Fruits are a distinctive characteristic of Angiosperms. They occur today in a wide variety of forms and types. The ancestral fruit, dry and dehiscent, probably emerged in the early Cretaceous period; fleshy fruits appeared later in the Cretaceous or early Tertiary (Eriksson et al., 2000). The diversification of fruits from a dry dehiscent form to a fleshy drupe or berry, correlated with the rise of vertebrates, main agents of seed dispersal (Knapp, 2002). The maturation of fruits is a complex and highly coordinated developmental process. In fleshy fruits, ripening results in the accumulation of succulent, flavorful, and soft pericarp that attract animals and facilitate seed dispersal (Giovannoni, 2001). In addition to softening, fruits normally exhibit increased accumulation of sugars, acids, pigments, and volatiles that increase interest and palatability to animals. Moreover, fruits are an important source of supplementary diet, providing minerals, vitamins, fibers, and antioxidants for humans. From an agronomical point of view, nutritional value, flavor, processing qualities, and shelf-life determine the quality of fruits.

The main changes associated with ripening include color (loss of green color and increase in non-photosynthetic pigments that vary depending on species and cultivar), firmness (softening by cell wall degrading activities and alterations in cuticle properties), taste (increase in sugar and decline in organic acids), and flavor (production of volatile compounds providing the characteristic aroma).

Analytical tools that allow comprehensive phenotyping at the level of transcriptome (Alba et al., 2003; Vierczynski et al., 2008; Matas et al., 2011; Röhrmann et al., 2011), proteome (Lee et al., 2004; Rose et al., 2004; Saravanan and Rose, 2004), and metabolome (Fait et al., 2008; Lombardo et al., 2011) facilitate an overview of the metabolic network (Carrari et al., 2006; Dehuc et al., 2007; Grimplet et al., 2007; Enfissi et al., 2010; Zamboni et al., 2010; Osorio et al., 2011; Lombardo et al., 2011; Lee et al., 2012; Pan et al., 2013) whilst network analysis is beginning to yield a detailed understanding of the systems regulation underlying fruit development.

**HORMONAL AND TRANSCRIPTIONAL REGULATION DURING RIPENING**

Fruits are generally classified into two physiological groups, climacteric and non-climacteric, according to their respiratory activity and associated ethylene biosynthesis profiles during ripening. Ethylene synthesis in climacteric fruits such as tomato, apple, and banana, is essential for normal fruit ripening and blocking either synthesis or perception of this hormone prevents ripening (Hamilton et al., 1990; Oeller et al., 1991; Röhrmann et al., 1991, Barry et al., 1996).

Efforts to uncover the transcriptional regulation underlying carpel and fruit development were first focused on the dry dehiscent siliques of the model plant Arabidopsis (Llebreger et al., 2000; Dinneny et al., 2005). These studies clarified the role of several MADS-box transcription factors in tissue specification and mechanism of dehiscence. Among these, the redundant SHATTERPROOF 1/2 genes (SHP; members of the AGAMOUS subfamily) specified valve margin identity in the siliqua: when mutated, fruits became indehiscent. However, despite the striking anatomical differences between dry and fleshy fruits, subsequent studies, primarily focused on tomato, have shown the involvement...
RIN target genes are major regulators of ripening control, such as regulating the expression of its targets by activation or repression. Using a combined approach based on chromatin immunoprecipitation and targeted metabolite analysis were combined during development and ripening of \textit{nor} and \textit{rin} mutants, has helped to refine the ethylene-regulated expression of downstream genes and added to our knowledge the role of this hormone in both protein- and metabolite regulation in tomato ripening (Osorio et al., 2011). This data supported the view that \textit{nor} and \textit{rin} act together in a cascade to control ripening (Giovannoni et al., 1995; Thompson et al., 1989; Ferrarese et al., 1995; Harpster et al., 1997; El-Kereamy et al., 2003). In apple, \textit{MADS2} gene expression is also associated with fruit firmness (Cevik et al., 2010), whereas in bilberry fruit, the SQUAMOSA MADS-box ortholog of the TDR4 gene in tomato, has a role in regulation of anthocyanin biosynthesis (Iakoula et al., 2010; see Figure 1).

Current knowledge about the role of hormones – other than ethylene – in the development and ripening of climacteric and non-climacteric fruits is limited. In tomato, pepper, banana, muskmelon, and strawberry, the most abundant free auxin, indole-3-acetic acid (IAA), has been reported to decline prior to the onset of ripening, this reduction was accompanied by an increase of its conjugated form (IAA-Asp; Bottcher et al., 2010). The conjugation reaction is catalyzed by the IAA-amino synthase (GH3). In tomato, 15 members of \textit{GH3} gene family have been described, but only for two of them is the pattern of expression associated with ripening (Kumar et al., 2012). Tomato fruits overexpressing the pepper \textit{GH3} gene show anticipation of ripening (Liu et al., 2005), which is in agreement with the view that the ratio between IAA and its AA-conjugated form, rather than the level of IAA itself, may contribute to the temporal regulation of ripening (Bottcher et al., 2010). In non-climacteric fruits, no single growth regulator appears to play a positive role analogous to that played by ethylene, but it has been observed that auxin can negatively control the ripening of some non-climacteric fruits. In strawberry, it has been shown that the expression of many ripening-specific genes previously characterized in \textit{Arabidopsis} (Pruell et al., 1994; Iftikhar et al., 2009; Vrebahol et al., 2009; Gimenez et al., 2010; Bemer et al., 2012). It is now clear that a part of the regulatory networks underlying fruit development have been conserved during the evolution of fleshy fruits (Sneh and Drummond, 2012; Seymour et al., 2013). A number of important advances in our understanding of mechanisms that regulate ripening have also come from the characterization of monogenic tomato mutants, including ripening-inhibitor (rin), non-ripening (Nor), colorless non-ripening (Cor), green-ripe (Gr), green flesh (gf), high pigmen (1 Ap), high pigmen (2 Ap), and never-ripe (Nr; Lanahan et al., 1994; Mustilli et al., 1999; Vrebahol et al., 2002; Liu et al., 2004; Barry and Giovannoni, 2006; Manning et al., 2006; Barry et al., 2008). The \textit{rin} mutant encodes a partially deleted MADS-box protein of the \textit{SEPALLATA} clade (\textit{SEP4}; Hileman et al., 2006), whereas \textit{Cor} is an epigenetic change which alters the promoter methylation of SQUAMOSA promoter binding (SPB) protein. \textit{Nor} is a member of the NAC-domain transcription factor family (Giovannoni, 2007). A recent study in which the transcriptome, proteome, and metabolome analysis were combined during development and ripening of \textit{nor} and \textit{rin} mutants, helped to refine the ethylene-regulated expression of downstream genes and added to our knowledge the role of this hormone in both protein- and metabolite regulation in tomato ripening (Osorio et al., 2011). This data supported the view that \textit{nor} and \textit{rin} act together in a cascade to control ripening (Giovannoni et al., 1995; Thompson et al., 1999) and also suggested that \textit{nor} has a more global effect on ethylene/ripening-related gene expression than \textit{rin}, which indicates that \textit{nor} likely operates upstream of \textit{rin}. Recently, using a combined approach based on chromatin immunoprecipitation and transcriptome analysis, it was provided evidence that RIN interacts with the promoters of more than 200 genes, modulating the expression of its targets by activation or repression. RIN target genes are major regulators of ripening control, such as \textit{CNR} and \textit{NOR}, or belong (Martel et al., 2011) to well-known pathways active during the transition from green to ripe fruits (e.g., carotenoid accumulation, chlorophyll breakdown, ethylene synthesis and perception; Fujisawa et al., 2013).

Fruits such as strawberry, citrus, and grape have been classified as non-climacteric based on the lack of the respiratory burst and on the low endogenous production of ethylene compared to standard climacteric fruits (Perkins-Veazie, 1995). In pepper fruits, some cultivars seem to be ethylene-insensitive, while other peppers cultivars treated with exogenous ethylene were able to stimulate the expression of ripening-specific genes (Armitage, 1989; Ferrarese et al., 1995; Harpster et al., 1997; El-Kereamy et al., 2003).

In strawberry, which has emerged as a prime model of non-climacteric fruit ripening, ethylene is relatively high in green fruits, decreases in white fruits, and finally increases again at the red stage of ripening (Perkins-Veazie et al., 1996; Lianette et al., 2006). Interestingly, this last increase is accompanied by an enhanced respiration rate that resembles the one that occurs in climacteric fruits at the onset of ripening (Lianette et al., 2006). For better understanding the function of ethylene during strawberry ripening, different approaches have been used. External application of ethylene caused the down-regulation of several cell wall-related genes, such as \textit{β}-galactosidase, pectin methyltransferase, or \textit{β}-xylosidase (Trainotti et al., 2001; Castillo et al., 2004; Bustamante et al., 2009), while the expression of other genes such as expansin, FaEXP2 (Civello et al., 1999) was ethylene-insensitive. Recent studies at transcriptomic and metabolomic levels in transgenic strawberry fruits with decreased ethylene sensitivity indicates that ethylene action is required for normal fruit development, acting differently in the two parts of strawberry fruit, achenes and receptacle (Merchant et al., unpublished data). These results show that, although not as relevant as in climacteric fruits, ethylene may nevertheless play a role in strawberry fruit ripening.

Recent comparative transcriptome and metabolome studies during the maturation processes of climacteric and non-climacteric fruits (tomato and pepper, respectively) suggest that both species have similar ethylene-mediated signaling components. In pepper, the regulation of these genes is, however, clearly different and may reflect altered ethylene sensitivity or regulators other than ethylene than in tomato (Osorio et al., 2012). Unlike the situation described in tomato the ethylene biosynthesis genes, aminoacylpropane-1-carboxylic acid (ACC) synthase, and ACC oxidase, are not induced in pepper. However, genes downstream of ethylene perception, such as cell wall-related genes, ethylene response factor 3 (ERF3), and carotenoid biosynthesis genes, are up-regulated during pepper fruit ripening (Osorio et al., 2012). Other commonly regulated genes between climacteric and non-climacteric fruits have been described. In strawberry, a \textit{SEPALLATA} gene (\textit{SEP1/2}; MADS-box) is needed for normal development and ripening (Seymour et al., 2011). Similarly, in banana, which is classified as a climacteric fruit, the MADS-box \textit{SEP3} gene also displays ripening-related expression (Eliazar et al., 2010). In apple, \textit{MADS2} gene expression is also associated with fruit firmness (Cevik et al., 2010), whereas in bilberry fruit, the SQUAMOSA MADS-box ortholog of the TDR4 gene in tomato, has a role in regulation of anthocyanin biosynthesis (Iakoula et al., 2010; see Figure 1).

Current knowledge about the role of hormones – other than ethylene – in the development and ripening of climacteric and non-climacteric fruits is limited. In tomato, pepper, banana, muskmelon, and strawberry, the most abundant free auxin, indole-3-acetic acid (IAA), has been reported to decline prior to the onset of ripening, this reduction was accompanied by an increase of its conjugated form (IAA-Asp; Bottcher et al., 2010). The conjugation reaction is catalyzed by the IAA-amino synthase gene (\textit{GH3}). In tomato, 15 members of \textit{GH3} gene family have been described, but only for two of them is the pattern of expression associated with ripening (Kumar et al., 2012). Tomato fruits overexpressing the pepper \textit{GH3} gene show anticipation of ripening (Liu et al., 2005), which is in agreement with the view that the ratio between IAA and its AA-conjugated form, rather than the level of IAA itself, may contribute to the temporal regulation of ripening (Bottcher et al., 2010). In non-climacteric fruits, no single growth regulator appears to play a positive role analogous to that played by ethylene, but it has been observed that auxin can negatively control the ripening of some non-climacteric fruits. In strawberry, it has been shown that the expression of many ripening-specific genes controlled by ethylene is also associated with fruit firmness (Cevik et al., 2010), whereas in bilberry fruit, the SQUAMOSA MADS-box ortholog of the TDR4 gene in tomato, has a role in regulation of anthocyanin biosynthesis (Iakoula et al., 2010; see Figure 1).
EPIGENETIC REMODELING DURING RIPENING

Epigenetic regulation of gene expression (inheritance without an alteration in the primary DNA sequence) is increasingly recognized as a mechanism for modulating gene activity. Naturally occurring epigenetic changes at a single gene locus in plants can result in inheritable morphological variation without alteration of the underlying DNA sequence (Patterson et al., 1993; Colbas et al., 1999; Manning et al., 2006). DNA methylation is one form of epigenetic regulation. It is involved in transcriptional regulation, stress responses and furthermore plays a major role in protecting the genome integrity against the activity of transposable elements (TEs) and other repetitive sequences (Chan et al., 2005).

In plants, DNA methylation occurs at cytosine residues in three different sequences (CG, CHG, and CHH, where H = A, C or T; Bakker et al., 2008) and is set in place and maintained by different factors (Law and Jacobsen, 2010). Analysis of epigenetic variation in Arabidopsis revealed that at least one-third of expressed genes are methylated in their coding region, and only 3% of genes are methylated within promoter regions (Zhang et al., 2006; Vaughn et al., 2007). However, the promoter-methylated genes have a higher degree of tissue-specific expression (Zhang et al., 2006; Zilberman and Henikoff, 2007).

The first survey of the frequency and distribution of cytosine methylation sites in tomato dates back to more than 20 years ago, when it was found that polymorphisms in cytosine methylation between two tomato species were relatively abundant and that methylation patterns were stably inherited, from parents to offspring, segregating in a Mendelian fashion. The presence of tissue-specific methylation patterns and the overall decrease of
5-mC frequency in developing tissues also led the authors to postulate variation of methylation status of selected alleles during plant development (Messeguer et al., 1991).

More recently, the impact of cytosine methylation on tomato fruit ripening has strikingly emerged in the definition of the molecular nature of the colorless non-ripening phenotype. The tomato non-ripening Cnr mutant fails to produce ripe berries; fruits exhibit green pericarps and do not respond to external applications of ethylene. The gene at the Cnr locus was identified as a SPB protein-like using positional cloning, but the non-ripening phenotype could not be attributed to any alteration in the coding gene sequence. Bisulfite sequencing of the Cnr mutant allele showed instead hypermethylation of cytosine in the region upstream the predicted ATG start site. This hypermethylation state correlated with a drastic reduction of Cnr gene expression (Manning et al., 2006). Therefore, the non-ripening phenotype was due to the heritable cytosine hypermethylation pattern of the region including the Cnr gene promoter. Additionally, in normal tomato fruit (cv. Liberto) development, the promoter of Cnr appears to be demethylated in a specific region just prior to the onset of ripening. This lead to the hypothesis that DNA methylation contributes to the regulation of fruit ripening (Seymour et al., 2008).

Recent work by Zhong et al. (2013) provides genome-wide insights into the link between the genetic program of fruit ripening and DNA methylation state. On the basis of the previous results on the nature of the Cnr (epi) mutation, the authors injected a chemical inhibitor of cytosine methylation, 5-azacytidine, directly in the locular spaces and columella of developing tomato fruits. The methylation inhibitor induced the formation of local ripe areas, red in appearance, where the expression of typical ripening-related genes (phytoene synthase 1 and polygalacturonase) was anticipated. Moreover, the Cnr promoter region was demethylated in red sectors with respect to green parts of the fruits, pointing at the demethylation of Cnr as the epigenetic signal sufficient to induce ripening. The authors then extended their views on the role of cytosine methylation reporting the full tomato methylome sequences of leaves, immature and ripe fruits, including the ripening-impaired mutants Cnr and rin. The sequencing of the entire epigenome revealed at least three important results: (i) in wild-type fruits, the degree of methylation of regions upstream the transcription start sites (TSS) decreased gradually along fruit development; (ii) this general decline was not observed for the fruits of the ripening-impaired mutants Cnr and rin, whose CG methylation levels were constantly higher at TSS and, for Cnr, also comparable to those observed in leaves; (iii) the promoters of typical ripening-related genes were gradually demethylated during development of wild-type fruits. Further evidences about the link between ripening and cytosine methylation came from...
the ChIP-Seq mapping of RIN binding sites during fruit development. The set of RIN targets included 292 genes with a known role in ripening. RIN binding sites were found in the promoters and the flanking regions, suggesting that RIN may be involved in the regulation of these genes. A previous study showed that the binding of RIN to a limited set of promoters was correlated with higher transcript levels of RIN target genes. A previous study showed that the binding of RIN to a limited set of promoters was correlated with higher transcript levels of RIN target genes. A previous study showed that the binding of RIN to a limited set of promoters was correlated with higher transcript levels of RIN target genes. A previous study showed that the binding of RIN to a limited set of promoters was correlated with higher transcript levels of RIN target genes. A previous study showed that the binding of RIN to a limited set of promoters was correlated with higher transcript levels of RIN target genes.

ACKNOWLEDGMENTS

This work was supported in part by grants from the Max-Planck-Gesellschaft (to Sonia Osorio and Alisdair R. Fernier), and by Ministerio de Ciencia e Innovación, Spain (Ramón y Cajal contract). Federico Nossco acknowledges the support of CRA-Young Investigator Program.

REFERENCES

Alba, R., Perrin, P., Fei, Z. J., McQuinn, R., Dubois, P., Martin, G. B., et al. (2005). Transcriptome and selected metabolite analyses reveal multiple points of ethylene control during tomato fruit development. Plant Cell 17, 2854–2865. doi: 10.1105/tpc.105.036053

Arntzen, A. M. (1989). Promotion of fruit ripening of ornamental poppies by ethylene. Plant Science 55, 962–964.

Barry, C. S., Blum, B., Bourayou, M., Coopet, W., Hamilton, J. A., and Giovannoni, J. (1996). Differences in the cyclopropane-1-carboxylate-methylester gene family of tomato. Plant J. 9, 525–535. doi: 10.1046/j.1365-313X.1996.00652.x

Barrero, C. S., and Giovannoni, J. J. (2008). Amino acid cyclization disrupts ethylene signaling. Proc. Natl. Acad. Sci. U.S.A. 105, 7923–7928. doi: 10.1073/pnas.0712191105

Barrero, C. S., McQuinn, R. P., Chung, M. Y., Benaulim, A., and Giovannoni, J. J. (2009). Local treatment of immature fruits with a DNA demethylating chemical accelerates ripening; and this lower level of methylation coexists with the analysis of conventional genetic variation in future plant breeding strategies. Epigenetic-based crop improvement approaches may radically impact fruit quality traits, especially for those plants whose allelic variation has been reduced during domestication or recent intense breeding pressure. As such future modeling work aimed at integrating epigenomic profiling and small RNA profiling along the more frequently used transcript, protein, enzyme, and metabolite profiling (as suggested in Figure 2) will allow for greater understanding of the complex dynamics underlying this tightly regulated biological process.
Dinneny, R. J., Weinig, D., and Yanofsky, M. F. (2005). A genetic framework for fruit patterning in Arabidopsis thaliana. Development 132, 4607–4617. doi: 10.1242/dev.2002
Elmore, T., Varanolo, J., Giovannoni, J., P. J., Goldschmidt, E. E., and Friedman, H. (2010). The regulation of MADS-box gene expression during ripening of tomato and its regulatory interac-
tion with ethylene. J. Exp. Bot. 61, 1725–1735. doi: 10.1093/jxb/erp176
Ehret, A., Celoria, C., Cortmann, A., Chum, M., Atienza, P., Orange, M. F., and Brummell, S. A. (2010). Functional analysis of the Arabidopsis mutant cor-
trols the essential role of the Arabidopsis TAL gene family in repro-
ductive development of tomato. Plant Cell 22, 1190–1215. doi: 10.1105/tpc.110.073866
Enfoido, E., Barbone, I., Ahmed, L. Lightl, A., Carrick, C., McGuire, R. P., et al. (2010). Integrative transcript and metabolite analyses of nutritional-enhanced DE-ETIOLATED1 downregulated tomato fruit. Plant Cell 22, 1190–1215. doi: 10.1105/tpc.110.073866
Eriksson, O., Friis, E. M., and Lof-gren, P. (2000). Seed size, fruit size, and dispersal systems in angiosperms from the early cretaceous to the late triassic. J. Mol. Evol. 51, 47–56. doi: 10.1007/3-540-46389-8
Fusi, A., Flamio, R., Bolognina, G., D. N., Righetti, L., Noci, E., Disord, V. I. (2008). 1995). Differen-
tial ethylene-inducible expression of genes related to anthocyanin biosyn-
drome: a phylogenetic perspective on plants. Nat. Genet. 32, 450–454. doi: 10.1038/ng1658
Fusco, M., Natale, T., Sharma, U., and Ito, Y. (2013). A large-scale identification of direct targets of the tomato MADS Box transcription factor RIPENING INHIBITOR reveals the regulatory network of fruit ripen-
ing. Plant Cell 25, 371–381. doi: 10.1105/tpc.112.109315
Gimenez, E., Pineda, B., Capel, J., Antoni, M. T., Atienza, P., Orange, M. F., and Brummell, S. A. (2010). Functional analysis of the Arabidopsis mutant cor-
trols the essential role of the Arabidopsis TAL gene family in repro-
ductive development of tomato. Plant Cell 22, 1190–1215. doi: 10.1105/tpc.110.073866
One of the main goals of plant biology is to understand how plants perceive and respond to various environmental stimuli. In this context, ethylene is a key hormone that regulates many developmental processes, including fruit ripening. Ethylene perception is mediated by the receptor Ethylene Insensitive 2 (EIN2), which activates a transcriptional cascade involving the protein Ethylene Response Factor 1 (ERF1). This cascade leads to the expression of target genes, including those encoding ethylene-responsive transcription factors (ERFs) and other genes involved in fruit ripening, such as Anthocyanin-1 (AN1). The regulation of EIN2 expression is critical for proper fruit ripening, and mutations in this gene can lead to impaired development and ripening. The role of EIN2 in fruit development is well-documented, with studies showing that EIN2 is required for the proper development of tomato fruit. The discovery of this role has led to a better understanding of the molecular mechanisms underlying fruit development and ripening. This knowledge is essential for the development of new strategies to improve fruit quality and yield.
in ripening processes in a COLORLESS NONRIpening-dependent mutant. Plant Physiol. 137, 1564–1579. doi: 10.1104/pp.111.181107

Martinez, G. A., Chlor, A., and Anon, M. C. (1996). Effect of exogenous application of gibberellic acid on color change and phenylalanine ammonia-lyase, chlorophyllase, and peroxidase activities during ripening of strawberry fruit (Fragaria × ananassa Duch.). J. Plant Growth Regul. 15, 139–146. doi: 10.1007/BF01989920

Matsun, A. I., Yate, T. H., Buda, J. Z., Zhong, Y., Chatterjee, S., Tohge, T., et al. (2011). Tissue- and cell-specific transcription profiling of expanding tomato fruit provides insights into metabolic and regulatory specialization and cuticle formation. Plant Cell 23, 3905–3916. doi: 10.1105/tpc.111.095117

Mousseau, R., Ganal, M. W., Stellman, J. C., and Tankely, S. D. (1991). Characterization of the leader sites and initiation of cistron methylation in tomato nuclear DNA. Plant Mol. Biol. 16, 755–770. doi: 10.1007/BF00013969

Muttil, A. C., Fenzi, F., Alfano, F., and Bowler, C. (1999). Phenotype of the tomato high pigmentation-2 mutant is caused by a mutation in the tomato homolog of DETELOTED. Plant Cell 11, 1443–1455. doi: 10.1105/tpc.11.11.1443

Oeller, P. W., Wong, L. M., Taylor, L. P., Pike, D. A., and Theologis, A. K. (1994). Isolation of the tomato MAMOSUS gene TaDAG and analysis of its homologous role in transgenic plants. Plant Cell 6, 165–173. doi: 10.1105/tpc.6.1.165

Peroncin-Vinzie, P. M., Houben, D. J., and Bruch, J. K. (1996). In vitro growth and ripening of strawberry fruit in presence of ACC, FTS or propylene. Am. J. Bot. 128, 105–116. doi: 10.1105/tpc.1160.105016

Zhong, S., Fei, Z., Chen, Y., Zheng, Y., Chatterjee, S., Tohge, T., et al. (2011). Combined transcriptional profiling of sample extraction techniques for enhanced proteomic analysis of recalcitrant plant tissue. Proteomics 11, 2522–2532. doi: 10.1002/pmic.201003799

Sayers, H., Menke, C., and King, G. J. (2008). Genomics and bioinformatics of fruit development and ripening. Curr. Opin. Plant Biol. 11, 58–63. doi: 10.1016/j.popbio.2007.09.005

Rohrmann, J., T ohge, T., Alba, R., Rounsley, S., Pnueli, L., Hareven, D., and Bowler, C. (2011). A SFPK-LAXA gene is involved in the development and ripening of strawberry (Fragaria × ananassa Duch.) fruit, a non-dimorphic species. J. Exp. Bot. 62, 1179–1188. doi: 10.1093/jxb/err049

Shahak, Y., Sargent, D. J., Chowdhuri, B. N., Meidke, T. C., Felker, O., Delhun, A. L., et al. (2011). The genome of woodland strawberry (Fragaria vesca). Nat. Genet. 43, 109–116. doi: 10.1038/ng.1970

Vrebalov, J., Ryder, C., Dvir, V., Hammond, J. J., Popovitch, A., and King, G. J. (2011). A SPIKE-LAXA gene is involved in the development and ripening of strawberry (Fragaria × ananassa Duch.) fruit, a non-dimorphic species. J. Exp. Bot. 62, 1179–1188. doi: 10.1093/jxb/err049

Zhang, X., Yamaki, S., and Asakura, T. (1991). Evolutionary diversity of plant MADS-domain DNA-binding domain from pepper and tomato ripening fruits. J. Exp. Bot. 42, 1189–1201. doi: 10.1093/jexpbot/42.361.1189

Zieminski, C., Immink, B. G., Angenent, G. C., and Kaufmann, K. (2012). Developmental and evolutionary diversity of plant MADS-domain factors: insights from recent studies. Development 139, 3081–3089. doi: 10.1242/dev.076784

Sun, L., Yang, X., Li, H., Liu, J., Ren, J., Cai, M., et al. (2012). Suppression of 8-cis-epoxycarotenoid dioxygenase, which encodes a key enzyme in abscisic acid biosynthesis, alters fruit texture in transgenic tomato. Plant Physiol. 158, 283, 298. doi: 10.1104/pp.111.180454

Thompson, A. J., Cox, M., Barry, C. S., Vrebalov, J., Orfilla, C., Jarvis, M. C., et al. (1999). Molecular and genetic characterization of a novel pleiotropic tomato-ripening mutant. Plant Physiol. 120, 351–360. doi: 10.1104/pp.120.2.351

Brettman, R., You, T., Cox, M. C., Medrano, D., Siegel, A. F., Spokos, S., and Cauadro, G. (2001). Beta-Galactosidases with a lectin-like domain are expressed in strawberry. J. Exp. Bot. 52, 1657–1665. doi: 10.1093/jxb/er1655

Vrebalov, J., Pan, L., L., Amaya, A. M., MacQueen, R., Cheng, M, Pudi, M., et al. (2009). Flaxyl fruit expansion and ripening are regulated by the tomato HEAT-TEMPER gene TAGL1. Plant Cell 21, 3901–3917. doi: 10.1105/tpc.108.066056

Viswanath, G. I., Thorpe, C. J., and Chaney, J. K. (1996). In vitro growth of DEETIOLA TED1. Plant Cell Physiol. 37, 431–439. doi: 10.1111/j.1744-7348.1996.tb07094.x

Yang, J., Cui, M., et al. (2012). Suppression of 8-cis-epoxycarotenoid dioxygenase (NCED) genes encoding a key enzyme during abscisic acid biosynthesis from peach and grape fruits. J. Plant Physiol. 169, 1241–1252. doi: 10.1016/j.jplph.2009.01.013

Zhang, X., Yanda, J., Sundaresan, A., Colbin, S., Chan, S. W., Chen, H., et al. (2006). Genome-wide high-resolution mapping and functional analysis of DNA methylation in Arabidopsis. Plant Cell 18, 1239–1250. doi: 10.1105/tpc.106.047373

Zhang, S., Fei, Z., Chen, Y. R., Zheng, Y., Huang, M, Vrebalov, J., et al. (2013). Single-base resolution methylation of tomato fruit development reveal
Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 06 March 2013; paper pending published: 23 April 2013; accepted: 28 May 2013; published online: 14 June 2013.

Citation: Osorio S, Scossa F and Fernie AR (2013) Molecular regulation of fruit ripening. Front. Plant Sci. 4:198. doi:10.3389/fpls.2013.00198

This article was submitted to Frontiers in Plant Systems Biology, a specialty of Frontiers in Plant Science.

Copyright © 2013 Osorio, Scossa and Fernie. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in other forums, provided the original authors and source are credited and subject to any copyright notices concerning any third-party graphics etc.

epigenome modifications associated with ripening. Nat. Biotechnol. 31, 154–159. doi: 10.1038/nbt.2462
Zilberman, D., and Henikoff, S. (2007). Genome-wide analysis of DNA methylation patterns. Development 134, 3959–3965. doi: 10.1242/dev.001131