LeRab11a*, a tomato homolog to ripening-related Rab-11–like GTPase from mango (Zainal and others 1996), shows higher expression during tomato fruit ripening than when the fruit is unripe (Lu and others 2001). The lack of expression of *LeRab11a* in *Never-ripe* (*Nr*) fruit suggests that the *LeRab11a* gene is regulated in an ethylene-dependent manner in fruit. The ripening-associated textural changes in the cell wall require a number of enzymes such as polygalacturonase (PG) and pectinesterase (PE), both of which are synthesized on the rough endoplasmic reticulum and presumably are trafficked through the endomembrane system of the cell and secreted to the apoplast. Transgenic *LeRab11a* antisense tomato lines generated to test the hypothesis that Rab GTPases might be essential for this transport, indeed reveal reduced softening

accompanied with reduced levels of PG and PE in the transgenic fruit compared with those in wild-type fruit (Lu and others 2001). The authors suggest that the varied abnormal phenotypes observed in these antisense transgenic lines could be an outcome of disrupted trafficking of hormone transporters or receptors to the cell membrane. Alternatively, the authors argue that if endocytotic receptor downregulatory mechanisms for Rab11-type GTPases exist in plants, then their disruption may result in failure to completely switch off hormone-mediated developmental programs or may lead to increased sensitivity to low levels of signaling molecules. A clear perception of the mode of Rab-GTPases action in plant systems is required to further understand their role and regulation during fruit development.

Ethylene-Regulated Fruit Ripening

In comparison to other hormones, impressive advances in understanding the mode of molecular regulation of ethylene action in tomato fruit development and ripening have been made. Ethylene has long been accepted as a ripening and senescence-inducing hormone in climacteric fruits (Oeller and others 1991; Theologis 1992; Picton and others 1993; Lanahan and others 1994). The ethylene biosynthesis pathway is well established in higher plants (Yang and Hoffman 1984) and exhibits a two-step regulatory control. The first step, catalyzed by the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACS), involves the formation of ACC from *S*-adenosyl-L-methionine, and the second step, catalyzed by ACC oxidase (ACO), converts this intermediate to ethylene (Kende 1993). In higher plants, two systems of ethylene regulation have been proposed to operate (Lelièvre and others 1998). System 1, functional during normal vegetative growth, is ethylene autoinhibitory and is responsible for producing the basal levels of ethylene detectable in all of the tissues, including non-ripening fruit. System 2 operates during the ripening of climacteric fruit and during petal senescence, when ethylene is auto-stimulatory and requires the induction of both ACS and ACO. *LeACS1A* and *LeACS6*, two members of the ACS gene family, have been shown to have regulatory effects on system 1 ethylene production. It has been suggested that a change in sensitivity to the basal levels of ethylene produced by system 1 results in a transition to system 2, leading to increased expression of *LEACS1A*, *LEACS2*, and *LEACS4* and higher ethylene production, and also resulting in negative feedback on the system 1 developmental pathway with reduction in *LEACS1A* and *LEACS6* expression (Barry and others 2000).

Many of the molecular components involved in ethylene perception and the signal transduction pathway during tomato fruit development and ripening have been unraveled using ripening mutants (Giovannoni 2001). Of the six ethylene receptors (*LeETR*s) isolated in tomato, five bind ethylene (Klee 2002; Klee and Tieman 2002), and studies with a subset (*NR* and *LeETR4*) that show induction during ripening reveal that the ethylene receptors act as negative regulators of ethylene signaling (Wilkinson and others 1995; Yen and others 1995; Hackett and others 2000; Tieman and others 2000; Ciardi and others 2000), a hypothesis consistent with the model predicted in *Arabidopsis*. *LeCTR1* (*Constitutive Triple Response 1*), a member of the multi-gene family, is another ethylene signaling component in tomato (LeClercq and others 2002; Adams-Phillip and others 2004) whose transient silencing confirms its negative regulation of ethylene responses (Liu and others 2002). Three functionally redundant *EIL* (*Ethylene Insensitive*-like) genes have been shown to regulate multiple ethylene responses throughout plant development (Tieman and others 2001) whereas a fourth member, *LeEIL4* shows ripening induction (Yokotani and others 2003). Among the four members of the *ERF* (*Ethylene Response Factors*) family, which show induction in response to wounding and ethylene treatment along with ripening, *LeERF2* exhibits ripening-associated expression and is not found in several ripening mutants (Tournier and others 2003), indicating a definite role in ripening.

Physiological studies of tomato ripening mutant lines, namely, *ripening inhibitor* (*rin*), *non-ripening* (*nor*), and *Colorless non-ripening* (*Cnr*) suggest that these genes may have a regulatory role prior to ethylene biosynthesis (Adams-Phillips and others 2004). Positional cloning and characterization of *rin* and *nor* loci have revealed *rin* to be MADS-box transcriptional factor (*LeMADS-RIN*) (Vrebalov and others 2002) and *nor* to be similar to a transcriptional factor, although not a MADS-box family member (Adams-Phillip and others 2004). The advancement in studies aimed at deciphering the mode of ethylene perception and signaling has arrived at a point where several of the key players in this process are now known. The model emerging from these studies suggests transcription factors like LeMADS-RIN, LeNOR, and other MADS-box proteins to be the components of developmental signaling systems that initiate ripening in climacteric fruits. Recovery of a *LeMADS-RIN* like sequence from strawberry, a non-climacteric fruit, is an

indication of a conserved link between climacteric and non-climacteric ripening control (Vrebalov and others 2002). The developmental signaling systems regulate ethylene synthesis, an autocatalytic process, along with non-ethylene–mediated ripening responses (Adams-Phillip and others 2004).

ABA and Seed Dormancy

Abscisic acid plays an important role during seed development, dormancy, and germination, and in plant responses to drought and osmotic stresses (Lee and others 2003). Overripe fruits of ABA-deficient *sit*^{w} tomato mutants display precocious germination (Liu and others 1996), indicating a role for ABA in maintaining seed dormancy. Berry and Bewley (1991) suggest that the osmotic environment of the fleshy fruits plays an important role in preventing precocious seed germination. It has been suggested that ABA controls seed dormancy by antagonizing the stimulation of seed germination by another hormone, gibberellic acid, which is an important essential hormone for germination (Karssen and others 1989; Bewley and Black 1994). Studies with GA-deficient *gib-1* and ABA-deficient *sit*^{w} tomato mutants and wild-type control plants indicate that precocious seed germination is prevented by the action of the fruit's osmotic environment and ABA on the seed tissues that surround the embryo and not the embryo itself (Liu and others 1996).

Roles of Other Plant Growth Regulators

Brassinosteroids

Brassinosteroids (BRs), a group of plant polyhydroxysteroids that have been identified as a class of phytohormones, play diverse roles in plant growth and development (Bishop 2003). Exogenous BR application to tomato pericarp discs leads to elevated levels of lycopene, lowered chlorophyll levels, decreased ascorbic acid, and increased carbohydrate contents (Vardhini and Rao 2002). Characterization of mutant tomato *d*^{x}-fruits (which are brassinosteroid-deficient) display delay in ripening, severely reduced levels of most carbohydrates resulting in a decreased dry mass, lower activity of acid invertases, and lower fruit yield. In contrast, amino acids levels in *d*^{x}- fruits are elevated, possibly as a result of enhanced protein degradation. Brassinosteroid treatment could partially complement all these observed effects (Lisso and Altman 2003). These results indicate a role for BR in tomato fruit development, with an effect on both the time of ripening and the tomato fruit composition. Additionally, BR-induced growth responses have been correlated with increased carbohydrate supply brought about by the increased levels of an extracellular invertase, namely, *Lin6* (Goetz and others 2000), further supporting the role of BRs in influencing fruit composition.

Jasmonic Acid

Jasmonic acid (JA) and its methyl ester (methyl jasmonate: MeJA), which are derivatives of linolenic acid, are known to modulate aspects of fruit ripening, pollen viability, root growth, and resistance to insect and pathogen attack (Creelman and Mullet 1997). Endogenous concentration of jasmonates increases at the onset of fruit ripening, and exogenous jasmonate application stimulates ethylene production and color change (Imanishi and Nagata 2003). Expression studies involving treatment of breaker stage tomato disks with methyl jasmonate reveals accumulation of mRNA for ACO, ACS2, and ACS6, but not for ACS4. Furthermore, JA-induced defense responses in tomato have profound effects on their reproductive fitness, and treatment of plants with high levels of JA produce fewer but larger fruits with fewer seeds per unit of fresh weight (Redman and others 2001). These studies indicate a role for JAs in ethylene-mediated fruit ripening, as well as in defense responses. Leucine aminopeptidase (LapA) expression increases under the influence of systemins, MeJA, ABA, ethylene, and under stress conditions such as water deficit and salinity in tomato. LapA1-::GUS transgenic tomato plants reveal that *LapA1*-promoter is active during floral and fruit development (Chao and others 1999).

Polyamines

Polyamines are ubiquitous low molecular weight, organic cations that affect a large number of developmental and physiological responses in a number of organisms, including plants (Walters 2003). They also influence early fruit development and ripening. Free polyamines are known to act as anti-senescence agents, causing retarded fruit color change, increased fruit firmness, delayed ethylene and respiration rate emissions, induced mechanical stress resistance, and reduced chilling symptoms (Valero and others 2002). In tomato, both ornithine decarboxylase (ODC) and arginine decarboxylase (ADC) pathways for PA biosynthesis are active (Alabadi and Carbonell 1998). As mentioned previously, application of PAs to wild-type unpollinated ovaries results in partial parthenocarpy. The

higher PA levels in unpollinated *pat-2* ovaries are correlated with the activation of the ODC pathway, which in turn is influenced by the elevated GA levels found in these ovaries (Fos and others 2003). The arginase and ODC activity decrease after tomato fruit set, and these observations suggest that the ADC pathway may be involved in cell expansion, whereas the ODC pathway may be active in the cell division process during early fruit growth of tomato (Cohen and others 1982; Alabadi and others 1996). Tomato transgenic lines over-expressing a yeast SAM-decarboxylase show increases in spermidine and spermine along with enhanced lycopene and ethylene levels and increased fruit juice viscosity in tomato fruit. The increased PAs in these lines seem to override the senescence effects of higher ethylene levels, indicating that both pathways, which share the precursor S-adenosylmethionine (SAM), can simultaneously exist *in vivo* and SAM levels are not limiting. Polyamines, along with salicylic acid, which is an inhibitor of wound-responsive genes in tomato, have been suggested to regulate ethylene biosynthesis at the level of ACC synthase transcript accumulation (Li and others 1992). Macroarray analyses indicate that transgenic tomato fruits accumulating spermidine and spermine due to over expression of SAM decarboxylase show quantitative changes of many transcripts, mainly those of ethylene receptor populations or component(s) of the ethylene signaling pathway (Srivastava and others unpublished results).

Future Perspectives

A comprehensive understanding of hormonal regulation of fruit development is important, both in terms of defining the process of fruit development and ripening at the molecular level and in improving the fruit quality in terms of shelf life and nutritional content. Substantial progress has been made in identifying the growth regulators involved in fruit development and ripening and the gene and protein receptor players. Most of these studies suggest cross talk and signaling among the classic hormones and the recently identified class of growth regulators. Given the complexity of the fruit development process, the task of deciphering the molecular basis of its regulation by hormones is made none too easy by the possible interactions between hormones. Despite the advances in recent years, many questions regarding the mode of action of various hormones remain unanswered. With further studies, many more signaling components playing roles in fruit set, development, and ripening are expected to come to light. A better comprehension of fruit development is expected when the question of how the genetic and molecular circuitries determine differential expression of the genes involved in the development of fruit is answered. The availability of expression arrays, proteomics, and functional genomic tools should, in the near future, reveal the expression of genes that are intimately associated with fruit development. One will also understand the mode of temporal and spatial expression of these genes, which is regulated by various developmental cues, including hormones, other growth regulators, and environmental stimuli. Such a foundation of knowledge of the development process is essential and will provide specific information necessary to ultimately develop designer fruits with longer shelf-lives and enhanced fruit quality.

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