ANNUAL REVIEWS

Annual Review of Plant Biology

Developmental Mechanisms of Fleshy Fruit Diversity in Rosaceae

Zhongchi Liu,[1] Hong Ma,[2] Sook Jung,[3] Dorrie Main,[3] and Lei Guo[1]

[1]Department of Cell Biology and Molecular Genetics, University of Maryland, College Park, Maryland 20742, USA; email: zliu@umd.edu, guo@umd.edu

[2]Department of Biology, Eberly College of Science, and The Huck Institutes of the Life Sciences, The Pennsylvania State University, University Park, Pennsylvania 16802, USA; email: hxm16@psu.edu

[3]Department of Horticulture, Washington State University, Pullman, Washington 99164, USA; email: sook_jung@wsu.edu, dorrie@wsu.edu

Annu. Rev. Plant Biol. 2020. 71:547–73

The *Annual Review of Plant Biology* is online at plant.annualreviews.org

https://doi.org/10.1146/annurev-arplant-111119-021700

Keywords

Rosaceae fruit type, Rosaceae phylogeny, fruit set, fruit identity, MADS box, genome resources

Abstract

Rosaceae (the rose family) is an economically important family that includes species prized for high-value fruits and ornamentals. The family also exhibits diverse fruit types, including drupe (peach), pome (apple), drupetum (raspberry), and achenetum (strawberry). Phylogenetic analysis and ancestral fruit-type reconstruction suggest independent evolutionary paths of multiple fleshy fruit types from dry fruits. A recent whole genome duplication in the Maleae/Pyreae tribe (with apple, pear, hawthorn, and close relatives; referred to as Maleae here) may have contributed to the evolution of pome fruit. MADS-box genes, known to regulate floral organ identity, are emerging as important regulators of fruit development. The differential competence of floral organs to respond to fertilization signals may explain the different abilities of floral organs to form fleshy fruit. Future comparative genomics and functional studies in closely related Rosaceae species with distinct fruit types will test hypotheses and provide insights into mechanisms of fleshy fruit diversity. These efforts will be facilitated by the wealth of genome data and resources in Rosaceae.

Contents

INTRODUCTION

Drupe: a simple fleshy fruit with a hard endocarp surrounding a seed, as in peach, plum, and cherry

Pome: a simple fleshy fruit derived from hypanthium, as in apple and pear

Drupetum: an aggregate fleshy fruit with many small drupe-like fruits, as in raspberry

Fruits represent a key evolutionary innovation for seed protection and disposal in angiosperms, and they show wide phenotypic diversity (28). Further, fruits are an indispensable part of animal and human diets and contribute greatly to agricultural output. They are diverse in morphology, size, texture, color, and taste as a result of evolutionary adaptation and human selection. Whereas some angiosperm families like Brassicaceae, Fabaceae, Vitaceae, and Poaceae produce rather similar fruit types, the Rosaceae family and a few others develop a wide array of fruit types, including drupe (a fleshy fruit with a hard endocarp surrounding a seed, as in peach, plum, and cherry), pome (a fleshy fruit derived from hypanthium as in apple and pear), drupetum (a fleshy fruit with many small drupe-like fruits, as in raspberry), achene (a dry fruit with a single seed), and achenetum (a fruit with multiple achenes, as in strawberry). The diverse fruit types in Rosaceae make it a favorite plant family for comparative developmental and evolutionary studies.

Fruits are derived from floral tissues after pollination, and differences in floral structure contribute to Rosaceae fruit diversity. Although Rosaceae species develop similar flowers characterized by five sepals, five petals, and numerous stamens, their pistils/carpels exhibit variations in number, shape, fusion, and relative position to other floral organs. For instance, peach (drupe)

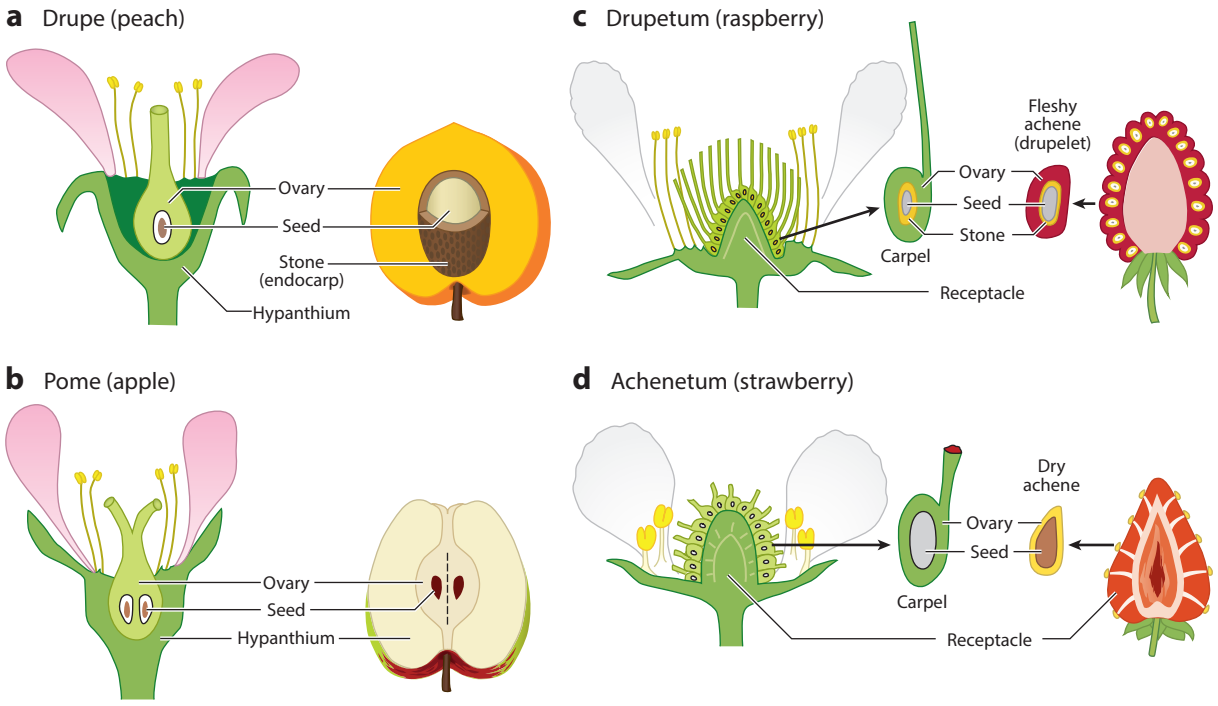


Figure 1

Four different Rosaceae flowers and their corresponding fruits representing drupe, pome, drupetum, and achenetum fruit types. (*a*) In peach, a drupe fruit, the ovary wall develops into the fruit flesh with a stone derived from the innermost layer (endocarp) of the ovary wall. Inside the stone is a seed. The hypanthium, which is a cup-like base resulting from the fusion of the lower half of the sepals, petals (and sometimes stamens), and senesces, does not become part of the fruit (see panel *b* for a contrasting example). (*b*) In apple, a pome fruit, the fruit flesh is derived from fusion between the hypanthium and the ovary, which contains five carpels that fuse to form a central core. (*c*) In raspberry, of the drupetum fruit type, the receptacle (raised stem tip) of the flower is connected to the base of numerous carpels (apocarpous gynoecium) with long styles. Each carpel (enlarged and in *green*), upon fertilization, develops into a fleshy drupe-like fruit (enlarged and in *red*), termed a drupelet. A drupelet is like a mini-peach with a fleshy ovary wall and a stone encasing a seed inside. The receptacle subtending these drupelets is not fleshy. (*d*) In strawberry, of the achenetum fruit type, the receptacle becomes fleshy while its numerous carpels develop into dry achenes. Each achene contains a seed surrounded by a thin and nonfleshy ovary wall.

has a single carpel that does not fuse with the surrounding hypanthium (**Figure 1*a***). In contrast, apple (pome) has five fused carpels that are positioned inferior to other floral organs and fuse with the cup-shaped hypanthium (**Figure 1*b***). In strawberry and raspberry, numerous unfused carpels emerge from a raised stem tip called a receptacle (**Figure 1*c*,*d***). These variations are the foundation for initial fruit diversity.

The second level of fruit diversity in Rosaceae comes from differential enlargement of specific floral tissue(s) in response to pollination and fertilization signals. For instance, peach is a typical botanical fruit with its fruit flesh derived from the ovary wall. On the other hand, apple and strawberry are accessory fruits as their fruits are derived from the hypanthium and receptacle, respectively. The differential ability of floral tissues to develop into fruit contributes greatly to fruit diversity in Rosaceae. A third level of diversity depends on whether a fruit becomes dry or fleshy. This review focuses primarily on the study of Rosaceae species with fleshy fruits because of their tremendous economic value and diversity.

Achene: a small and dry one-seeded fruit, often mistaken for a seed, that is produced by many plants, such as the dry achenes on the surface of strawberry fruit

Achenetum: a fruit with multiple achenes, as in strawberry

Hypanthium: the basal portion of the sepals and petals (and sometimes stamens) that are fused with each other to form a cup-like base

Receptacle: usually enlarged and dome-shaped stem tip supporting the development of floral organs

Botanical fruit: the seed-bearing structure derived from the ovary wall, such as peach and grape

Accessory fruit: atypical fruit where fruit flesh is derived from nonovary tissue such as the receptacle of strawberry and the hypanthium of apple

Apocarpous gynoecium: the female reproductive organ of a flower with multiple unfused carpels, as in the case of strawberry and raspberry

Follicetum: a dry fruit with multiple follicles that dehisce to release seeds

The Rosaceae family includes four main fruit types (**Figure 1**). In the drupe type, which includes peaches, plums, and cherries, the single ovary upon fertilization develops into a botanical fruit with a fleshy ovary wall (**Figure 1*a***). The innermost layer of ovary wall, the endocarp, becomes lignified and forms a hard shell, the stone, encasing the single seed inside. In the pome fruit type, which includes apples and pears, the fleshy fruit is derived from the fusion of the hypanthium, a cup-like base resulting from the fusion of the lower half of the sepals and petals, with the ovary (**Figure 1*b***) (80, 123). The five carpels of the ovary fuse with one another to develop into the central core of the pome fruit (**Figure 1*b***). For the drupetum-type fruit, such as the raspberry, the receptacle, the raised stem tip, gives rise to numerous unfused carpels, which are part of the apocarpous gynoecium. Each of the carpels develops into a fleshy achene (**Figure 1*c***). Interestingly, each drupelet forms its own stone encasing a seed inside, as in the drupe fruit of the peach. The receptacles subtending these drupelets are not fleshy (**Figure 1*c***). In contrast to the raspberry, the achenetum-type fruit of the strawberry develops a fleshy receptacle while its numerous carpels develop into dry achenes (**Figure 1*d***). Given the relatively close phylogenetic relationship between *Fragaria* and *Rubus* and their similar flower structures (**Figure 1*c,d***), it is intriguing that homologous floral organs possess distinct fruit-forming ability.

Most of our current understanding of fleshy fruit development was learned through the study of tomato (*Solanum lycopersicum*), an excellent model for fleshy fruit development. Genes that control fruit size and shape have been identified (84), and de novo domestication can be attained in the span of a few years (57, 130). Comparisons of fleshy fruit development between Rosaceae and tomato will reveal their conserved and unique mechanisms. Furthermore, recent progress in phylogeny, genomics, and functional studies in Rosaceae will help advance our understanding of the molecular bases underlying the evolution of different fleshy fruit types.

ROSACEAE PHYLOGENOMICS AND FRUIT TYPE EVOLUTION

Nuclear Rosaceae Phylogeny and Implication on Evolution of Fleshy Fruit Types

Rosaceae has ~100 genera with over 3,000 species (44). Traditional taxonomy, using fruit morphologies and other characteristics, grouped Rosaceae species into four subfamilies: Rosoideae (e.g., roses, strawberries, and raspberries, mostly with aggregate fruits); Amygdaloideae (e.g., peaches, plums, and cherries, with drupes); Maloideae (e.g., apples, pears, and hawthorns, mostly with pomes or related fruits); and Spiraeaoideae (e.g., *Spiraea*, many with follicetum, a type of dry fruit) (90). However, molecular phylogenetic analyses using chloroplast genes indicated that neither Rosoideae (s.l.) nor Spiraeaoideae are monophyletic (all members forming a single clade), leading to the reclassification of Rosaceae into three subfamilies: Rosoideae (s.s.), Amygdaloideae (s.l.), and Dryadoideae (79).

Most of the members of the previous Rosoideae (s.l.) form the slightly smaller Rosoideae (s.s.), with the remainder forming the newly defined Dryadoideae, consisting of four genera and approximately 20 species that produce achenes or achenetums (79). According to the phylogeny using plastid genes, Maloideae and Amygdaloideae (s.s.) are monophyletic and nested within Spiraeaoideae, prompting the naming of the combined clade of all three subfamilies into the newly expanded Amygdaloideae (s.l.) (79). Rosoideae (s.s.) and Amygdaloideae (s.l.) are further divided, respectively, into six and nine tribes; roses, strawberries, and raspberries belong to three different tribes, respectively, whereas the previously defined Maloideae (with pomes) and Amygdaloideae (s.s., with drupes) groups are given the tribe names Maleae and Amygdaleae in this classification system supported by phylogeny using chloroplast genes (79). However, in the chloroplast-gene-based Rosaceae phylogeny, the relationships among the subfamilies and among the tribes are not

clear. Therefore, a more informative, strongly supported, and well-resolved phylogeny is needed to understand the evolution of fruit types.

Recent phylogenetic analyses using nuclear genes have been effective in resolving difficult relationships, including those among members of relatively large families (43, 120, 127, 128). To provide a clearer understanding of Rosaceae evolutionary relationships, researchers performed a phylogenetic study using nuclear genes from 125 Rosaceae species, representing all 16 tribes and most of the genera (118) (**Figure 2**). In this nuclear phylogeny, all three subfamilies and all 16 tribes, including Maleae (apple and pear, with pomes), Amygdaleae (peach and cherry, with drupes), Rubeae (raspberry and blackberry, with drupetum), and Potentilleae (strawberry, with fleshy receptacle), are maximally supported as monophyletic. In addition, Dryadoideae was the first to separate, whereas Rosoideae (s.s.) and Amygdaloideae (s.l.) are sister groups. Furthermore, in Rosoideae, the Ulmarieae tribe was the first to separate from the other five tribes, with Rubeae being the second earliest branch; in Amygdaloideae (s.l.), the relationships among the nine tribes are highly supported, not only reaffirming the sister relationship of Maleae and Gillenieae (with follicetum), but also identifying the sister lineage for the drupe-producing Amygdaleae as the small tribe Lyonothamneae, which has only a single species, *Lyonothamnus floribundus*. This species is a tall tree (more than 10 m) with the unusual property of producing dry fruits from an ovary with only two to three carpels.

Using the new Rosaceae phylogeny, a statistical analysis (i.e., ancestral character reconstruction) has traced a possible evolutionary history of fruit types in Rosaceae (118). According to this analysis (**Figure 2**), the ancestral fruit type for Rosaceae, Rosoideae (s.s.), and Dryadoideae was achenetum, whereas the ancestral fruit type for Amygdaloideae (s.l.) was follicetum. For most Rosoideae tribes, the ancestral fruit type was also achenetum, although the ancestral fruit type for Rubeae could be drupetum. For most tribes in Amygdaloideae (s.l.), including Maleae, the ancestral fruit type was follicetum, but the ancestral fruit type of Amygdaleae could be drupe.

Accordingly, the ancestral dry fruit types have given rise in parallel to different fleshy fruits in various Rosaceae groups. In Rosoideae (s.s.) (**Figure 2*b***), individual achenes have evolved fleshy outer tissues to form the drupetum of Rubeae, while the receptacle in strawberries has become enlarged and fleshy, without dramatic changes in the achenes themselves. In roses (Roseae), yet another evolutionary path resulted in the increased fleshiness of the hypanthium, which has extended upward to enclose the achenes, whereas the receptacle did not appear to enlarge. In the nuclear phylogeny (**Figure 2*a***), the *Fragaria* genus is part of a large tribe (Potentilleae) that also includes many other genera with the dry fruit achenetum, whereas raspberry/blackberry belong to another tribe (Rubeae) with a separate history. Therefore, despite the structural similarities between strawberries and raspberries/blackberries, their fleshy components are different and likely evolved via different pathways.

In Amygdaloideae (s.l.), two major fleshy fruit types, drupe and pome, were derived from the dry fruit follicetum, via two rather different evolutionary paths (**Figure 2*c***). For the drupes of peach, plum, apricot, and cherry (in the tribe Amygdaleae), the nuclear phylogeny placed Amygdaleae as sister to the tribe Lyonothamneae, which produces a follicetum with two to three carpels, a reduction from the ancestral type of five or more carpels. This relationship strongly supports the gradual reduction of carpel number from five to two or three, eventually leading to the one-carpelled drupe-type fruit in the ancestor of peach, plum, and cherry that became fleshy after the separation from Lyonothamneae. Separately, the pome-fruit bearing species all belong to the Maleae tribe, which is sister to the dry-fruit-producing Gillenieae tribe. Because the dry fruits from members of both Gillenieae and the early-divergent genera of Maleae have five carpels, and the pome fruit is a product of the fusion between the hypanthium and the five-carpelled ovary,

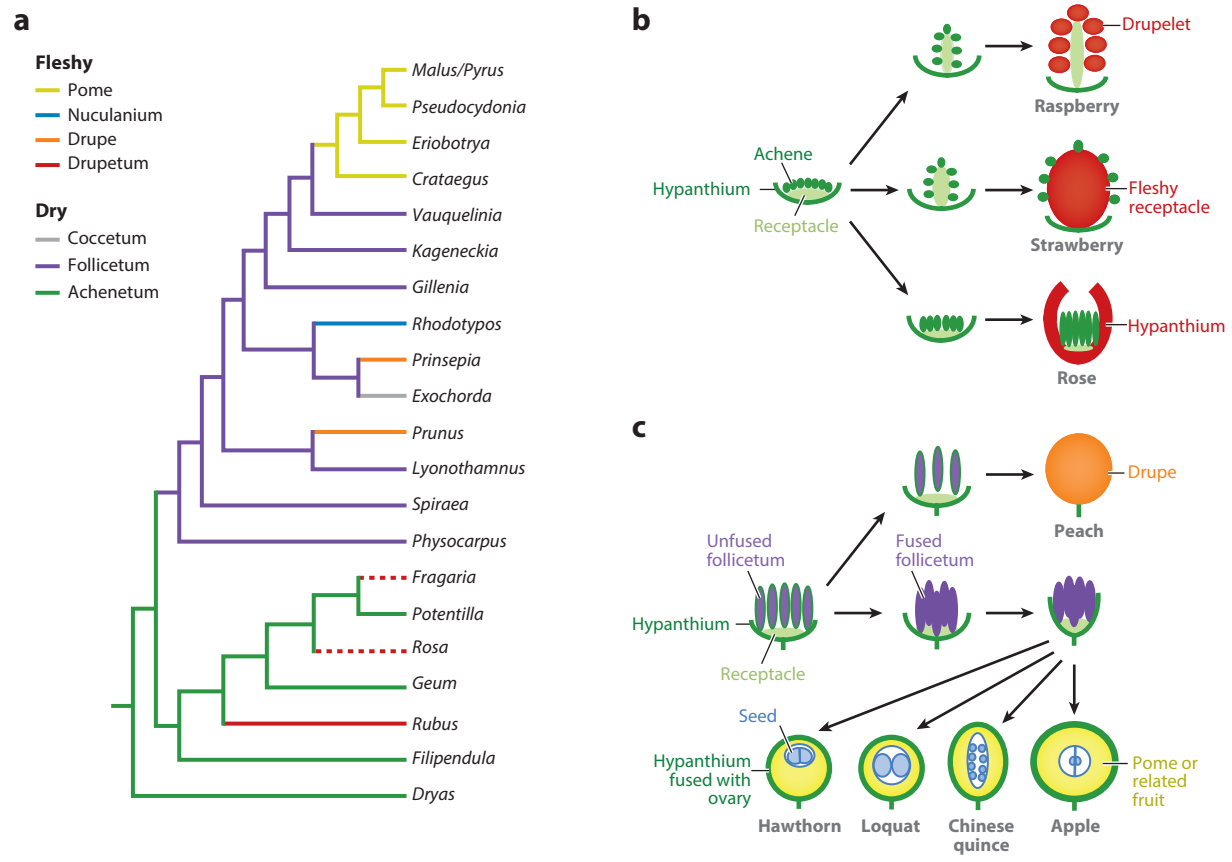


Figure 2

Nuclear Rosaceae phylogeny and fruit-type evolution. (*a*) A nuclear phylogeny of Rosaceae, showing genera representative of various tribes with different fruit types: Maleae (pome and related fruit types, *Malus*, *Pyrus*, *Pseudocydonia*, *Eriobotrya*, *Crataegus*; follicetum, *Vauquelinia*, *Kageneckia*), Gillenieae (follicetum, *Gillenia*), Kerrieae [nuculanium (a type of berry, fleshy fruit), *Rhodotypos*], Exochordeae [coccetum (a dehiscent dry fruit with multiple carpels that open along two sutures), *Exochorda*; drupe, *Prinsepia*], Amygdaleae (drupe, *Prunus*), Lyonothamneae (follicetum, *Lyonothamnus*), Spiraeeae (follicetum, *Spiraea*), Neillieae (follicetum, *Physocarpus*), Potentilleae (achenetum with fleshy receptacle, *Fragaria*; achenetum, *Potentilla*), Roseae (achenetum with fleshy hypanthium, *Rosa*), Colurieae (achenetum, *Geum*), Rubeae (drupetum, *Rubus*), Ulmarieae (achenetum, *Filipendula*), and Dyadeae (achenetum, *Dryas*). The differently colored lines represent the ancestral character reconstruction of the fruit types. The dashed red lines corresponding to *Fragaria* and *Rosa* indicate achenetum with fleshy receptacle and hypanthium, respectively. (*b*) A proposed evolutionary history of fleshy fruits in three genera in Rosoideae: *Rubus* (drupetum, raspberries), *Fragaria* (achenetum with fleshy receptacle), and *Rosa* (achenetum with fleshy hypanthium). The green cup-like structures and the red urn-like structure represent the hypanthium, the light green ovals represent the receptacle, the small green ovals represent achenes, the red ovals represent drupelets, and the large red oval represents a fleshy receptacle. (*c*) A proposed evolutionary history of fleshy fruits in the tribes Amygdaleae (drupe, peach) and Maleae (pome and related fruits, apple/pear, Chinese quince, loquat, and hawthorn) in Amygdaloideae (s.l.). The green cup-like structures represent the hypanthium, the large orange oval represents the drupe, the purple long ovals with a thin green outline represent unfused follicetum, the purple long ovals without green outlines represent fused follicetum, and the yellow circles with green outlines indicate pome or related fruits. The green outlines represent the hypanthium that has been fused with the ovary, and the light blue shapes inside the pomes represent seeds. This figure was adapted from Reference 118.

a possible evolutionary history is the change from five unfused carpels to fused carpels to further fusion of the ovary with the hypanthium, with additional changes to various fleshy types related to the typical pome of apples and pears (**Figure 2*c***). The nuclear phylogeny of a number of genera in the subtribe Malinae supports the successive divergence of the ancestors of *Crataegus* (with the partial enclosure of the ovary by the hypanthium), *Eriobotrya* (with thin flesh), and *Pseudocydonia* (with many ovules), suggesting somewhat different evolutionary paths from that of apples and pears.

Whole Genome Duplications, MADS-Box Gene Duplications, and Pome Fruit Evolution

The MADS-box genes are intimately linked to the evolution of developmental novelties such as floral organs in angiosperms (76, 101). The most well-studied MADS-box proteins all belong to the MIKC type or type II groups because of the presence of four domains (from N to C terminus), the MADS-box (M), intervening (I), keratin-like (K), and C-terminal (C) domains. During flower development, the identity of four floral organ types—sepal, petal, stamen, and carpel—is determined by the combinatorial action of four classes of MADS-box genes: A, B, C and E. Specifically, sepals are specified by A and E genes; petals are specified by A, B, and E; stamens are determined by B, C, and E; and carpel identity is determined by C and E MADS-box genes (70, 101).

Whole genome duplication (WGD) events followed by preferential gene retention and subsequent divergence may have contributed to angiosperm diversification. Duplicated MADS-box genes resulting from an ancient WGD in the common ancestor of angiosperms may have led to the origin of flowers as well as other innovative traits, including fruits (98, 104). Similarly, whole genome sequencing of apple and pear identified a relatively recent (~50 million years ago) WGD in the Maleae tribe that was proposed as a contributor to the formation of Maleae-tribe-specific pome fruit (107). Further, a group of type II MADS-box genes containing *SVP* and *AGL24* was found to have substantially expanded, suggesting that members of this group potentially served as regulator(s) of pome fruit formation (107).

To further test this hypothesis, researchers performed phylogenomic analysis using genomic and transcriptomic data sets to uncover further evidence for WGDs in Rosaceae, especially in the ancestors of Maleae and Amygdaleae, with pome and drupe fruits, respectively (118). The results suggest that WGDs might have contributed to the origins of the pome and drupe types of fleshy fruits. In addition, the WGD that was placed at the origin of the Malinae subtribe with pome-bearing genera (**Figure 3*a***) was also strongly supported by large syntenic chromosome regions in the apple and pear genomes (56).

Studies in *Arabidopsis* indicated that MADS-box genes *AG*, *FUL*, and *SHP* are important for fruit development (19). Moreover, the *SVP* gene was found to cause enlarged sepals when overexpressed (65). Homologs of *AG*, *FUL*, and *SVP* in apple are expressed during the development of the pome fruit, suggesting a role in pome fruit development (46, 122). Since the pome fruit is derived from a hypanthium, with fused basal portions of sepals and petals, the class A *AP1* gene, required for sepal and petal identities, may also participate in pome fruit formation. Indeed, molecular phylogenetic analyses revealed that homologs of *AG*, *FUL*, *SHP*, *SVP*, and *AP1* experienced a duplication event corresponding to the WGD at the origin of Malinae (**Figure 3**) (56). The coincidental occurrences of both the duplication of multiple MADS-box genes, due to the WGD event, and the origin of the pome and related fruits in Malinae support the idea that the increased MADS-box gene copies might have allowed the functional innovations necessary for the evolution of the pome fruit.

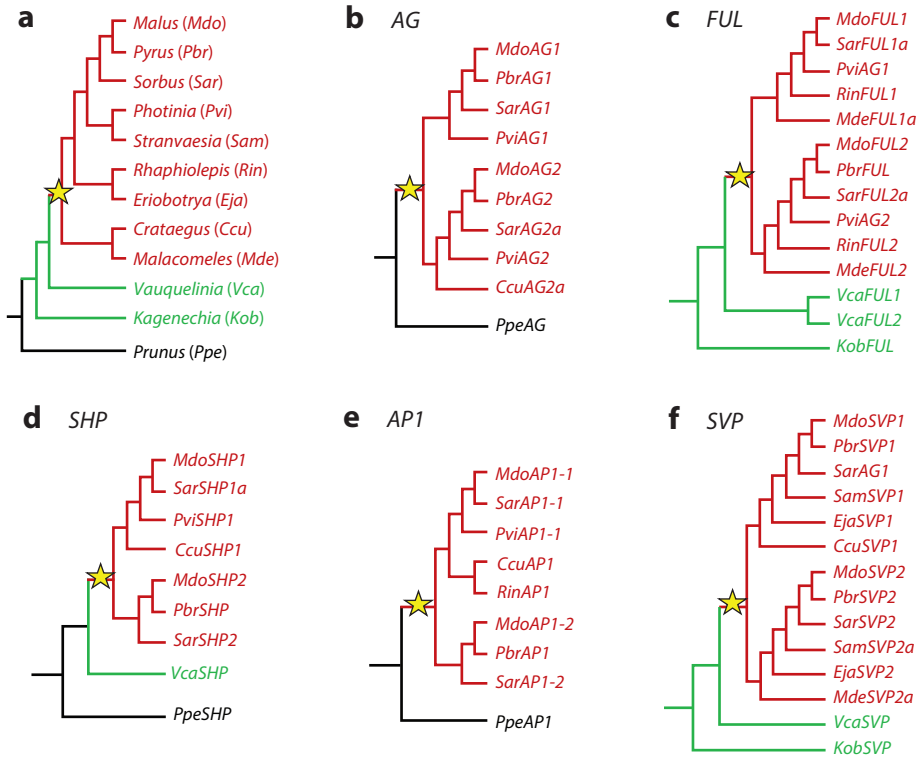


Figure 3

A Maleae phylogeny and duplication of several MADS-box genes. (*a*) A diagram of the phylogenetic tree of representative Maleae genera, including those producing pomes and related fleshy fruits (*red*) and two genera with follicetum (*green*). A proposed whole genome duplication (WGD) event is indicated with a star. *Prunus* is in the tribe Amygdaleae. (*b*) The *AG* gene tree. (*c*) The *FUL* gene tree. (*d*) The *SHP* gene tree. (*e*) The *AP1* gene tree. (*f*) The *SVP* gene tree. The star in panels *b–f* indicates a gene-duplication event consistent with the position of the WGD. The gene names use three-letter abbreviations for the species, as indicated in panel *a*, and the gene name of the closest homolog in *Arabidopsis thaliana*. Figure adapted with permission from Reference 56.

FERTILIZATION-INDUCED SIGNALING AND FRUIT SET

Fertilization-Induced Signaling in Fruit Set Is Conserved in Flowering Plants

To understand fleshy fruit diversity from a developmental perspective, it is important to introduce the concept of fruit set, the decision to abort or to proceed with fruit development (34, 50). After a flower is fully developed, further development is blocked. Successful fertilization induces the production of hormonal signals in the seed. These hormonal signals relieve the developmental block and promote botanical or accessory fruit development.

Fruit set: the initiation of or commitment to start fruit development

The phytohormones auxin and gibberellic acid (GA) are identified as the fertilization-induced signals. Removal of the achenes (individual ovaries) from cultivated strawberries (*Fragaria* × *ananassa*) completely arrested the receptacle from developing into fruit, while exogenous application of synthetic auxin or GA can restore the receptacle fruit growth (71, 102). Free auxin is found to accumulate in the achenes, in contrast to the low level of auxin in receptacles, demonstrating that auxin is synthesized within the fertilized achenes (71, 72). In the diploid strawberry *Fragaria vesca*, the application of exogenous auxin, GA, or both to emasculated flowers also induced

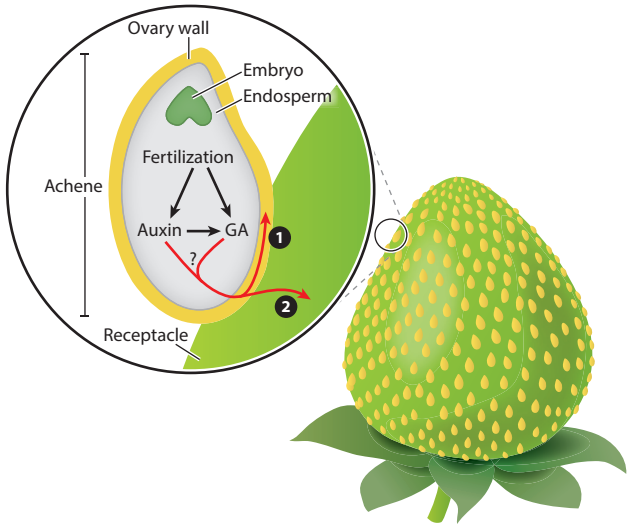


Figure 4

Fertilization-induced signal production in the achene of the strawberry. In the enlarged achene (a single ovary), double fertilization leads to the formation of the embryo (*green heart*) and endosperm (*gray*). Auxin biosynthesis in the endosperm may also promote GA biosynthesis in the endosperm. Together, auxin and GA are transported to the ovary wall (❶) or receptacle (❷) to stimulate fleshy fruit development. Abbreviation: GA, gibberellic acid. Figure adapted from Reference 52.

fertilization-independent (parthenocarpic) fruit (52, 60). RNA-sequencing (RNA-seq) profiling of staged and finely dissected *F. vesca* fruit revealed transcript accumulation of auxin and GA biosynthesis genes in the ghost (endosperm and seed coat) soon after fertilization. Subsequently, promoters of auxin biosynthesis genes fused to the gene for β-glucuronidase in transgenic strawberry revealed strong expression of auxin biosynthesis genes in the endosperm (25). In contrast to auxin and GA biosynthesis in the achenes, auxin-signaling genes, auxin-response factors (ARFs), and auxin/indole-3-acetic acid (AUX/IAA) repressor genes are highly expressed in the receptacle (52), indicating that the receptacle is the site of auxin perception and response (**Figure 4**).

In addition to strawberry, exogenous applications of auxin or GA were shown to cause parthenocarpic fruits in other Rosaceae species, including rose, apple, pear, loquat, and several *Prunus*, as well as in other flowering plants, including *Arabidopsis*, tomato, and grape (12–14, 31, 66, 73, 81, 91, 97, 110). Furthermore, ectopic overexpression of the auxin biosynthesis gene *defH9-iaaM* in strawberry and raspberry (67) and overexpression of the GA biosynthesis gene *gibberellin 20-oxidase* in tomato (32) led to parthenocarpic fruits. In addition to biosynthetic genes, overexpressing the auxin receptor *TIR1* led to parthenocarpic tomato fruit, probably as a result of auxin hypersensitivity (24, 83). Parthenocarpy can also be induced when repressors of auxin or GA-signaling pathways were mutated or suppressed, as demonstrated by *arf8* mutants in *Arabidopsis* and transgenic knockdowns of tomato *ARF7*, *ARF8*, or *IAA9* (18, 35, 36, 112, 113). These results led to the proposal that the IAA9/ARF7/ARF8 repressor complex inhibits fruit set in the ovary tissue of *Arabidopsis* and tomato. DELLA proteins are repressors of GA signaling (99); a tomato *procera* mutant with a point mutation in the *SlDELLA* as well as a transgenic tomato containing an antisense construct against *SlDELLA* developed parthenocarpic fruits (8, 64). *Arabidopsis della* mutants form seedless fruit due to constitutive activation of GA signaling (30). Together, these results indicate that auxin and GA are evolutionarily conserved signals for the induction of fruit set across angiosperm species.

Parthenocarpy: fruit formation in the absence of pollination

Epigenetic Regulation of Fertilization-Induced Signals May Coordinate Seed Set and Fruit Set

While little is known about the molecular mechanisms by which pollination and fertilization induce auxin/GA production in seed, recent studies in fertilization-induced seed development shed some light on this process, as seed set and fruit set appear to respond to the same fertilization-induced signal (50, 86). In *Arabidopsis*, the initiation of seed development is repressed by histone H3K27 methylation, mediated before fertilization by the evolutionarily conserved Polycomb Repressive Complex 2 (PRC2). Mutations in any of four PRC2 components, MEDEA (MEA), FERTILIZATION-INDEPENDENT ENDOSPERM (FIE), FERTILIZATION-INDEPENDENT SEED2 (FIS2), and MULTICOPY SUPPRESSOR OF IRA1 (MSI1), lead to the fertilization-independent autonomous endosperm development and derepression of target gene expression (10, 38, 55, 74). The PRC2 complex is also required to block the development of the maternally derived seed coat prior to fertilization (85). After the fertilization of the central cell, an auxin signal is produced in the endosperm and subsequently transported to the maternal integuments to release the block on seed coat development. The transport of auxin to the seed coat depends on the type I MADS-box transcription factor AGAMOUS-LIKE 62 (AGL62), as *agl62* mutants displayed retention of auxin in the endosperm and impaired seed coat development (29). By responding to the same signal, fruit set and seed set are coordinated, which is likely critical for the appropriate timing of seed dissemination.

Recently, loss-of-function mutations in a type II MADS-box gene, *AGL6*, led to facultative parthenocarpy in tomato (53), suggesting a repressive role for *AGL6* in fruit set. RNA-seq data from finely dissected tomato fruit tissues showed that *AGL6* expression peaks in the ovule at 0 days postanthesis (DPA); however, at 5 DPA, *AGL6* expression declines rapidly (**Figure 5*a***) (27, 77, 94). An examination of *AGL6* homolog (*gene38250*) in wild strawberry *F. vesca* reveals a similar expression trend: highly specific expression in the ovule followed by gradual decline postfertilization (**Figure 5*b***). Given its strong expression in the ovule prefertilization, *AGL6* may repress auxin/GA signal production in the ovule. Nevertheless, mutants of *AGL6* in *Arabidopsis*, petunia, and rice exhibit a range of phenotypes unrelated to fruit development, implicating that *AGL6* may function as a SEP-like protein (20). Therefore, despite expression similarity in tomato and strawberry, the specific mechanism of *AGL6* function in fruit development requires further investigation.

FRUIT IDENTITY IS INTIMATELY LINKED TO FLORAL ORGAN IDENTITY

Type II MADS-Box Genes May Also Determine Fruit Identity

An intriguing question is why certain floral organs can form fruit flesh while other floral organs cannot. Exogenous auxin or GA application does not change the species-unique fleshy fruit type, suggesting that genetic factors may underlie fruit identity, which endows a specific floral organ with the competence to respond to the fertilization signal. Surprisingly, we know almost nothing about the genes involved in bestowing this tissue-specific fruit identity.

Given that fruits, like flowers, function to ensure reproductive success in angiosperms, type II MADS-box genes could also determine fruit identity. Indeed, ectopic expression of C class genes *TAGL1* (*SHP*) or *TAG1* in tomato results in fleshy sepals (75, 78). The partial homeotic transformation from sepals to carpels in these tomato plants might have also converted the nonfruit identity of sepals to the fruit identity of carpelloid sepals. The above study indicates that C class MADS-box genes may specify fruit identity in species with ovary-derived botanical fruits.

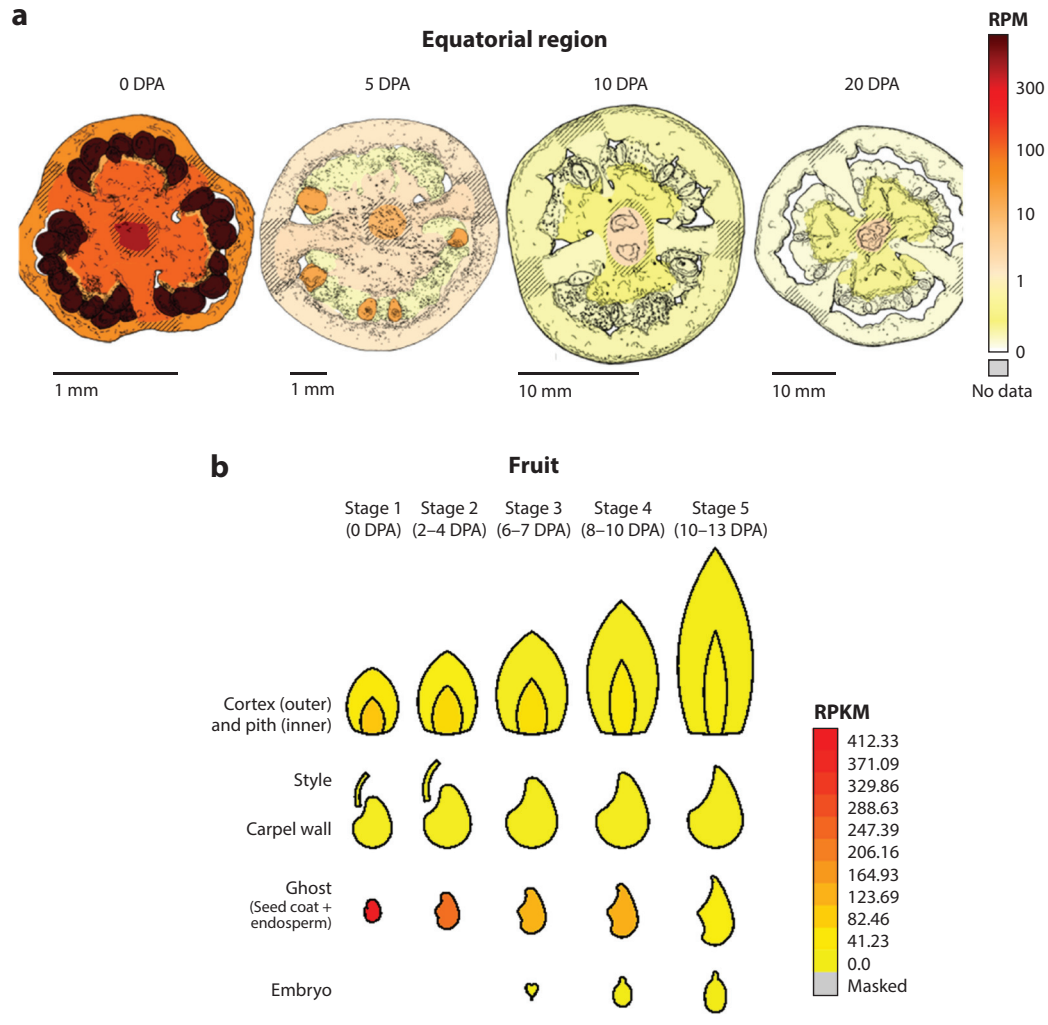


Figure 5

AGL6 is most highly expressed in the ovule at 0 DPA in tomato (*a*) and diploid strawberry (*b*). The expression of *AGL6* declines soon after fertilization in both species. In strawberry (*b*), stages are defined as 0 DPA (stage 1), 2–4 DPA (stage 2), 6–7 DPA (stage 3), 8–10 (stage 4), and 10–13 (stage 5). Abbreviations: DPA, days postanthesis; RPKM, reads per kilobase per million; RPM, reads per million. The tomato data are from Tomato Expression Atlas (**http://tea.solgenomics.net**) (see also 27, 77, 94). The strawberry data are from Strawberry Genome Resources (**http://mb3.towson.edu/efp/cgi-bin/efpWeb.cgi**) (see also 40).

Interestingly, some insect species have acquired the ability to induce the growth of fruit-like galls from vegetative tissues. Transcriptome profiling of leaves of wild grapevine (*Vitis riparia*) infected by a galling parasite called phylloxera (*Daktulosphaira vitifoliae*) revealed that the phylloxera leaf gall is both phenotypically and transcriptionally similar to carpel (89). The expression of 39 orthologs of *Arabidopsis* gynoecium development genes, including *AG*, *SHP2*, *FUL*, *SEP1*, and *AGL6*, is elevated in the phylloxera leaf gall when compared with age-matched leaves, supporting the hypothesis that carpel identity is tied to fruit identity in species with ovary-derived fruits.

miR172 and AP2 Regulate Fruit Identity and Fruit Size

While apple's hypanthium is often considered a fusion of the bases of sepals, petals, and stamens (80), recent studies indicate that the sepal base contributes most to the apple fruit flesh (123, 124). Hence, sepal identity might be tied to fleshy fruit identity in apple, and as such, class A genes such as *AP1* and *AP2* could be involved in specifying fruit identity in apple or other species with hypanthium-derived fruits. A transposon insertion in an apple microRNA gene, *miR172*, was identified that led to twofold reduction of the *miR172* transcripts and larger fruit size (125). Conversely, overexpression of *miR172* in transgenic apple partially converted sepals to petals and dramatically reduced fruit size. In transgenic lines with 20- to 24-fold increase of *miR172* transcripts, the flowers consisted entirely of carpels that did not develop into fleshy fruit even after hand pollination. This is not surprising given that apple carpels only contribute to the core of the apple and may not possess the flesh-forming competence. In contrast, sepal tissues that are reduced or absent due to their conversion to petal or carpel in the *miR172* overexpression lines may underlie the reduced ability to form fleshy fruits and hence the development of thin hypanthium and smaller-sized fruit.

In *Arabidopsis*, *miR172* functions to repress class A floral homeotic gene *AP2* post-transcriptionally (11), and AP2 represses the expression of class C MADS-box genes *AG* and *FUL* (21, 49, 121). Therefore, the effect of *miR172* on apple fruit size is likely mediated by *AP2*. Increased AP2 activity due to transposon insertion in *miR172* may positively promote fruit identity while reduced AP2 activity due to overexpressed *miR172* may lead to a loss of fruit identity.

Interestingly, tomato plants that strongly overexpressed *miR172* also developed abnormal flowers consisting entirely of carpel tissues. However, unlike the apple flowers, these carpel-only tomato flowers developed parthenocarpic fruit (124). The ectopic and extra carpels may somehow bypass the requirement of auxin/GA signals for fruit set, perhaps as a result of interorgan communication (111). The findings that *miR172* overexpression lines have similar floral phenotypes but distinct fruit phenotypes in apple and tomato suggest that, while the regulation of floral organ identity by *miR172* is similar in apple and tomato, their floral organs possess distinct competencies to form fleshy fruits.

Class E Genes *SEP1/2/4* and Related *FBP9* Clade Promote Fleshy Fruit

Several publications have suggested *SEPALLATA1/2/4* and related *FBP9* genes promote fruit flesh formation in apple. Antisense suppression of *SEPALLATA1/2/4*-like genes *MdMADS8* and *MdMADS9*, as well as *FBP9*-like *MdMADS7*, caused sepaloid petals and severely reduced apple fruit flesh in the cortex layer (45). This reduction of fruit flesh may be mediated partly through a reduction of *MdMADS6* found in *MdMADS7*, *MdMADS8*, and *MdMADS9* antisense apple plants. Interestingly, in wild type apple, *MdMADS7* and *MdMADS6* exhibit low expression early in fruit development but then show a gradual increase of expression as fruit develops (45). The expression and phenotype suggest a positive role of *SEP1/2/4* and *FBP9* MADS-box genes in fruit flesh formation in apple. In the cultivated strawberry, another Rosaceae species with accessory fruit, suppression of a *SEP1/2*-like gene, *FaMADS9*, led to the repression of receptacle fruit development similar to the loss of fruit flesh in apple described above (92). Hence, the activities of *SEP1/2/4* and the closely related *FBP9*-clade MADS-box genes are required for fleshy fruit development in apple and strawberry. Unlike the C and A class floral genes discussed above, the role of *SEP1/2/4* and *FBP9* might be directly linked to fleshy fruit development instead of to floral organ identity. Nevertheless, their positive roles in fruit development in other Rosaceae species are yet to be demonstrated.

Based on the studies discussed above, we propose that MADS-box proteins, including SEP1/2/4, FBP9, and other unidentified members, likely define a new class of MADS-box

transcriptional complexes, which we name the F (fruit) class. MADS-box genes belonging to this class should fulfill the following criteria: (*a*) They show expression in the species-specific fruit tissue(s), (*b*) their expression increases soon after fruit set and continues to increase as fruit enlarges, (*c*) their loss-of-function mutants arrest fruit development, and (*d*) their ectopic expression may cause ectopic fleshy fruit. We hypothesize further that the functions of F class MADS-box genes may not be as conserved as those of the ABCE genes for floral development. Thus, these F class genes may act differently in different species, reflecting the apparently greater plasticity of fleshy fruit development and suggesting possible convergent evolution of such gene functions.

B CLASS MADS-BOX GENES SUPPRESS THE PHOTOSYNTHESIS REQUIRED FOR FLESHY FRUIT DEVELOPMENT

B Class MADS-Box Genes May Encode a General Repressor of Cell Division, Expansion, and Fruit Flesh Formation

In apple, the B class *MdPISTILLATA* (*MdPI*) gene (MDP0000286643) is a single-copy gene (107). Several apple varieties, including Rae Ime, Spencer Seedless, and Wellington Bloomless, develop abnormal flowers resembling B class mutants with an increased number of sepals and pistils and a lack of petals and stamen. Interestingly, these abnormal flowers develop parthenocarpic apple fruit. A transposon insertion in the *MdPI* gene is responsible for the flower and fruit phenotype (123). Transgenic downregulation of *MdPI* also produced similar parthenocarpic apple fruit (126), suggesting that *MdPI* inhibits fruit set. In contrast, overexpression of *MdPI* in transgenic apple caused sepal-to-petal conversion and flattened fruit shape due to inhibition of cell expansion toward the base of the fruit (126). Since apple fruit flesh is derived mostly from the fused sepal base, the increased number of sepals in *MdPI* loss-of-function mutants may somehow bypass the requirement of auxin/GA signal for fruit set. An alternative interpretation is that during the evolution of pome fruit, *MdPI* may have gained new functions to inhibit cell division and cause floral organ development to arrest prior to pollination/fertilization.

The inhibitory effect of PI on cell division is supported by studies in grape (*Vitis vinifera)*. The *fleshless berry* mutant in the grape cultivar Ugni Blanc was caused by ectopic expression of the grapevine homolog of *VvPISTILLATA* (*VvPI*). An insertion of a miniature inverted-repeat transposable element in the promoter of *VvPI* caused its ectopic expression in fruit, shoot, and leaves, instead of its normal expression in flower organs (26). Depending on the cell layer in which the transposon insertion occurs, the phenotypes are different. When the mutation occurs in the L1 and L2 cell layer, fruit set is blocked. When the insertion occurs in the L2 layer, *VvPI* misexpression prevents fleshy pericarp development by blocking the differentiation of vacuolated cells that are characteristic of mesocarp tissues. This suggests that *VvPI* might encode a general inhibitor of fruit flesh development that is not normally expressed in the fruit tissues of grape.

In *Arabidopsis*, the B class genes *PI/AP3* promote petal and stamen differentiation by repressing photosynthesis and nutritional signals (63). *AtPI* directly binds and represses two GATA transcription factors, GNA and GNL; these two GATA factors redundantly promote chlorophyll biosynthesis in flowers and leaves (63). Given the role of *MdPI* and *VvPI* in repressing fruit flesh in apple and grape (26, 126), *PI* may repress fruit flesh development in part by repressing photosynthesis.

Photosynthesis May Be Required for Fleshy Fruit Development

An interesting observation is that fleshy fruit, irrespective of their fruit type, all develops from formerly green floral tissues such as the sepal/hypanthium in apple, the ovary wall in raspberry and peach, and the receptacle (stem tip) in strawberry. Thus, photosynthesis and related metabolic

processes might be required for fleshy fruit formation and may contribute to competence for fruit development.

Supporting the hypothesized positive role of photosynthesis in fruit formation, microarray analysis revealed the upregulation of a large number of photosynthesis-related genes at postanthesis (4 DPA) in tomato. Further, antisense-*IAA9* tomato plants, which exhibit parthenocarpy, showed strong and precocious activation of photosynthesis-related genes at 0 DPA as well as at 4 DPA. A similar dramatic upregulation of genes in sucrose catabolism was also observed in antisense-*IAA9* during fruit set. Therefore, activation of photosynthesis and sucrose metabolism appears to accompany fruit set (113).

With abundant RNA-seq data from the flower and fruit of diploid wild strawberry, robust consensus coexpression networks have been established (93). Clusters of genes correlating to specific tissue or stages could be identified by mining the consensus network at **http://www.fv.rosaceaefruits.org**. The clusters of genes associated with the postfertilization ghost (endosperm and seed coat) and receptacle fruit are enriched for Gene Ontology terms related to iron transport. This is likely due to the requirement of active iron transport for photosynthesis and other biochemical activities during fleshy fruit initiation and development.

SUMMARY AND HYPOTHESES ON FLESHY FRUIT DIVERSITY

Active Repression Mechanisms Prevent Fruit Development in the Absence of Successful Fertilization

An emerging theme from the studies presented above is that active repression mechanisms must exist to prevent precocious fleshy fruit development without pollination/fertilization. This active repression occurs in two ways. The first is the repression of the synthesis of fertilization signals auxin and GA at the ovule. The second is the active repression of floral tissues (ovary wall, sepals, hypanthium, and receptacle) from forming fruits, fleshy or dry, in the absence of fertilization. Epigenetic regulators such as PRC2 and transcription factors including MADS-box genes are critical in repressing the synthesis of fertilization signals in the ovule, while repressors in auxin signaling (IAA9/ARF8/ARF7) and GA signaling (DELLA) act at floral tissues to prevent them from developing into fruit. These repression activities are inactivated upon successful fertilization.

While the fertilization-induced signals, auxin and GA, are highly conserved across angiosperms, significant diversity exists in Rosaceae fleshy fruit types, where different floral organs in the same species possess different competence to develop into fleshy fruit. This fruit-type diversity is likely driven by their mode of seed dissemination and specific interactions with animals and their environment.

Competence to Respond to the Fertilization Signals May Determine Whether a Floral Organ Develops into the Fruit

The exogenous application of auxin, GA and cytokinin as well as genetic mutations remove the active repression mechanisms described above and lead to parthenocarpic fruit characteristic of a given species. For instance, application of auxin to strawberry flowers does not cause them to form fruits resembling raspberry. How could a specific organ develop into fleshy fruits in each different species? The studies described above support the hypothesis that the fertilization-induced signals are transported equally to all floral organs/tissues, yet only certain floral tissue(s) are competent to respond to the signals. This competence to develop fruit flesh appears to depend on both positive and negative genetic factors. First, photosynthetic capability appears to be needed for a floral organ to develop into fruit, as nonphotosynthetic organs such as petals and stamens do not normally form

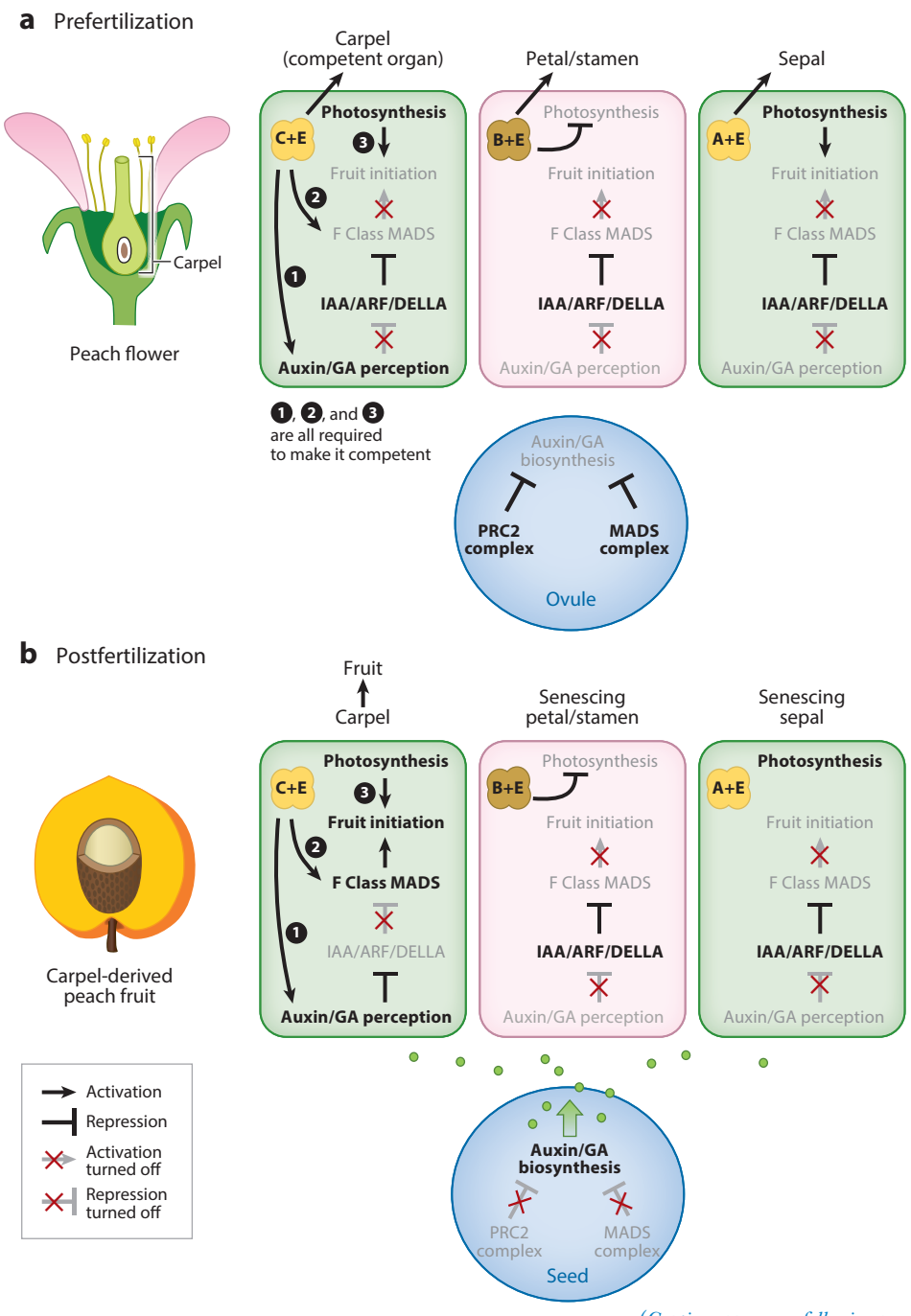
fruits. Second, the floral organ should be of correct organ identity. The expression of C and E class MADS-box genes (*AG*, *SEP*) is required to specify carpel identity; this carpel identity is tied to the fruit-forming competence in species with ovary-derived fruit such as peach. Conversely, the expression of A class genes such as *AP2* and *AP1* is needed to preserve sepal/hypanthium identity, which is tied to fruit formation and larger fruit size in apple. Third, the competent floral organ should be sensitive to the fertilization-induced signal. Genes acting in auxin, GA, and cytokinin perception and signaling pathways should be expressed in the competent floral organ. A final condition is that the floral organ may need to repress the expression of B class MADS-box genes and their partner *SEP* genes to allow photosynthesis and other cellular and biochemical activities required for fruit development.

A Model Based on a Competence Hypothesis

Figure 6 specifically illustrates the competence hypothesis, highlighting the role of differential competence factors in specifying fruit type. In an unfertilized ovule, auxin and GA biosynthesis are repressed by MADS-box genes (such as *AGL6*) and PRC2 (**Figure 6*a***); mature floral tissues arrest their development due to the repressor activities of auxin and GA signaling components (IAA/ARF/DELLA) (**Figure 6*a***). However, competent and incompetent floral organs are distinct, as illustrated by the competent carpel (ovary wall) and incompetent petal/stamen and sepal. In the competent carpel, the C + E MADS complex not only specifies carpel identity but also promotes competence by ❶ activating the expression of auxin/GA receptors, ❷ promoting the expression of F class MADS-box genes, and ❸ coexisting with the photosynthetic capability. By contrast, in petal/stamen tissue, the A + B + E or C + B + E (B + E for short) MADS complexes specify their respective floral organ identity but at the same time repress photosynthesis, which may preclude the competence of the petal/stamen to develop into fruit. Finally, sepal (an example of a noncompetent organ) is specified by A + E genes and could undergo photosynthesis but fails to activate the expression of auxin/GA receptors and/or F class MADS-box genes.

Upon pollination and fertilization (**Figure 6*b***), auxin and GA produced in the fertilized seed are perceived only by the competent organ (the carpel in **Figure 6*b***), where signal perception causes the degradation of IAA and DELLA, removing inhibition of F class MADS-box genes and leading to subsequent fruit development. In incompetent petal/stamen and sepal, however, the auxin/GA receptor genes are not expressed and will not respond to the auxin/GA. As a result, F class MADS-box genes remain inhibited. Even in the presence of mutations that knock out DELLA or IAA, the F class MADS-box genes will not be expressed due to an absence of activators (i.e., C + E genes in the example here) (**Figure 6*b***).

To sum up, a fruit-competent floral organ should possess the ability to express auxin and GA receptors, to activate F class MADS-box genes, and not to repress photosynthesis. During the evolution of different fruit types, different floral organs have acquired competence. If sepal/hypanthium is the competent organ, as in the case of apple, the A + E genes may have acquired the ability to activate F class MADS-box genes and auxin/GA receptors in the sepal/hypanthium. In strawberry, the putative GA receptor GID1c is specifically expressed in the receptacle but not in the ovary wall (52), which may underlie the receptacle's competence in strawberry. Future comparative genomic analyses of closely related species with distinct fruit type may help uncover mechanisms and genes that contribute to the evolution of differential competence. For example, the genus *Potentilla* is very closely related to strawberry, with an estimated 24 million year divergence (5, 118). While they share similar floral characteristics, most *Potentilla* do not develop fleshy fruit (5). Large-scale differences in transposons between the genomes of *Potentilla micrantha* and *F. vesca* were reported (5); these differences could contribute to gene expression changes affecting fruit development.



(Caption appears on following page)

Figure 6 (*Figure appears on preceding page*)

Proposed hypothesis explaining floral organ-specific competence in developing into fleshy fruit. It illustrates, using peach as an example, carpel (ovary wall) as the competent organ. (*a*) In the ovule right before fertilization (*blue circle*), MADS-box repressive complexes and epigenetic regulators such as PRC2 repress auxin/GA biosynthetic genes. In the competent floral organ (carpel as an example here), the MADS-box complex (C + E) acts to specify fruit-forming competence by promoting the expression of auxin and GA receptors (❶) as well as F class MADS-box genes (❷). Photosynthesis in green organs also contributes to competence (❸). The floral organs that do not possess competence either are nonphotosynthetic (petal/stamen) or fail to express auxin/GA receptors or F class MADS-box genes (sepal as an example here). A, B, C, and E are different MADS-box proteins that form C + E, B + E, or A + E MADS-box complexes that regulate downstream gene expression. (*b*) Upon successful fertilization, the fertilized seed (*blue circle*) gains the ability to synthesize auxin/GA (*green dots*), which are then transported to all floral organs. However, only the competent organ (carpel as an example here) is expressing auxin/GA receptors and is able to remove repressive IAA/ARF/DELLA, allowing the activation of F class MADS-box genes that stimulate fruit development. Bold black font indicates active processes/genes, while gray font indicates inactive processes/genes. Abbreviations: ARF, auxin-response factor; GA, gibberellic acid; IAA, AUX/IAA repressor protein; PRC2, polycomb repressive complex 2.

GENOMIC RESOURCES FOR ROSACEAE

With the rapid progress in sequencing technologies, Rosaceae research is poised to enter a new era with the marked increase of available whole genome sequences (**Table 1**). In addition to comparative genomic studies, whole genome sequences are the foundation for designing various research platforms, including high-density genotyping tools and genome-wide association studies, to identify key genes, address biological questions, and improve fruit yield. A summary of genomic resources for Rosaceae follows.

The cultivated strawberry *Fragaria* × *ananassa* is an allo-octoploid. For the first time, a near-complete chromosome-scale assembly of the *F. ananassa* genome was recently published (22). A previous draft genome assembly for *F. ananassa* is also available (42). For the wild diploid strawberry *F. vesca*, four genome assemblies, including the newest v4.0 (23), help establish diploid strawberry *F. vesca* as a model for the cultivated strawberry and other Rosaceae species. Among these assemblies, the *F. vesca* genome v1.1 (96), v2.0 (100), and the recent v4.0 (23) received additional annotations: They are v1.1.a2 (16), v2.0.a2 (59), and v4.0.a2 (58), respectively (**Table 1**). The draft genome of *P. micrantha* (5), a species that does not develop fleshy fruit but is closely related to *Fragaria*, is also available (**Table 1**).

For *Malus*, whole genome data for apple include a de novo assembly of a Golden Delicious doubled haploid (GDDH13) (15) along with three versions of assembly for the heterozygous apple genome (107). Recently, an anther-derived homozygous line of apple, Hanfu, was used for a high-quality assembly (HFTH1) (129). For *Pyrus*, which is closely related to *Malus* and develops pome fruit, the whole genome sequences of the European pear *Pyrus communis* Bartlett double haploid genome v2.0 (61) and Chinese white pear *Pyrus bretschneideri* v1.1 genome (119) have recently become available following the initial whole genome sequencing of *P. bretschneideri* v1.0 (117) and *P. communis* v1.0 (9). Recently, genomes of 113 *Pyrus* accessions, including 63 Asian and 50 European pears, were sequenced and analyzed, providing abundant genomic data (116).

For *Prunus*, peach (*Prunus persica*) genome v1.0 (108) and v2.0 (109) have been serving as the reference genome for the other *Prunus* species. However, whole genome sequences of other *Prunus* are now becoming available, including whole genome assemblies of sweet cherry *Prunus avium* genome v1.0 (95); two almond genomes, *Prunus dulcis* Texas (1) and *Prunus dulcis* Lauranne (87); and apricot *Prunus armeniaca* (47). The draft genomes of hexaploid plum *Prunus domestica* v1.0 (6) and wild cherry *Prunus yedoensis var. nudiflora* genome v1.0 (3) are also available (see **Table 1**).

Allo-octoploid: indicates eight sets of chromosomes coming from parents of two or more species

Table 1 A list of Rosaceae species, ploidy, and genome sequencing paper/data

Species	Ploidy	Whole genome sequence	Whole genome sequence reference(s)
Fragaria vesca (wild strawberry)	$2n = 2x = 14$	*Fragaria vesca* genome v4.0 (v4.0.a1/v4.0.a2)	23, 58
		Fragaria vesca genome v2.0	100
		Fragaria vesca genome v1.1 (v1.1.a1 | v1.1.a2)	16, 96
		Fragaria vesca genome v1.0	96
Fragaria × *ananassa* (cultivated strawberry)	$2n = 8x = 56$	*Fragaria* × *ananassa* Camarosa genome v1.0	22
		Fragaria × *ananassa* genome v1.0 (FAN_r1.1)	42
		Fragaria × *ananassa* reference genome v1.0 (FANhybrid_r1.2)	42
Fragaria iinumae (wild strawberry)	$2n = 2x = 14$	*Fragaria iinumae* genome v1.0 (FII_r1.1)	42
Fragaria nipponica (wild strawberry)	$2n = 2x = 14$	*Fragaria nipponica* genome v1.0 (FNI_r1.1)	42
Fragaria nubicola (wild strawberry)	$2n = 2x = 14$	*Fragaria nubicola* genome v1.0 (FNU_r1.1)	42
Fragaria orientalis (wild strawberry)	$2n = 4x = 28$	*Fragaria orientalis* genome v1.0 (FOR_r1.1)	42
Malus × *domestica* (apple)	$2n = 2x = 34$	*Malus* × *domestica* HFTH1 genome v1.0	129
		Malus × *domestica* genome (GDDH13 v1.1)	15
		Malus × *domestica* v3.0.a1	107
		Malus × *domestica* v1.0	107
Prunus avium (sweet cherry)	$2n = 2x = 16$	*Prunus avium* genome v1.0.a1	95
Prunus domestica (plum)	$2n = 6x = 48$	*Prunus domestica* draft genome v1.0.a1	6
Prunus dulcis (almond)	$2n = 2x = 16$	*Prunus dulcis* Texas genome v2.0	1
		Prunus dulcis Lauranne genome v1.0	87
Prunus persica (peach)	$2n = 2x = 16$	*Prunus persica* genome v2.0.a1	109
		Prunus persica genome v1.0	108
Prunus yedoensis (Yoshino cherry)	$2n = 2x = 16$	*Prunus yedoensis* genome v1.0	3
Prunus armeniaca (apricot)	$2n = 2x = 16$	*Prunus armeniaca* genome v1.0	47
Potentilla micrantha (pink barren strawberry)	$2n = 2x = 14$	*Potentilla micrantha* v1.0	5
Pyrus communis (European pear)	$2n = 2x = 34$	*Pyrus communis* Bartlett DH genome v2.0	61
		Pyrus communis v1.0 draft genome	9
Pyrus bretschneideri (Chinese white pear)	$2n = 2x = 34$	*Pyrus bretschneideri* v1.1 genome	119
		Pyrus bretschneideri v1.0 genome	117

(*Continued*)

Table 1 (*Continued*)

Species	Ploidy	Whole genome sequence	Whole genome sequence reference(s)
Rosa multiflora (multiflora rose, baby rose, or Japanese rose)	$2n = 2x = 14$	*Rosa multiflora* genome v1.0	69
Rosa chinensis (China rose)	$2n = 2x = 14$	*Rosa chinensis* Old Blush homozygous genome v2.0	82
		Rosa chinensis homozygous genome v2.0	41
Rubus occidentalis (black raspberry)	$2n = 2x = 14$	*Rubus occidentalis* genome v1.0.a1	105
		Rubus occidentalis genome v1.1	48
		Rubus occidentalis genome v3.0	106
Rubus idaeus (red raspberry)	$2n = 2x = 14$	*Rubus idaeus* draft genome v1.0	115

Raspberry is appreciated for its high antioxidant and vitamin content in addition to its interesting fruit. The black raspberry (*Rubus occidentalis*) has a high-quality chromosome-scale genome assembly (106) that improves upon two previous versions, v1.1 (48) and v1.0 (105). The closely related red raspberry (*Rubus idaeus*) also has a draft genome (115).

Rose is the world's most important ornamental plant. Doubled haploid lines of *Rosa chinensis* Old Blush were used by two groups of researchers to assemble the rose genome (41, 82). Extensive synteny was found with the *F. vesca* genome even though rose and strawberry have evolved distinct fleshy fruits (**Figure 2*b***). A draft genome of a wild rose, *Rosa multiflora*, was also published (69).

The Genome Database for Rosaceae (GDR) is the central repository and data-mining resource for Rosaceae genomics, genetics, and breeding (51). In addition to hosting whole genome assemblies, GDR now provides a reference transcriptome (RefTrans) that combines published RNA-seq and expressed sequence tag data. Both the genes from the whole genome assemblies and the transcripts in RefTrans are annotated for homology to the genes of other plant species and the assignment of InterPro domains (68) and Gene Ontology terms (2, 33). The data can be accessed through the species page, gene/transcript search page, Jbrowse (4), and BLASTX (7). GDR also contains extensive marker, quantitative trait loci (QTL), and genetic maps and phenotypic and genotypic data for publicly available cultivars. In addition, recent genome assemblies in each species are used in synteny analysis using MCScanX (114) with the results available through the new Synteny Viewer. The synteny analysis along with functional annotation of gene models using sequence similarity enabled GDR to integrate data among species. The alignment of transcripts and markers, used in genotyping and QTL mapping, to the whole genome sequences, allows scientists to utilize data from different types, species, and disciplines. Some of the Rosaceae whole genome sequence data are also available from three primary sequence databases: GenBank (88), European Nucleotide Archive (39), and the DNA Data Bank of Japan (54). Some of the comparative genomics resources also have whole genome data for a limited number of Rosaceae species. This includes Phytozome (37), CoGe (Comparative Genomics) (62), and Plaza (103) (**Table 2**). There are also project databases where the whole genome data are available, such as The Apple Genome and Epigenome, The Pear Genome Project, the Institute of Applied Genomics, and Strawberry Genome Resources (**Table 2**).

Table 2 A list of websites with genomic resources for Rosaceae

Type	Name	URL	Reference
Community database	Genome Database for Rosaceae (GDR)	**https://www.rosaceae.org/**	51
Primary databases	GenBank	**http://www.ncbi.nlm.nih.gov/genbank/**	88
	European Nucleotide Archive (ENA)	**http://www.ebi.ac.uk/ena/**	39
	DNA Data Bank of Japan (DDBJ)	**http://www.ddbj.nig.ac.jp/**	54
Comparative genomics databases	Phytozome	**http://www.phytozome.net**	37
	CoGe (Comparative Genomics)	**https://genomevolution.org**	62
	Plaza	**https://bioinformatics.psb.ugent.be/plaza**	103
Project databases	The Apple Genome and Epigenome	**https://iris.angers.inra.fr/gddh13/**	N/A
	The Pear Genome Project	**http://peargenome.njau.edu.cn/**	N/A
	Institute of Applied Genomics (IGA)	**http://services.appliedgenomics.org/projects/prunus_persica_v2/prunus_persica_v2/intro/index.html**	N/A
	Strawberry Genome Resources (SGR)	**http://bioinformatics.towson.edu/strawberry/**	17, 40

Abbreviation: N/A, not available.

SUMMARY POINTS

1. Rosaceae exhibits diverse fruit types and is an excellent plant family for investigating the evolutionary mechanisms that shaped them.
2. Nuclear gene-based phylogeny of Rosaceae and ancestral fruit-type reconstruction support separate (independent) origins and evolution paths of multiple fleshy fruit types from dry fruit types.
3. Whole genome duplication (WGD) and resulting MADS-box gene duplication may underlie the evolution of pome and drupe fruits.
4. Parthenocarpic Rosaceae fruits can be induced if fertilization signals, auxin, gibberellic acid (GA), or cytokinin is provided through transgenes or exogenous sprays.
5. Different floral organs might have different abilities or competencies to develop into fruits upon exposures to hormonal signals. This competence is likely tied to floral organ identity.
6. MADS-box genes likely encode key regulators of fruit identity and development.
7. Abundant genomic resources in the Rosaceae family provide important tools for comparative studies of fruit development, evolution, and breeding.

FUTURE ISSUES

1. Genomic resources, including genome sequencing and carefully staged and dissected tissue RNA-sequencing, are needed for many more Rosaceae species, facilitating comparative analyses of closely related species with distinct fruit characteristics.

2. Tools for functional studies, including methods of facile transformation and CRISPR/Cas9, should be developed for additional Rosaceae species.
3. Robust and reliable bioinformatic methods of assigning orthologs and comparative transcriptome/network analysis tools across related species are needed.
4. Identification of key genes such as fruit identity genes and mechanisms of fruit-type evolution will enable the manipulation of genes to increase fruit yield, the creation of new fruit types, and the de novo domestication of wild Rosaceae species.
5. Breakthroughs in this field will require close collaborations among developmental biologists, molecular biologists, evolutionary biologists, ecologists, bioinformaticians, and breeders.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We apologize to colleagues whose work was not included due to space limitations. We thank Dirk Joldersma for his comments. The research of Z.L. is supported by the National Science Foundation (IOS 1444987) and the Maryland Agricultural Experiment Station Hatch Project (MD-CBMG-8881), and the research of D.M. is supported by the US Department of Agriculture (USDA) Specialty Crop Research Initiative (SCRI) and the USDA National Institute of Food and Agriculture National Research Support Project 10 (NRSP10).

LITERATURE CITED

1. Alioto T, Alexiou KG, Bardil A, Barteri F, Castanera R, et al. 2019. Transposons played a major role in the diversification between the closely related almond and peach genomes: results from the almond genome sequence. *Plant J.* 101(2):455–72
2. Ashburner M, Ball CA, Blake JA, Botstein D, Butler H, et al. 2000. Gene ontology: tool for the unification of biology. *Nat. Genet.* 25(1):25–29
3. Baek S, Choi K, Kim G-B, Yu H-J, Cho A, et al. 2018. Draft genome sequence of wild *Prunus yedoensis* reveals massive inter-specific hybridization between sympatric flowering cherries. *Genome Biol.* 19(1):127
4. Buels R, Yao E, Diesh CM, Hayes RD, Munoz-Torres M, et al. 2016. JBrowse: a dynamic web platform for genome visualization and analysis. *Genome Biol.* 17:66
5. Buti M, Moretto M, Barghini E, Mascagni F, Natali L, et al. 2018. The genome sequence and transcriptome of *Potentilla micrantha* and their comparison to *Fragaria vesca* (the woodland strawberry). *Gigascience* 7(4):giy010
6. Callahan A, Zhebentyayeva T, Humann J, Saski C, Galimba K, et al. 2020. Defining the 'HoneySweet' insertion event utilizing NextGen sequencing and a de novo genome assembly of plum (*Prunus domestica*). *Hortic. Res.* In press
7. Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, et al. 2009. BLAST+: architecture and applications. *BMC Bioinform.* 10:421
8. Carrera E, Ruiz-Rivero O, Peres LEP, Atares A, Garcia-Martinez JL. 2012. Characterization of the *procera* tomato mutant shows novel functions of the SlDELLA protein in the control of flower morphology, cell division and expansion, and the auxin-signaling pathway during fruit-set and development. *Plant Physiol.* 160(3):1581–96

9. Chagné D, Crowhurst RN, Pindo M, Thrimawithana A, Deng C, et al. 2014. The draft genome sequence of European pear (*Pyrus communis* L. 'Bartlett'). *PLOS ONE* 9(4):e92644
10. Chaudhury AM, Ming L, Miller C, Craig S, Dennis ES, Peacock WJ. 1997. Fertilization-independent seed development in *Arabidopsis thaliana*. *PNAS* 94(8):4223–28
11. Chen X. 2004. A microRNA as a translational repressor of *APETALA2* in *Arabidopsis* flower development. *Science* 303(5666):2022–25
12. Cong L, Yue R, Wang H, Liu J, Zhai R, et al. 2019. 2,4-D-induced parthenocarpy in pear is mediated by enhancement of GA_4 biosynthesis. *Physiol. Plant.* 166(3):812–20
13. Coombe BG. 1960. Relationship of growth and development to changes in sugars, auxins, and gibberellins in fruit of seeded and seedless varieties of Vitis vinifera. *Plant Physiol.* 35(2):241–50
14. Crane JC, Primer PE, Campbell RC. 1960. Gibberellin induced parthenocarpy in *Prunus*. *Proc. Am. Soc. Hortic. Sci.* 75:129–37
15. Daccord N, Celton J-M, Linsmith G, Becker C, Choisne N, et al. 2017. High-quality *de novo* assembly of the apple genome and methylome dynamics of early fruit development. *Nat. Genet.* 49(7):1099–106
16. Darwish O, Shahan R, Liu Z, Slovin JP, Alkharouf NW. 2015. Re-annotation of the woodland strawberry (*Fragaria vesca*) genome. *BMC Genom.* 16:29
17. Darwish O, Slovin JP, Kang C, Hollender CA, Geretz A, et al. 2013. SGR: an online genomic resource for the woodland strawberry. *BMC Plant Biol.* 13:223
18. de Jong M, Wolters-Arts M, Feron R, Mariani C, Vriezen WH. 2009. The *Solanum lycopersicum* auxin response factor 7 (*Sl*ARF7) regulates auxin signaling during tomato fruit set and development. *Plant J.* 57(1):160–70
19. Dinneny JR, Weigel D, Yanofsky MF. 2005. A genetic framework for fruit patterning in *Arabidopsis thaliana*. *Development* 132(21):4687–96
20. Dreni L, Zhang D. 2016. Flower development: the evolutionary history and functions of the *AGL6* subfamily MADS-box genes. *J. Exp. Bot.* 67(6):1625–38
21. Drews GN, Bowman JL, Meyerowitz EM. 1991. Negative regulation of the Arabidopsis homeotic gene *AGAMOUS* by the *APETALA2* product. *Cell* 65(6):991–1002
22. Edger PP, Poorten TJ, VanBuren R, Hardigan MA, Colle M, et al. 2019. Origin and evolution of the octoploid strawberry genome. *Nat. Genet.* 51(3):541–47
23. Edger PP, VanBuren R, Colle M, Poorten TJ, Wai CM, et al. 2018. Single-molecule sequencing and optical mapping yields an improved genome of woodland strawberry (*Fragaria vesca*) with chromosome-scale contiguity. *Gigascience* 7(2):gix124
24. El-Sharkawy I, Sherif S, El Kayal W, Jones B, Li Z, et al. 2016. Overexpression of plum auxin receptor *PslTIR1* in tomato alters plant growth, fruit development and fruit shelf-life characteristics. *BMC Plant Biol.* 16:56
25. Feng J, Dai C, Luo H, Han Y, Liu Z, Kang C. 2019. Reporter gene expression reveals precise auxin synthesis sites during fruit and root development in wild strawberry. *J. Exp. Bot.* 70(2):563–74
26. Fernandez L, Chaïb J, Martinez-Zapater J-M, Thomas MR, Torregrosa L. 2013. Mis-expression of a *PISTILLATA*-like MADS box gene prevents fruit development in grapevine. *Plant J.* 73(6):918–28
27. Fernandez-Pozo N, Zheng Y, Snyder SI, Nicolas P, Shinozaki Y, et al. 2017. The Tomato Expression Atlas. *Bioinformatics* 33(15):2397–98
28. Ferrandiz C. 2011. Fruit structure and diversity. In *eLS*. **https://doi.org/10.1002/9780470015902.a0002044.pub2**
29. Figueiredo DD, Batista RA, Roszak PJ, Hennig L, Köhler C. 2016. Auxin production in the endosperm drives seed coat development in *Arabidopsis*. *eLife* 5:e20542
30. Fuentes S, Ljung K, Sorefan K, Alvey E, Harberd NP, Østergaard L. 2012. Fruit growth in *Arabidopsis* occurs via DELLA-dependent and DELLA-independent gibberellin responses. *Plant Cell* 24(10):3982–96
31. Galimba KD, Bullock DG, Dardick C, Liu Z, Callahan AM. 2019. Gibberellic acid induced parthenocarpic "Honeycrisp" apples (*Malus domestica*) exhibit reduced ovary width and lower acidity. *Hortic. Res.* 6:41

32. García-Hurtado N, Carrera E, Ruiz-Rivero O, López-Gresa MP, Hedden P, et al. 2012. The characterization of transgenic tomato overexpressing *gibberellin 20-oxidase* reveals induction of parthenocarpic fruit growth, higher yield, and alteration of the gibberellin biosynthetic pathway. *J. Exp. Bot.* 63(16):5803–13
33. Gene Ontol. Consort.. 2019. The Gene Ontology Resource: 20 years and still GOing strong. *Nucleic Acids Res*. 47(D1):D330–38
34. Gillaspy G, Ben-David H, Gruissem W. 1993. Fruits: a developmental perspective. *Plant Cell* 5(10):1439–51
35. Goetz M, Hooper LC, Johnson SD, Rodrigues JCM, Vivian-Smith A, Koltunow AM. 2007. Expression of aberrant forms of *AUXIN RESPONSE FACTOR8* stimulates parthenocarpy in Arabidopsis and tomato. *Plant Physiol*. 145(2):351–66
36. Goetz M, Vivian-Smith A, Johnson SD, Koltunow AM. 2006. *AUXIN RESPONSE FACTOR8* is a negative regulator of fruit initiation in *Arabidopsis. Plant Cell* 18(8):1873–86
37. Goodstein DM, Shu S, Howson R, Neupane R, Hayes RD, et al. 2012. Phytozome: a comparative platform for green plant genomics. *Nucleic Acids Res*. 40(D1):D1178–86
38. Grossniklaus U, Vielle-Calzada JP, Hoeppner MA, Gagliano WB. 1998. Maternal control of embryogenesis by *MEDEA*, a *Polycomb* group gene in *Arabidopsis. Science* 280(5362):446–50
39. Harrison PW, Alako B, Amid C, Cerdeño-Tárraga A, Cleland I, et al. 2019. The European Nucleotide Archive in 2018. *Nucleic Acids Res*. 47(D1):D84–88
40. Hawkins C, Caruana J, Li J, Zawora C, Darwish O, et al. 2017. An eFP browser for visualizing strawberry fruit and flower transcriptomes. *Hortic. Res.* 4:17029
41. Hibrand Saint-Oyant L, Ruttink T, Hamama L, Kirov I, Lakhwani D, et al. 2018. A high-quality genome sequence of *Rosa chinensis* to elucidate ornamental traits. *Nat. Plants* 4(7):473–84
42. Hirakawa H, Shirasawa K, Kosugi S, Tashiro K, Nakayama S, et al. 2014. Dissection of the octoploid strawberry genome by deep sequencing of the genomes of *Fragaria* species. *DNA Res*. 21(2):169–81
43. Huang C-H, Sun R, Hu Y, Zeng L, Zhang N, et al. 2016. Resolution of Brassicaceae phylogeny using nuclear genes uncovers nested radiations and supports convergent morphological evolution. *Mol. Biol. Evol.* 33(2):394–412
44. Hummer KE, Janick J. 2009. Rosaceae: taxonomy, economic importance, genomics. In *Genetics and Genomics of Rosaceae*, ed. KM Folta, SE Gardiner, pp. 1–17. New York: Springer
45. Ireland HS, Yao J-L, Tomes S, Sutherland PW, Nieuwenhuizen N, et al. 2013. Apple *SEPALLATA1/2*-like genes control fruit flesh development and ripening. *Plant J.* 73(6):1044–56
46. Janssen BJ, Thodey K, Schaffer RJ, Alba R, Balakrishnan L, et al. 2008. Global gene expression analysis of apple fruit development from the floral bud to ripe fruit. *BMC Plant Biol*. 8(1):16
47. Jiang F, Zhang J, Wang S, Yang L, Luo Y, et al. 2019. The apricot (*Prunus armeniaca* L.) genome elucidates Rosaceae evolution and beta-carotenoid synthesis. *Hortic. Res.* 6:128
48. Jibran R, Dzierzon H, Bassil N, Bushakra JM, Edger PP, et al. 2018. Chromosome-scale scaffolding of the black raspberry (*Rubus occidentalis* L.) genome based on chromatin interaction data. *Hortic. Res.* 5:8
49. Jofuku KD, den Boer BGW, Van Montagu M, Okamuro JK. 1994. Control of Arabidopsis flower and seed development by the homeotic gene *APETALA2. Plant Cell* 6(9):1211–25
50. Joldersma D, Liu Z. 2018. The making of virgin fruit: the molecular and genetic basis of parthenocarpy. *J. Exp. Bot.* 69(5):955–62
51. Jung S, Lee T, Cheng C-H, Buble K, Zheng P, et al. 2019. 15 years of GDR: new data and functionality in the Genome Database for Rosaceae. *Nucleic Acids Res*. 47(D1):D1137–45
52. Kang C, Darwish O, Geretz A, Shahan R, Alkharouf N, Liu Z. 2013. Genome-scale transcriptomic insights into early-stage fruit development in woodland strawberry *Fragaria vesca*. *Plant Cell* 25(6):1960–78
53. Klap C, Yeshayahou E, Bolger AM, Arazi T, Gupta SK, et al. 2017. Tomato facultative parthenocarpy results from Sl*AGAMOUS-LIKE 6* loss of function. *Plant Biotechnol. J.* 15(5):634–47
54. Kodama Y, Mashima J, Kosuge T, Kaminuma E, Ogasawara O, et al. 2018. DNA Data Bank of Japan: 30th anniversary. *Nucleic Acids Res*. 46(D1):D30–35
55. Köhler C, Hennig L, Bouveret R, Gheyselinck J, Grossniklaus U, Gruissem W. 2003. *Arabidopsis* MSI1 is a component of the MEA/FIE *Polycomb* group complex and required for seed development. *EMBO J.* 22(18):4804–14

56. Li H, Huang C-H, Ma H. 2019. Whole-genome duplications in pear and apple. In *The Pear Genome*, ed. SS Korban, pp. 279–99. Cham, Switz.: Springer
57. Li T, Yang X, Yu Y, Si X, Zhai X, et al. 2018. Domestication of wild tomato is accelerated by genome editing. *Nat. Biotechnol.* 36:1160–63
58. Li Y, Pi M, Gao Q, Liu Z, Kang C. 2019. Updated annotation of the wild strawberry *Fragaria vesca* V4 genome. *Hortic. Res.* 6(1):61
59. Li Y, Wei W, Feng J, Luo H, Pi M, et al. 2017. Genome re-annotation of the wild strawberry *Fragaria vesca* using extensive Illumina- and SMRT-based RNA-seq datasets. *DNA Res.* 25(1):61–70
60. Liao X, Li M, Liu B, Yan M, Yu X, et al. 2018. Interlinked regulatory loops of ABA catabolism and biosynthesis coordinate fruit growth and ripening in woodland strawberry. *PNAS* 115(49):E11542–50
61. Linsmith G, Rombauts S, Montanari S, Deng CH, Celton J-M, et al. 2019. Pseudo-chromosome length genome assembly of a double haploid 'Bartlett' pear (*Pyrus communis* L.). bioRxiv 651778. **https://doi.org/10.1101/651778**
62. Lyons E, Freeling M. 2008. How to usefully compare homologous plant genes and chromosomes as DNA sequences. *Plant J.* 53(4):661–73
63. Mara CD, Irish VF. 2008. Two GATA transcription factors are downstream effectors of floral homeotic gene action in Arabidopsis. *Plant Physiol.* 147(2):707–18
64. Martí C, Orzáez D, Ellul P, Moreno V, Carbonell J, Granell A. 2007. Silencing of *DELLA* induces facultative parthenocarpy in tomato fruits. *Plant J.* 52(5):865–76
65. Masiero S, Li M-A, Will I, Hartmann U, Saedler H, et al. 2004. *INCOMPOSITA*: a MADS-box gene controlling prophyll development and floral meristem identity in *Antirrhinum*. *Development* 131(23):5981–90
66. Mesejo C, Reig C, Martínez-Fuentes A, Agustí M. 2010. Parthenocarpic fruit production in loquat (*Eriobotrya japonica* Lindl.) by using gibberellic acid. *Sci. Hortic.* 126(1):37–41
67. Mezzetti B, Landi L, Pandolfini T, Spena A. 2004. The *defH9-iaaM* auxin-synthesizing gene increases plant fecundity and fruit production in strawberry and raspberry. *BMC Biotechnol.* 4:4
68. Mitchell AL, Attwood TK, Babbitt PC, Blum M, Bork P, et al. 2019. InterPro in 2019: improving coverage, classification and access to protein sequence annotations. *Nucleic Acids Res.* 47(D1):D351–60
69. Nakamura N, Hirakawa H, Sato S, Otagaki S, Matsumoto S, et al. 2018. Genome structure of *Rosa multiflora*, a wild ancestor of cultivated roses. *DNA Res.* 25(2):113–21
70. Ng M, Yanofsky MF. 2001. Function and evolution of the plant MADS-box gene family. *Nat. Rev. Genet.* 2(3):186–95
71. Nitsch JP. 1950. Growth and morphogenesis of the strawberry as related to auxin. *Am. J. Bot.* 37(3):211–15
72. Nitsch JP. 1955. Free auxins and free tryptophane in the strawberry. *Plant Physiol.* 30(1):33–39
73. Niu Q, Wang T, Li J, Yang Q, Qian M, Teng Y. 2015. Effects of exogenous application of GA_{4+7} and N-(2-chloro-4-pyridyl)-*N′*-phenylurea on induced parthenocarpy and fruit quality in *Pyrus pyrifolia* 'Cuiguan.' *Plant Growth Regul.* 76(3):251–58
74. Ohad N, Margossian L, Hsu YC, Williams C, Repetti P, Fischer RL. 1996. A mutation that allows endosperm development without fertilization. *PNAS* 93(11):5319–24
75. Pan IL, McQuinn R, Giovannoni JJ, Irish VF. 2010. Functional diversification of *AGAMOUS* lineage genes in regulating tomato flower and fruit development. *J. Exp. Bot.* 61(6):1795–806
76. Parenicová L, de Folter S, Kieffer M, Horner DS, Favalli C, et al. 2003. Molecular and phylogenetic analyses of the complete MADS-box transcription factor family in Arabidopsis: new openings to the MADS world. *Plant Cell* 15(7):1538–51
77. Pattison RJ, Csukasi F, Zheng Y, Fei Z, van der Knaap E, Catalá C. 2015. Comprehensive tissue-specific transcriptome analysis reveals distinct regulatory programs during early tomato fruit development. *Plant Physiol.* 168(4):1684–701
78. Pineda B, Giménez-Caminero E, García-Sogo B, Antón MT, Atarés A, et al. 2010. Genetic and physiological characterization of the *Arlequin* insertional mutant reveals a key regulator of reproductive development in tomato. *Plant Cell Physiol.* 51(3):435–47

79. Potter D, Eriksson T, Evans RC, Oh S, Smedmark JEE, et al. 2007. Phylogeny and classification of Rosaceae. *Plant Syst. Evol.* 266(1–2):5–43
80. Pratt C. 1988. Apple flower and fruit: morphology and anatomy. In *Horticultural Reviews*, Vol. 10, ed. J Janick, pp. 273–308. New York: Wiley
81. Prosser MV, Jackson GAD. 1959. Induction of parthenocarpy in *Rosa arvensis* Huds. with gibberellic acid. *Nature* 184(4680):108
82. Raymond O, Gouzy J, Just J, Badouin H, Verdenaud M, et al. 2018. The *Rosa* genome provides new insights into the domestication of modern roses. *Nat. Genet.* 50(6):772–77
83. Ren Z, Li Z, Miao Q, Yang Y, Deng W, Hao Y. 2011. The auxin receptor homologue in *Solanum lycopersicum* stimulates tomato fruit set and leaf morphogenesis. *J. Exp. Bot.* 62(8):2815–26
84. Rodríguez GR, Muños S, Anderson C, Sim S-C, Michel A, et al. 2011. Distribution of *SUN*, *OVATE*, *LC*, and *FAS* in the tomato germplasm and the relationship to fruit shape diversity. *Plant Physiol.* 156(1):275–85
85. Roszak P, Köhler C. 2011. Polycomb group proteins are required to couple seed coat initiation to fertilization. *PNAS* 108(51):20826–31
86. Ruan Y-L, Patrick JW, Bouzayen M, Osorio S, Fernie AR. 2012. Molecular regulation of seed and fruit set. *Trends Plant Sci.* 17(11):656–65
87. Sánchez-Pérez R, Pavan S, Mazzeo R, Moldovan C, Aiese Cigliano R, et al. 2019. Mutation of a bHLH transcription factor allowed almond domestication. *Science* 364(6445):1095–98
88. Sayers EW, Cavanaugh M, Clark K, Ostell J, Pruitt KD, Karsch-Mizrachi I. 2019. GenBank. *Nucleic Acids Res.* 47(D1):D94–99
89. Schultz JC, Edger PP, Body MJA, Appel HM. 2019. A galling insect activates plant reproductive programs during gall development. *Sci Rep.* 9(1):1833
90. Schulze-Menz GK. 1964. Rosaceae. *Engler's Syllabus der Pflanzenfamilien*, Vol. 2, ed. H Melchior, pp. 209–18. Berlin: Gerbrüder Borntraeger
91. Serrani JC, Ruiz-Rivero O, Fos M, García-Martínez JL. 2008. Auxin-induced fruit-set in tomato is mediated in part by gibberellins. *Plant J.* 56(6):922–34
92. Seymour GB, Ryder CD, Cevik V, Hammond JP, Popovich A, et al. 2011. A *SEPALLATA* gene is involved in the development and ripening of strawberry (*Fragaria* × *ananassa* Duch.) fruit, a non-climacteric tissue. *J. Exp. Bot.* 62(3):1179–88
93. Shahan R, Zawora C, Wight H, Sittmann J, Wang W, et al. 2018. Consensus coexpression network analysis identifies key regulators of flower and fruit development in wild strawberry. *Plant Physiol.* 178(1):202–16
94. Shinozaki Y, Nicolas P, Fernandez-Pozo N, Ma Q, Evanich DJ, et al. 2018. High-resolution spatiotemporal transcriptome mapping of tomato fruit development and ripening. *Nat. Commun.* 9(1):364
95. Shirasawa K, Isuzugawa K, Ikenaga M, Saito Y, Yamamoto T, et al. 2017. The genome sequence of sweet cherry (*Prunus avium*) for use in genomics-assisted breeding. *DNA Res.* 24(5):499–508
96. Shulaev V, Sargent DJ, Crowhurst RN, Mockler TC, Folkerts O, et al. 2011. The genome of woodland strawberry (*Fragaria vesca*). *Nat. Genet.* 43(2):109–16
97. Sjut V, Bangerth F. 1982. Induced parthenocarpy—a way of changing the levels of endogenous hormones in tomato fruits (*Lycopersicon esculentum* Mill.) 1. Extractable hormones. *Plant Growth Regul.* 1(4):243–51
98. Soltis PS, Soltis DE. 2016. Ancient WGD events as drivers of key innovations in angiosperms. *Curr. Opin. Plant Biol.* 30:159–65
99. Sun T-P. 2010. Gibberellin-GID1-DELLA: a pivotal regulatory module for plant growth and development. *Plant Physiol.* 154(2):567–70
100. Tennessen JA, Govindarajulu R, Ashman T-L, Liston A. 2014. Evolutionary origins and dynamics of octoploid strawberry subgenomes revealed by dense targeted capture linkage maps. *Genome Biol Evol.* 6(12):3295–313
101. Theißen G, Melzer R, Rümpler F. 2016. MADS-domain transcription factors and the floral quartet model of flower development: linking plant development and evolution. *Development* 143(18):3259–71
102. Thompson PA. 1969. The effect of applied growth substances on development of the strawberry fruit. II. Interactions of auxins and gibberellins. *J. Exp. Bot.* 20(3):629–47

103. Van Bel M, Diels T, Vancaester E, Kreft L, Botzki A, et al. 2018. PLAZA 4.0: an integrative resource for functional, evolutionary and comparative plant genomics. *Nucleic Acids Res*. 46(D1):D1190–96
104. Van de Peer Y, Maere S, Meyer A. 2009. The evolutionary significance of ancient genome duplications. *Nat. Rev. Genet.* 10(10):725–32
105. VanBuren R, Bryant D, Bushakra JM, Vining KJ, Edger PP, et al. 2016. The genome of black raspberry (*Rubus occidentalis*). *Plant J*. 87(6):535–47
106. VanBuren R, Wai CM, Colle M, Wang J, Sullivan S, et al. 2018. A near complete, chromosome-scale assembly of the black raspberry (*Rubus occidentalis*) genome. *Gigascience* 7(8):giy094
107. Velasco R, Zharkikh A, Affourtit J, Dhingra A, Cestaro A, et al. 2010. The genome of the domesticated apple (*Malus* × *domestica* Borkh.). *Nat. Genet.* 42(10):833–39
108. Verde I, Abbott AG, Scalabrin S, Jung S, Shu S, et al. 2013. The high-quality draft genome of peach (*Prunus persica*) identifies unique patterns of genetic diversity, domestication and genome evolution. *Nat. Genet.* 45(5):487–94
109. Verde I, Jenkins J, Dondini L, Micali S, Pagliarani G, et al. 2017. The Peach v2.0 release: High-resolution linkage mapping and deep resequencing improve chromosome-scale assembly and contiguity. *BMC Genom*. 18(1):225
110. Vivian-Smith A, Koltunow AM. 1999. Genetic analysis of growth-regulator-induced parthenocarpy in Arabidopsis. *Plant Physiol*. 121(2):437–51
111. Vivian-Smith A, Luo M, Chaudhury A, Koltunow A. 2001. Fruit development is actively restricted in the absence of fertilization in *Arabidopsis*. *Development* 128(12):2321–31
112. Wang H, Jones B, Li Z, Frasse P, Delalande C, et al. 2005. The tomato *Aux/IAA* transcription factor *IAA9* is involved in fruit development and leaf morphogenesis. *Plant Cell* 17(10):2676–92
113. Wang H, Schauer N, Usadel B, Frasse P, Zouine M, et al. 2009. Regulatory features underlying pollination-dependent and -independent tomato fruit set revealed by transcript and primary metabolite profiling. *Plant Cell* 21(5):1428–52
114. Wang Y, Tang H, Debarry JD, Tan X, Li J, et al. 2012. MCScanX: a toolkit for detection and evolutionary analysis of gene synteny and collinearity. *Nucleic Acids Res*. 40(7):e49
115. Wight H, Zhou J, Li M, Hannenhalli S, Mount S, Liu Z. 2019. Draft genome assembly and annotation of red raspberry *Rubus idaeus*. bioRxiv 546135. **https://doi.org/10.1101/546135**
116. Wu J, Wang Y, Xu J, Korban SS, Fei Z, et al. 2018. Diversification and independent domestication of Asian and European pears. *Genome Biol*. 19(1):77
117. Wu J, Wang Z, Shi Z, Zhang S, Ming R, et al. 2013. The genome of the pear (*Pyrus bretschneideri* Rehd.). *Genome Res*. 23(2):396–408
118. Xiang Y, Huang C-H, Hu Y, Wen J, Li S, et al. 2017. Evolution of Rosaceae fruit types based on nuclear phylogeny in the context of geological times and genome duplication. *Mol. Biol. Evol.* 34(2):262–81
119. Xue H, Wang S, Yao J-L, Deng CH, Wang L, et al. 2018. Chromosome level high-density integrated genetic maps improve the *Pyrus bretschneideri* "DangshanSuli" v1.0 genome. *BMC Genom*. 19(1):833
120. Yang Y, Moore MJ, Brockington SF, Soltis DE, Wong GK-S, et al. 2015. Dissecting molecular evolution in the highly diverse plant clade Caryophyllales using transcriptome sequencing. *Mol. Biol. Evol.* 32(8):2001–14
121. Yant L, Mathieu J, Dinh TT, Ott F, Lanz C, et al. 2010. Orchestration of the floral transition and floral development in *Arabidopsis* by the bifunctional transcription factor APETALA2. *Plant Cell* 22(7):2156–70
122. Yao J-L, Dong Y-H, Kvarnheden A, Morris B. 1999. Seven MADS-box genes in apple are expressed in different parts of the fruit. *J. Am. Soc. Hortic. Sci.* 124(1):8–13
123. Yao J-L, Dong Y-H, Morris BAM. 2001. Parthenocarpic apple fruit production conferred by transposon insertion mutations in a MADS-box transcription factor. *PNAS* 98(3):1306–11
124. Yao J-L, Tomes S, Xu J, Gleave AP. 2016. How microRNA172 affects fruit growth in different species is dependent on fruit type. *Plant Signal Behav*. 11(4):e1156833
125. Yao J-L, Xu J, Cornille A, Tomes S, Karunairetnam S, et al. 2015. A microRNA allele that emerged prior to apple domestication may underlie fruit size evolution. *Plant J*. 84(2):417–27
126. Yao J-L, Xu J, Tomes S, Cui W, Luo Z, et al. 2018. Ectopic expression of the *PISTILLATA* homologous *MdPI* inhibits fruit tissue growth and changes fruit shape in apple. *Plant Direct* 2(4):e00051

127. Zeng L, Zhang N, Zhang Q, Endress PK, Huang J, Ma H. 2017. Resolution of deep eudicot phylogeny and their temporal diversification using nuclear genes from transcriptomic and genomic datasets. *New Phytol.* 214(3):1338–54
128. Zeng L, Zhang Q, Sun R, Kong H, Zhang N, Ma H. 2014. Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. *Nat. Commun.* 5:4956
129. Zhang L, Hu J, Han X, Li J, Gao Y, et al. 2019. A high-quality apple genome assembly reveals the association of a retrotransposon and red fruit colour. *Nat. Commun.* 10(1):1494
130. Zsögön A, Čermák T, Naves ER, Notini MM, Edel KH, et al. 2018. *De novo* domestication of wild tomato using genome editing. *Nat. Biotechnol.* 36:1211–16