CHAPTER THREE

To Have and to Hold: Selection for Seed and Fruit Retention During Crop Domestication

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Contents

Abstract

Crop domestication provides a useful model system to characterize the molecular and developmental bases of morphological variation in plants. Among the most universal changes resulting from selection during crop domestication is the loss of seed and fruit dispersal mechanisms, which greatly facilitates harvesting efficiency. In this review, we consider the molecular genetic and developmental bases of the loss of seed shattering and fruit dispersal in six major crop plant families, three of which are primarily associated with seed crops (Poaceae, Brassicaceae, Fabaceae) and three of which are associated with fleshy-fruited crops (Solanaceae, Rosaceae, Rutaceae). We find that the developmental basis of the loss of seed/fruit dispersal is conserved in a number of independently domesticated crops, indicating the widespread occurrence of developmentally convergent evolution in response to human selection. With regard to the molecular genetic approaches used to characterize the basis of this trait, traditional biparental quantitative trait loci mapping remains the most commonly used strategy; however, recent advances in next-generation sequencing technologies are now providing new avenues to map and characterize loss of shattering/dispersal alleles. We

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anticipate that continued application of these approaches, together with candidate gene analyses informed by known shattering candidate genes from other crops, will lead to a rapid expansion of our understanding of this critical domestication trait.

1. INTRODUCTION

Plant domestication is a complex evolutionary process in which human selection acts on morphological and physiological traits, resulting in phenotypic changes that distinguish domesticated species from their wild progenitors (Diamond, 2002; Hancock, 2005; Purugganan & Fuller, 2009). Domesticated plants have provided outstanding systems for the study of evolutionary processes due to the well-defined time frame in which domestication has occurred (largely within the last 10,000 years) and, for at least some species, clear archeological and historical evidence on their dispersal and varietal diversification history (Gross & Olsen, 2010; Meyer & Purugganan, 2013). Domesticated plants typically possess a suite of traits that distinguish them from their wild progenitors and collectively comprise the "domestication syndrome" (Hammer, 1984; Harlan, 1971; Harlan & De Wet, 1972). Depending on the particular crop species, these traits may include the loss of seed dormancy, shifts to determinate growth and apical dominance, reduction in physical and chemical defenses, mating system shifts toward self-fertilization and/or asexual reproduction, synchronization of flowering time, enlargement of reproductive organs (seeds or fruits), and loss of seed or fruit dispersal mechanisms (Doebley, Gaut, & Smith, 2006; Hammer, 1984; Meyer & Purugganan, 2013; Olsen & Wendel, 2013).

Of these different domestication traits, the loss of seed and fruit dispersal mechanisms is one of the most characteristic features of the domestication process. While seed dispersal is adaptive in most wild species, retention of mature seeds or fruit on a cultivated plant allows for the plant's entire yield to be harvested at once (for example, through reaping of grain stalks by sickle), with minimal loss and spoilage from dropped seed or fruit (Estornell, Agustí, Merelo, Talón, & Tadeo, 2013). Not only does this change vastly increase harvesting efficiency, but it also renders domesticated plants primarily dependent on humans for survival and propagation, thereby marking a critical transition between wild and domesticated species. Consistent with the importance of seed/fruit retention in domestication, both genetic and archeological studies have documented evidence for the repeated, convergent evolution of this trait in diverse crops worldwide

(Fuller et al., 2014; Lenser & Theißen, 2013; Meyer, DuVal, & Jensen, 2012; Meyer & Purugganan, 2013). Among seed crops, where loss of seed dispersal is commonly referred to as a loss of shattering, this phenomenon has been best documented in the cereals (Poaceae), legumes (Fabaceae), and mustard family (Brassicaceae). In the case of fleshy-fruited crops, less is known overall about the genetic and developmental bases of fruit retention, but some insights have been gained for species of the Rosaceae (eg, pomes and stone fruits), Solanaceae (eg, chilies, tomato, and eggplant), and Rutaceae (citrus crops). Domesticated species within these six families are the focus of our review.

For cereal crops in particular, archeological and genetic data have together provided a wealth of insights into the approximate timing and locations for the emergence of nonshattering phenotypes in several important cereal crops. While there is variation in the geographical locations and timing of these domestication events, most nonshattering or reduced-shattering alleles in cereals appear to have been fixed prior to 4000 years ago (YA) (Meyer et al., 2012) (Fig. 1). In East Asia, for example, the nonshattering phenotype is estimated to have emerged in Asian rice (*Oryza sativa*) about 6600–6900 YA (Fuller, Allaby, & Stevens, 2010; Fuller et al., 2009). The fixation of nonshattering alleles in einkorn wheat (*Triticum monococcum*) and barley (*Hordeum vulgare*) appeared ~8000–11,000 YA in the Middle East (Purugganan & Fuller, 2011). In Mesoamerica, the domestication and evolution of nonshattering maize (*Zea mays* spp. *mays*) are suggested to have occurred before 8700 YA (Piperno, Ranere, Holst, Iriarte, & Dickau, 2009). The domestication of nonshattering sorghum (*Sorghum bicolor*) possibly took place in Africa between 6000 and 4000 YA (Fuller et al., 2014). Among the millets, the nonshattering trait appears in pearl

Fig. 1 Occurrence and fixation of the nonshattering phenotypes in the major cereal crops. Dates are estimated based on archeological evidence.

millet (*Pennisetum glaucum*), Indian millet (*Pennisetum typhoides*), and foxtail millet (*Setaria italica*) about 4000, 4500, and 7500–8000 YA, respectively (Bettinger, Barton, & Morgan, 2010; Fuller, 2011; Liu, Hunt, & Jones, 2009; Manning, Pelling, Higham, Schwenniger & Fuller, 2011).

Among legume crops, indehiscent pods have also arisen independently in multiple species throughout the world (Meyer & Purugganan, 2013). For example, indehiscent phenotypes emerged in both soybean (*Glycine max*) and common bean (*Phaseolus vulgaris*), which were domesticated in Old and New World, respectively (Harlan, 1992; Hymowitz, 1970; Schmutz et al., 2014). In the case of the mustard family, loss of silique or silicle dehiscence has similarly evolved independently in several genera (Appel & Al-Shehbaz, 2003). Among fleshy-fruited crop species, fruit shedding is widely observed in the wild progenitors of cultivated species within the Rosaceae, Rutaceae, and Solanaceae, and the emergence of fruit retention is a key characteristic of most domesticated fruit tree varieties (Meyer & Purugganan, 2013).

In this review, we focus our discussion on the genetic and developmental bases of the loss of seed shattering and fruit dispersal mechanisms in domesticated crops. We have reviewed the domestication genetics literature and have compiled a list of currently known candidate genes for this trait (Table 1); using this information, we examine how molecular genetic changes have led to the convergent evolution of nonshattering phenotypes across independently domesticated crop species. These observations together suggest a large degree of conservation in the developmental and molecular genetic mechanisms that underlie the convergent evolution of nondispersing seeds/fruits in different crop species. From this finding, we propose that the existing genetic and developmental knowledge derived from species studied to date can provide an important foundation for characterizing this trait in heretofore unstudied crop species.

2. DEVELOPMENTAL BASIS FOR THE LOSS OF SEED AND FRUIT DISPERSAL IN CROPS

One of the remarkable features of higher plants is their capacity to selectively shed organs or parts of organs, such as fruits, leaves, and flowers, during development and reproduction (Gasser & Simon, 2011; Lewis, Leslie, & Liljegren, 2006; Liljegren, 2012). Anatomically, the shedding of seeds and/or fruits in crop species usually corresponds to the detachment of seeds or fruits from pedicel (Dong & Wang, 2015). Abscission is the

Table 1 Seed and Fruit Dispersal-Related Candidate Genes Identified in Crop Species and Their Relatives

Plant Family	Species	Gene	Putative Function	Causative Mutation	References
Poaceae					
	Oryza sativa	*sh4*	Myb3 DNA-binding domain protein	G → T	Li, Zhou, and Sang (2006)
		qSH1	BEL1-type homeobox protein	G → T	Konishi et al. (2006)
		SHAT1	APETALA2 transcription factor	1 bp deletion	Zhou et al. (2012)
		OsCPL1	Carboxy-terminal domain phosphatase-like 1 protein	A → T	Ji et al. (2010)
		OsSh1	YABBY transcription factor	~4 kb insertion	Lin et al. (2012)
		SH5	BEL1-type homeobox protein	Unclear[a]	Yoon et al. (2014)
	Oryza glaberrima	*OgSh1*	YABBY transcription factor	~45 kb deletion	Wang et al. (2014)
		OgSh4	Myb3 DNA-binding domain protein	Unclear	Wang et al. (2014)
	Sorghum bicolor	*SbSh1*	YABBY transcription factor	Point mutations and 2.2 kb deletion[b]	Lin et al. (2012)
	Sorghum propinquum	*SpWRKY*	WRKY transcription factor	A → G	Tang et al. (2013)
	Hordeum vulgare	*Btr1*	Membrane-bound protein	1 bp deletion	Pourkheirandish et al. (2015)

Continued

Table 1 Seed and Fruit Dispersal-Related Candidate Genes Identified in Crop Species and Their Relatives—cont'd

Plant Family	Species	Gene	Putative Function	Causative Mutation	References
		Btr2	Soluble protein	11 bp deletion	Pourkheirandish et al. (2015)
	Triticum spp.	*Q/q*	AP2-like protein	G → A	Simons et al. (2006)
	Zea mays	*ZmSh1*	YABBY transcription factor	83 bp insertion and structural variation[c]	Lin et al. (2012)
Fabaceae					
	Glycine max	*Pdh1*	Dirigent-like protein	A → T	Funatsuki et al. (2014)
		SHAT1–5	NAC domain transcription factor	Unclear	Dong et al. (2014)
Solanaceae					
	Solanum esculentum	*JOINTLESS*	MADS-box transcription factor	939 bp deletion	Mao et al. (2000)
		MC	MADS-box transcription factor	*Cis* regulatory deletion	Vrebalov et al. (2002) and Nakano et al. (2012)

[a]Association between expression level and nonshattering phenotype was found in these genes, but the causative mutations were unclear so far.
[b]Two types of mutations, single-nucleotide mutation and deletion, were reported in the cultivated sorghum.
[c]Two distinct *Sh1* orthologs, *ZmSh1–1* and *ZmSh1–5*, were found in maize, of which, a 83 bp insertion occurred in the third exon of *ZmSh1–1*. In contrast, structural variation was detected in the two tandemly arranged copies of *ZmSh1–5*.

crucial process that enables the separation of the reproductive structure from the remainder of the plant (Addicott, 1982; Estornell et al., 2013; Gasser & Simon, 2011; Taylor & Whitelaw, 2001). In selecting for a loss of seed and fruit dispersal mechanisms in cultivated plants, early farmers favored developmental mutants where the abscission and dehiscence zones (AZ or DZ) have been modified and disarticulation disrupted (Pickersgill, 2007).

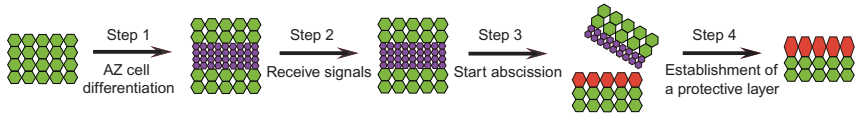

Fig. 2 Differentiation and formation of the abscission and dehiscence zone in plants. *Green*, normal cells; *purple*, abscission cells; *red*, protective layer. *The original model was retrieved from Patterson, S. E. (2001). Cutting loose. Abscission and dehiscence in Arabidopsis.* Plant Physiology, 126, *494–500; Estornell, L. H., Agustí, J., Merelo, P., Talón, M., & Tadeo, F. R. (2013). Elucidating mechanisms underlying organ abscission.* Plant Science, 199, *48–60.*

The current model of the establishment of the AZ and DZ involves four major developmental steps (Fig. 2): (i) initial differentiation of a functionally specialized tissue where the detachment zone will be formed; (ii) development in the newly formed detachment zone of the ability to respond to abscission signals such as ethylene, abscisic acid, and other plant hormones; (iii) phytohormone-mediated signaling to trigger the abscission process within the AZ and DZ; and (iv) formation of a protective layer over the separation surface of the AZ and DZ (Estornell et al., 2013; Patterson, 2001). In principle, this developmental process could be initiated in any number of locations within vegetative or inflorescence tissue. Indeed, as detailed later, empirical studies have revealed differences in the location of AZ and DZ formation among plant species that has led to distinct developmental strategies for seed and fruit dispersal. Correspondingly, distinct developmental bases for the nondispersing phenotype have emerged in different crop species as a result of selection during domestication.

Variation in developmental basis for nonshattering (or reduced shattering) seed is especially well illustrated by the cereal crops and their relatives within the Poaceae (Doust, Mauro-Herrera, Francis, & Shand, 2014). In the case of the grass tribe *Oryzeae*, which includes domesticated Asian and African rice (*O. sativa* and *Oryza glaberrima*, respectively) and American wild rice (*Zizania palustris*), the wild progenitors of the cultivated crops shatter their seeds as individual caryopses with glumes attached (Fig. 3A). In contrast, the wild barley species *Hordeum pusillum* (tribe Triticeae) shatters whole spikelets that contain multiple individual florets (Fig. 3B). Yet another mechanism is found in the wild dune grass genus *Spinifex* (tribe Paniceae), where the dispersal unit consists of the entire inflorescence which is shed from the base of the inflorescence branch. Thus, while the developmental basis of AZ formation is similar among cereal crops and their relatives, the location where it forms can vary widely, leading to diverse forms of diaspores.

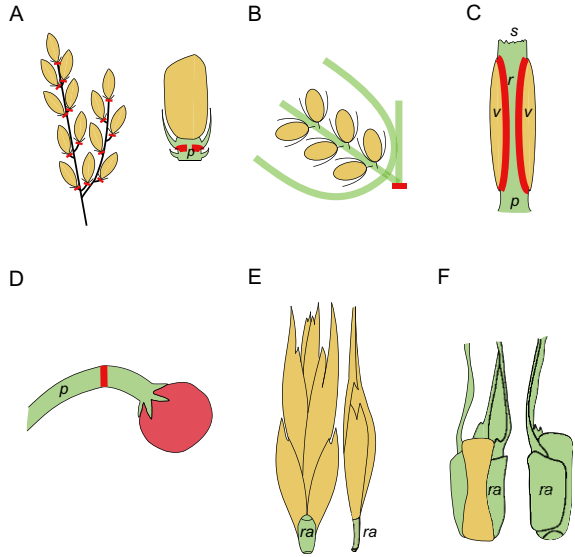

Fig. 3 Seed and fruit dispersal unit of rice (A), barley (B), *Brassica* (C), tomato (D), wheat barrel-shaped (E), and wedge-shaped (F) spikelet disarticulation. *Red* color represents the occurrence of abscission and dehiscence zone in the inflorescence. The characters *p*, *s*, *r*, *v*, and *ra* indicate pedicel, stigma, replum, valve, and rachis, respectively. *The original models were retrieved from Li, W., & Gill, B. S. (2006). Multiple genetic pathways for seed shattering in the grasses.* Functional and Integrative Genomics, 6, *300–309; Gasser, C. S., & Simon, M. K. (2011). Seed dispersal: Same gene, different organs.* Current Biology, 21, *R546–R548; Doust, A. N., Mauro-Herrera, M., Francis, A. D., & Shand, L. C. (2014). Morphological diversity and genetic regulation of inflorescence abscission zones in grasses.* American Journal of Botany, 101, *1759–1769.*

In contrast to the Poaceae, fruits of the Brassicaceae and Fabaceae show greater conservation within each family in the developmental mechanism of seed dispersal. In the Brassicaceae, a typical dry fruit contains two valves that are connected by a replum (Fig. 3C) (Ferrándiz, Pelaz, & Yanofsky, 1999). The valve margin differentiates into lignified and separation layers throughout the silique development, and these two layers together form the DZ along the silique (Ferrándiz, 2002; Ferrándiz et al., 1999). In oilseed rape, for example, as the silique dries during senescence, pod dehiscence is initiated at the base of the pod where the pedicel and replum are fused together (Morgan, Ladbrooke, Bruce, Child, & Arthur, 2000). Similarly, wild legume species also disperse their seeds by shattering the pod along the ventral suture after maturation (Tiwari & Bhatia, 1995).

Compared to the seed crops, fleshy-fruited crop species possess yet another strategy to shed their fruits. In the tomato (Solanaceae), the AZ

usually forms in the knuckle region of the pedicle that leads to the shedding of the entire ripe fruit (Fig. 3D) (Estornell et al., 2013; Roberts, Elliott, & Gonzalez-Carranza, 2002). The AZ of tomato consists of several layers of cytoplasmic cells which are predetermined at the initial stage of fruit development (Roberts et al., 2002; van Nocker, 2009). Similar abscission processes are also observed in the Rosaceae and Rutaceae, although not necessarily at the same time point during development (Rascio, Casadoro, Ramina, & Masia, 1985; Tadeo et al., 2008). These features indicate that common and conserved mechanisms might regulate the cell separation in fleshy fruit abscission processes.

3. MOLECULAR GENETIC BASIS OF SHATTERING IN SEED CROPS

3.1 Poaceae

The domestication of cereal crops from their wild grass progenitors had a unique importance in the history of human civilization (Sang, 2009). Cereals have constituted the primary staple food for most of the world's population since their domestication (Doebley et al., 2006; Varshney, Hoisington, & Tyagi, 2006). A variety of cereal crops, including rice, wheat, and sorghum, are cultivated worldwide and now provide more than 60% of the calories and proteins in our daily diet (FAO, 2013). As noted earlier, while the cereal crops were domesticated independently from multiple distinct genera throughout the world, convergent and parallel selections during the domestication process resulted in repeated occurrences of nonshattering phenotypes among cereal crops. The molecular genetic basis of nonshattering seed is better understood for cereals than for any other crop family; we review this information in this section.

3.1.1 Asian Rice (O. sativa)

Asian rice (*O. sativa*) was domesticated from the wild species *Oryza rufipogon* and provides the staple food for more than half of the world's population (Huang et al., 2012; Sang & Ge, 2007a, 2007b; Sweeney & McCouch, 2007). The mature grains of the wild progenitor dissociate easily from the panicle to ensure the successful dispersal of offspring. In contrast, reduced-shattering phenotypes of the two cultivated Asian rice subspecies (*indica* and *japonica*) were selected for improved grain yield during the domestication process. Although the degree of seed shattering varies widely

among cultivars, the mature seeds of *indica* varieties generally shatter more easily than those of *japonica* varieties (Konishi et al., 2006; Lin et al., 2007).

Genetic analyses of seed shattering between cultivated rice and its wild ancestor have revealed two major quantitative trait loci (QTLs), *sh4* and *qSH1*, that contribute to the nonshattering phenotype (Konishi et al., 2006; Li & Gill, 2006; Li et al., 2006) (Table 1). In the case of *sh4* (LOC_Os04g57530), a single nonsynonymous substitution in the Myb3 DNA-binding domain of this transcription factor results in the incomplete development and partial function of the AZ; this single mutation explains ~70% of phenotypic difference between the *indica* and wild parents of the mapping population in which *sh4* was identified (Li et al., 2006). In the case of *qSH1*, a causative nucleotide substitution located ~12 kb upstream of the BEL1-type homeobox gene (LOC_Os01g62920) decreases its expression level and interferes with the development of the AZ; this mutation was found to explain 68.6% of the shattering variation between *indica* and *japonica* mapping line parents (Konishi et al., 2006). Population genetic analyses based on a wide sampling of cultivated rice and wild progenitors revealed the single origin of the nonshattering allele of *sh4*, which may have been fixed across all cultivated rice within a period as short as c.100 years (Zhang et al., 2009). In contrast, the nonshattering allele of *qSH1* has been found in *temperate japonica* varieties only and was apparently not a target of selection outside of this group (Zhang et al., 2009).

Interestingly, evidence from wild *O. rufipogon* and weedy rice (ie, feral *O. sativa* strains), both of which are typically highly shattering, has indicated that the nonshattering allele of *sh4* is not by itself sufficient to generate the reduced-shattering phenotype in all genetic backgrounds (Thurber et al., 2010; Zhu, Ellstrand, & Lu, 2012). In *O. rufipogon*, for example, more than 25% of accessions in one survey were found to carry the reduced-shattering allele while showing the shattering phenotype (Zhu et al., 2012). Likewise, both straw-hulled (SH) and black-hulled awned (BHA) populations of U.S. weedy rice possess the *sh4* nonshattering allele common to the cultivated rice, even though nearly all U.S. weedy rice shows a similar degree of shattering as wild rice (Thurber et al., 2010). Yan et al. (2015) recently found that the expression pattern of *sh4* gene is regulated by its promoter *pSH4*, which, apart from its major role in seed shattering, may have additional functions in the growth and development of cultivated rice. In the case of *qSH1*, the degree of nonshattering varies dramatically among different varieties that carry the nonshattering allele (Konishi et al., 2006). These observations together suggest that while *sh4* and *qSH1* have played

important roles during the domestication and improvement of cultivated rice, other loci have also apparently been involved in the evolution of the reduced-shattering phenotype during rice domestication.

Consistent with this expectation, a series of other genes related to the nonshattering phenotype have been identified in rice through QTL mapping, including *OsCPL1*, *OsSh1*, *OsWRKY*, *SH5*, and *SHAT1* (Ji et al., 2010; Lin et al., 2012; Tang et al., 2013; Yoon et al., 2014; Zhou et al., 2012) (Table 1). While it is a relatively minor shattering QTL in rice, *OsSh1* is notable in that parallel selection on the underlying *Shattering1* (*Sh1*) gene has apparently contributed to the evolution of nonshattering phenotype in other cereals, including maize and sorghum (Lin et al., 2012). *OsSh1* (LOC_Os03g44710) encodes a YABBY transcription factor, which in rice shows an overlapping distribution with the QTL *qSH3* (Donini et al., 2007; Gu, Kianian, Hareland, Hoffer, & Foley, 2005; Lin et al., 2012; Onishi et al., 2007). Gene structure and expression analyses based on the nonshattering mutant SR-5 and a wild-type rice breeding line Nanjing 11 revealed that an insertion of a ~4 kb fragment occurs in the third intron of *OsSh1*, resulting in the reduced levels of transcription and shattering-resistant phenotype (Lin et al., 2012). Population genomic studies have also suggested that *OsSh1* was a target of selection during rice domestication (He et al., 2011; Xu et al., 2012).

Recent studies have further revealed that the gene *OsWRKY* is localized within another shattering QTL, *qSH3*, and that *OsSh1* and *qSH3* may interact with *qSH1* and *sh4* in regulating AZ development in the pedicel (Htun, Inoue, Chhourn, Ishii, & Ishikawa, 2014; Inoue et al., 2015). Previous work has demonstrated that the ortholog *SpWRKY* confers shattering phenotype to a wild sorghum species *Sorghum propinquum* (Tang et al., 2013). These observations together suggest that *OsWRKY* is also a candidate gene that might play roles in the grain rice abscission process.

The *SHAT1* gene, which encodes an *APETALA2* transcription factor, is another candidate gene associated with the nonshattering phenotype in cultivated rice (Zhou et al., 2012). Through recurrent introgression of chromosome 4 from a shattering *O. rufipogon* line into an *indica* crop line with reduced shattering, two introgression lines, *shat1* and *shat2*, were generated from the substitution line SL4; both of them show a nonshattering phenotype. From these lines, map-based cloning was used to identify two corresponding genes, *SHAT1* and *SHAT2*, associated with the nonshattering phenotype. *SHAT1* was mapped to a 9-kb interval within which only one annotated gene (LOC_Os0455560) was found. By comparing the

sequences of this candidate gene between *shat1* and the wild type, Zhou et al. (2012) found that a 1-bp deletion occurs at the first exon between the nucleotide sites +41 and +42 in the introgression line *shat1*, which leads to a frame shift at the *SHAT1* gene. Similarly, fine mapping narrowed down the *SHAT2* to a 9.7 kb genomic region which overlapped with the previously identified locus *sh4*. However, unlike the single amino acid replacement characterizing the *sh4* domestication allele, the *SHAT2* allele carries a frameshift mutation in the nuclear localization signal region. The *SHAT1* gene is expressed at the early stage of the AZ formation and affects the formation of the AZ with the other shattering-related genes (eg, *qSH1* and *sh4*). Likewise, *SHAT2* is a null-function mutant and shows different phenotypes of the AZ compared to the *sh4* allele. The loss of functions of *SHAT1* and *SHAT2* prevents the development of AZ in the pedicel and results in the occurrence of the nonshattering phenotype.

In contrast to genes such as *sh4* and *OsWRKY*, population genomic analysis does not reveal evidence of artificial selection acting on the *SHAT1* gene in the process of rice domestication, because there is no obvious decrease in nucleotide diversity in cultivated rice compared to its wild ancestor (Zhou et al., 2012). For the BEL1-type homeobox gene *SH5* (LOC_Os05g38120), a recently identified shattering-related gene on chromosome 5 (Yoon et al., 2014), and for the carboxy-terminal domain phosphatase-like 1 (*OsCPL1*, LOC_Os07g10690), which acts as a repressor of abscission layer (AL) differentiation, no test for signatures of artificial selection at these loci has been reported. Genetic analyses revealed that *SH5* is homologous to *qSH1* and is highly expressed at the AZ in the pedicel. Suppression of *SH5* expression in the shattering *indica* variety Kasalath can prevent the AZ development and reduce the degree of shattering. Likewise, overexpression of *SH5* in the nonshattering Korean *japonica* variety IIpum can lead to an increase in seed shattering because lignin levels are decreased in the basal region of spikelets. These features suggest that *SH5* induces the shattering in the presence of the nonshattering *qSH1* allele, although it remains unknown whether this gene has undergone artificial selection during rice domestication.

Besides the loci described earlier, numerous additional shattering QTLs across the 12 rice chromosomes have been detected in several distinct mapping populations derived from shattering and nonshattering parents (reviewed in Subudhi et al., 2014); shattering QTLs have been detected on rice chromosomes 1, 3, 4, 7, 8, and 11 (Bres-Patry, Lorieux, Clement, Bangratz, & Ghesquière, 2001; Cai & Morishima, 2000; Thomson et al., 2003; Xiong, Liu, Dai, Xu, & Zhang, 1999). However, relatively few of

the underlying candidate genes have been identified from these mapped QTLs. In a recent study, Qi et al. (2015) generated two recombinant inbred line populations through crosses between a nonshattering *indica* crop variety and individuals representing the two major U.S. weedy rice strains (SH and BHA). This comparative QTL mapping study revealed that shattering QTLs are largely not shared between the two types of weedy rice. In the SH population, for example, two QTLs, *qSH2S* and *qSH11S*, are detected in chromosomes 2 and 11, respectively, and neither is detected in the BHA population. Instead, a total of six shattering QTLs (*qSH1Bb*, *qSH3Bb*, *qSH5Bb*, *qSH6B*, *qSH8Bb*, and *qSH12B*) were identified on chromosomes 1, 3, 5, 5, 8, and 12, respectively. These map-based studies indicate that there are very likely several as-yet unidentified loci that affect shattering differences between cultivated and weedy rice.

The diversity of rice shattering QTLs described herein suggests that multiple, interacting genes have likely been involved in the emergence of nonshattering cultivated rice. These loci might also play distinct roles during the development of the AZ. However, the regulatory network specifying AZ development in rice has remained unclear so far. As a step toward elucidating these interactions, we updated recent progress in rice inflorescence development and propose a modified evolutionary model of the shattering phenotype based on Zhou et al. (2012) (Fig. 4). Current data suggest that *sh4* and *qSH1* play crucial roles in the formation of AZ and seed shattering (Konishi et al., 2006; Li et al., 2006; Zhang et al., 2009), while *qSH1* is epistatic to *sh4* (Onishi et al., 2007). Of the two loci, *sh4* acts largely upstream of the other

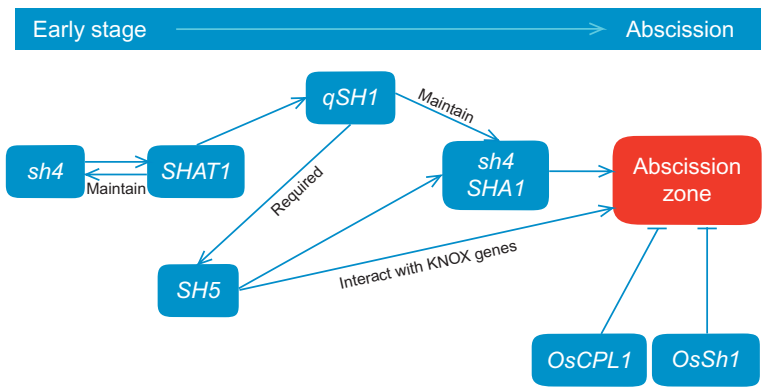

Fig. 4 Molecular genetic regulatory network of the nonshattering trait in the Asian rice. This model was modified based on Zhou et al. (2012). The expression stage of *OsCPL1* and *OsSh1* is unknown.

shattering-related genes. The *SHAT1* gene functions downstream of *sh4* and activates the expression of *qSH1* while maintaining expression of *sh4* (Zhou et al., 2012). In contrast, *qSH1* shows strong effects in the genetic background of *japonica* Nipponbare cultivars (Ishikawa et al., 2010; Onishi et al., 2007) and maintains the expression level of *sh4* and *SHAT1* in the AZ (Zhou et al., 2012). Similarly, the *SH5* gene is expressed at the early stage of the abscission process and positively affects the expression level of *sh4* and *SHAT1* (Yoon et al., 2014). In addition, *SH5* can interact with *KNOX* genes which together enhance the development of the AZ, but the presence of *qSH1* is required for this function (Hay & Tsiantis, 2010; Yoon et al., 2014).

Besides these genes that have known interactions, both *OsCPL1* and *qSH3* show obvious effects on the formation of the AZ in the pedicel (Hunt et al., 2014; Inoue et al., 2015; Ji et al., 2010); however, their roles in the regulatory network of seed shattering are unknown at present. Ji et al. (2010) proposed that *OsCPL1* represses the formation of AZ, possibly by reducing phosphatase activity of genes involved in the abscission process. Likewise, *qSH3*, including both *OsSh1* and *OsWRKY*, can repress the formation of the AZ in the pedicel (Hunt et al., 2014; Inoue et al., 2015; Lin et al., 2012), but how exactly they interact with the other shattering-related genes is still unclear. Further investigations based on mutant complementation, which carry one or more of these identified genes, might provide new insight into the evolution of the rice nonshattering phenotype. The present regulatory network model (Fig. 4) is thus best viewed as a work in progress.

3.1.2 *African Rice* (O. glaberrima)

African rice (*O. glaberrima*) is thought to have been domesticated from the African wild rice species *Oryza barthii* (Sarla & Swamy, 2005; Sweeney & McCouch, 2007; Wang et al., 2014). Archeological evidence, including ceramic impressions of rice grains, suggests that this domestication may have occurred 2000–3000 YA (Klee, Zach, & Neumann, 2000). Harlan (1971) proposed that African rice was selected by ancient hunting–gathering human populations from distinct places within the vast forest and savanna areas. In contrast, Fage and Oliver (1970) and Porteres (1962) proposed an alternative hypothesis that African rice primarily originated from the Inland Delta of the Upper Niger River and was then dispersed to two secondary centers along the Sahelian Rivers. The latter was supported by a recent population genomic study based on a total of 114 African rice accessions (Wang et al., 2014). At the present time, African rice is mainly cultivated in tropical West Africa

and has been largely displaced on that continent by Asian rice cultivation (Semon, Nielsen, Jones, & McCouch, 2005). Although African rice and Asian rice were domesticated independently from distinct wild progenitors, only slight morphological differences are observed between them (Linares, 2002). In comparison with Asian rice, for example, African rice usually has small grains that are pear-shaped and have a red bran (pericarp) and an olive-to-black seed coat, straight panicles, and short ligules (Linares, 2002). Most relevant to the present discussion, the seed of African rice shatters more easily than that of Asian rice.

The molecular mechanisms underlying the reduced-shattering phenotype of African rice remain less resolved than Asian rice. However, as a congeneric species that is phylogenetically close to its Asian counterpart, orthologs of genes that control shattering in Asian rice have been proposed to show similar functions in African rice. To this end, Wang et al. (2014) have compared the gene structures and expression patterns of three shattering-related genes, *OsSh1*, *sh4*, and *qSH1*, between African and Asian cultivated rice based on whole genome data (Table 1). In the case of *OsSh1*, a ~4-kb insertion found at the third intron in Asian rice leads to the decreased expression level of *OsSh1* that results in a nonshattering phenotype compared to the wild progenitor *O. rufipogon*. Interestingly, the genome of cultivated African rice harbors a ~45-kb deletion which leads to the absence of the ortholog of *OsSh1* and three additional genes, whereas the ortholog of *OsSh1* is present in the wild ancestor, *O. barthii* (Wang et al., 2014). These observations suggest the possibility that selection for a deletion of the *OsSh1* ortholog might have contributed to the evolution of nonshattering phenotype in cultivated African rice.

The African rice ortholog of the major rice shattering gene *sh4* may also be important in the reduced shattering of this species. Although the causative mutation reported in Asian rice is not found in African rice (Wang et al., 2014), RNA-seq from the panicle tissue revealed that the ortholog of *sh4* is expressed in the wild progenitor *O. barthii*, while no transcription is detected in African cultivated rice. Further investigation based on the promoter region of the *sh4* gene showed that nucleotide diversity of African cultivated rice is obviously lower at this locus than that of its wild progenitor *O. barthii*, suggesting that it was a target of selection during domestication. In addition, substantial deviation from neutral expectations was also observed at the promoter region of *sh4* gene in African cultivated rice. As noted earlier, Yan et al. (2015) have reported that in Asian cultivated rice the expression pattern of *sh4* gene is regulated by its promoter *pSH4*. These findings

together suggest that orthologs of *sh4* might have played important roles in the evolution of nonshattering phenotype in both African and Asian rice.

In the case of *qSH1*, there is no strong evidence that the African rice ortholog of this gene played a role in domestication. Like *sh4*, the *O. glaberrima qSH1* sequence has not been found to carry the causal mutation detected in Asian rice (Wang et al., 2014). In addition, transcriptome profiling showed that the *qSH1* ortholog is expressed in both African cultivated rice and its wild progenitor and functions normally in the panicle tissue (Wang et al., 2014). Given that even in Asian rice the causal variation at this locus is restricted to a small subset of all varieties (*temperate japonicas*), broader sampling of African rice germplasm might be helpful in detecting any role for *qSH1* in African rice domestication.

Taken together, these studies in African rice suggest that although African and Asian rice were domesticated independently from distinct wild parental species, convergent selection on orthologous genes has played at least some role in the emergence of reduced-shattering varieties of both crop species. Based on these findings, we propose that the orthologs of the other Asian rice shattering genes described earlier, such as *SH5*, *OsCPL1*, and *SHAT1*, might have also played roles in the evolution of nonshattering phenotype in African rice. The recent availability of the African rice reference genome (Wang et al., 2014) and extensive population samples deposited in GenBank make it possible to now investigate the gene structures and expression patterns of these orthologs in African rice. In addition, the feasibility of interspecific hybridization between Asian and African rice suggest that forward genetics approaches such as QTL mapping can provide an efficient avenue to detect the shattering-related genes.

3.1.3 American Wild Rice

American wild rice (*Z. palustris*) is an annual aquatic grain that is native to the shallow lakes and streams in the north-central North America and has long been utilized by Native Americans for food (Hanten, Ahlgren, & Carlson, 1980; Oelke, Schreiner, & Council, 2007). Unlike Asian rice, traditional harvesting practices for this species did not select for reduced-shattering phenotypes. This is because the natural ecotypes are usually harvested by repeated gathering of freely shattering grains as they mature over an extended period of the growing season (Elliott & Perlinger, 1977). Commercial cultivation of wild rice is a recent development and was made possible in large part due to the discovery of a reduced-shattering phenotype, allowing for industrialized crop production with mechanized harvesting

(Everett & Stucker, 1983; Grombacher, Porter, & Everett, 1997; Oelke et al., 1982). Anatomical features of the wild rice AZ are similar to those described for the seed and fruit of other species (Hanten et al., 1980). This suggests that the developmental basis is likely similar between wild rice and other crops, such as Asian and African cultivated rice. To date, several non-shattering wild rice cultivars (eg, Johnson, Manomin1, and Kosbau 2) have been developed and are now cultivated widely in Minnesota and California (Hayes, Stucker, & Wandrey, 1989; Kahler, Kern, Porter, & Phillips, 2014). These cultivars are sufficiently shatter resistant to confer the possibility of harvesting all seeds on the plant at one time. However, yield losses from shattering are still high in commercial wild rice, and progress in developing stable nonshattering varieties has been hindered due to inbreeding depression in this naturally outcrossing species and the intense labor requirements for large-scale production (Kennard, Phillips, Porter, Grombacher, & Phillips, 1999).

Recent work on the improvement of nonshattering wild rice has shifted toward comparative genetics at both gene and chromosome levels (Hass, Pires, Porter, Phillips, & Jackson, 2003; Kennard, Phillips, & Porter, 2002; Kennard et al., 1999). American wild rice is phylogenetically fairly closely related to Asian cultivated rice, with both crops belonging to the *Oryzoideae* subfamily of the *Oryzeae* grass tribe (Duvall, Peterson, Terrell, & Christensen, 1993). As a consequence, the two crops show a high degree of genomic conservation. For example, one study found that as much as 85% of restriction fragment length polymorphism markers are collinear between American wild rice and Asian rice (Kennard et al., 1999). QTL mapping analyses based on F_2 and F_3 generations revealed that three QTLs account can for ~87% of the observed phenotypic variations between shattering and nonshattering wild rice parents (Kennard et al., 2002). With the availability of an annotated reference genome for Asian rice, anchored loci can provide a reference point for identifying orthologs of Asian rice shattering genes and examining their functional significance within American wild rice. Whole genome and transcriptome sequencing of diverse *Z. palustris* lines may provide the most efficient strategy for applying this approach to identify shattering-related genes in this American crop.

3.1.4 *Sorghum* (S. bicolor)

Sorghum (*S. bicolor*) is the fifth most important grain crop in the world and an emerging cellulosic biofuel crop (Paterson, 2008, 2009). Cultivated sorghum (*S. bicolor* ssp. *bicolor*) was domesticated from its wild progenitor

S. bicolor ssp. *verticilliflorum* in Africa about 8000 YA (Wendorf et al., 1992; Wiersema & Dahlberg, 2007). Five major morphological forms have traditionally been recognized, namely *caudatum*, *durra*, *guinea*, *kafir*, and *bicolor*, of which *bicolor* is considered the most primitive form as it contains both shattering and nonshattering phenotypes (Brown, Myles, & Kresovich, 2011; Harlan & De Wet, 1972; Olsen, 2012).

As with other cereal crops, reduction of seed dispersal was a critical step in sorghum domestication (Paterson, Schertz, Lin, Liu, & Chang, 1995; Tang et al., 2013). To identify the molecular genetic basis underlying the seed shattering in sorghum, Paterson et al. (1995) crossed an elite breeding line (BTx623) of domesticated sorghum with the wild relative species *S. propinquum*. Surprisingly, a single locus, *Shattering 1* (*Sh1*), was found to account for nearly 100% of phenotypic variance explained (PVE) between shattering and nonshattering types (Paterson et al., 1995) (Table 1). An F_2 QTL population was then constructed from the cross between a wild sorghum *Sorghum virgatum* with complete seed shattering and a nonshattering domesticated sorghum line Tx430 (Lin et al., 2012). The F_1 individuals showed the same complete shattering phenotype as the wild sorghum species, and the F_2 segregation ratio confirmed the hypothesis that the gene *Sh1* corresponds to the shattering phenotype in sorghum with a complete dominance effect (Lin et al., 2012). Further investigation based on fine mapping placed the *Sh1* within a ~17-kb region on sorghum chromosome 1, within which only two candidate genes, a hypothetical gene and a transcription factor gene belonging to the YABBY transcription factor family, are annotated. This YABBY gene is orthologous to the Asian rice *OsSh1* gene described earlier. Sequences from the YABBY gene further revealed that domesticated sorghum carries three haplotypes at the *Sh1* locus, all of which lead to reduced gene function and a reduction in shattering. One haplotype carries mutations at regulatory sites in the promoter and intronic regions that reduce *Sh1* expression in domesticated sorghum. In contrast, the haplotype with a 2.2-kb deletion results in a truncated transcript that lacks exons 2 and 3, and a GT-GG splice-site variant in intron 4 of the third haplotype causes the removal of exon 4 (Lin et al., 2012).

SpWRKY is another transcription factor that affects shattering variation between wild and domesticated sorghum (Tang et al., 2013). A single-nucleotide mutation that creates an early start codon of *SpWRKY* leads to a 132-bp longer transcript in *S. propinquum* than that of *SbWRKY* in *S. bicolor* (Table 1). The WRKY superfamily of plant transcriptional factors

has been suggested to play roles in a variety of physiological and developmental processes unique to plants, such as leaf senescence and trichome initiation (Johnson, Kolevski, & Smyth, 2002; Robatzek & Somssich, 2001, 2002). Low *SpWRKY* expression in *S. propinquum* results in the end of floral development that may derepress its downstream cell wall biosynthesis genes, allowing for the deposition of lignin in a manner similar to that found in the AZ of the seed pedicel junction (Tang et al., 2013). Positional analysis revealed that the *SpWRKY* and YABBY genes are colocalized within a ~300-kb genomic region and may have appeared to be a single locus in some sorghum populations. Therefore, Tang et al. (2013) proposed that the ancestral species which predated the divergence of *S. propinquum* and *S. bicolor* may have carried a shattering allele of YABBY and a nonshattering allele of WRKY. The nonshattering alleles of YABBY emerged in *S. bicolor* only and have been targets of artificial selection during the sorghum domestication process, while the occurrence of the start codon mutation of *SpWRKY* might have reinforced the level of shattering in *S. propinquum*. Taken together, the evolutionary trajectories of *SpWRKY* and *Sh1* in sorghum species suggested that although *Sh1* can explain ~100% of the PVE in domesticated sorghum, the molecular mechanisms underlying the evolution of shattering in wild relatives might be controlled by different loci.

3.1.5 *Barley* (H. vulgare *ssp.* vulgare)

Barley (*H. vulgare* ssp. *vulgare*), which is the world's fourth most important cereal crop, was domesticated from its wild progenitor *H. vulgare* ssp. *spontaneum* (Harlan & Zohary, 1966; Tanno & Willcox, 2012; Weiss, Kislev, & Hartmann, 2006). As one of the first domesticated crops, barley was initially cultivated in the Fertile Crescent ~9500 to 12,000 YA and thereafter spread throughout temperate regions of the Old World (Tanno & Willcox, 2006; Willcox, 2013; Willcox, Fornite, & Herveux, 2008; Zohary, Hopf, & Weiss, 2012). As with other cereal crops such as rice and sorghum, an early step in barley domestication was the modification of seed dispersal mechanisms to increase efficient harvesting and avoid yield losses due to shattering (Haberer & Mayer, 2015). The dispersal unit of barley consists of a central fertile spikelet along with two sterile lateral spikelets (Pourkheirandish et al., 2015) (Fig. 3B). This phenotype is referred to as "brittle rachis" which is equivalent to grain shattering in rice and sorghum. The brittle rachis character is specific to the Triticeae tribe (Pourkheirandish et al., 2015).

The brittle rachis of barley is controlled by two dominant complementary genes, *Btr1* and *Btr2* (Takahashi & Hayashi, 1964). QTL mapping showed that the two genes are tightly linked on the short arm of barley chromosome 3 (Franckowiak & Konishi, 1997a, 1997b; Takahashi & Hayashi, 1964). Wild barley carries the haplotype *Btr1Btr1/Btr2Btr2*. Recent molecular genetic work has demonstrated that 1 and 11 bp deletions occur in *Btr1* and *Btr2*, respectively, and have led to the occurrence of two recessive alleles, *btr1* and *btr2* (Pourkheirandish et al., 2015) (Table 1). Thereafter, the two mutants underwent independent artificial selection during the barley domestication process. The homozygous recessive genotype at one of the two loci confers the nonbrittle phenotype to cultivated barley, of which *btr1btr1/Btr2Btr2* is mainly found in occidental cultivars and *Btr1Btr1/btr2btr2* exists in Asian cultivars (Azhaguvel & Komatsuda, 2007; Takahashi, 1955; Takahashi & Hayashi, 1964; Takahashi, Yasuda, & Daigaku, 1983). Population genetic analyses further revealed that the *btr1btr1/Btr2Btr2* haplotype originated from the southern Levant, whereas the *Btr1Btr1/btr2btr2* haplotype was derived from the northern Levant (Pourkheirandish et al., 2015). Comparative genetic analysis based on the available whole genome sequences demonstrated that a duplication event had occurred before the divergence between the Pooideae and Ehrhartoideae, which has led to each of the extant species carrying two copies, namely *Btr1* and *Btr1-like*, *Btr2* and *Btr-like2* (Haberer & Mayer, 2015; Pourkheirandish et al., 2015). Neofunctionalization of the *Btr1* and *Btr2* genes then conferred new roles in determining the development of AZ. Although the biological functions of *Btr1* and *Btr2* proteins are unknown so far, they are hypothesized to function as a receptor and ligand, respectively. In wild barley, the two genes work together and produce a thin cell wall in the AZ of brittle rachis, which results in the disarticulation of mature spikelets (Pourkheirandish et al., 2015).

3.1.6 *Wheat* (Triticum *spp.)*

Wheat is the world's third cereal crop and provides more than 20% of the calories consumed by humans (Dubcovsky & Dvorak, 2007; FAO, 2013). There are six species of wheat at three different ploidy levels: the diploid species *T. monococcum* (A^mA^m) and *Triticum urartu* (AA); the tetraploid species *Triticum turgidum* (BBAA) and *Triticum timopheevii* (GGAA); and the hexaploid species *Triticum aestivum* (BBAADD) and *Triticum zhukovskyi* ($GGAAA^mA^m$) (Dvorak et al., 2012). The evolution of loss of seed dispersal in domesticated wheat is much more complicated than for other cereal

crops, mainly due to its complex domestication process and inflorescence structure. For example, hybridizations and whole genome duplications of three diploid species, *T. urartu*, *Aegilops speltoides* (SS), and *Aegilops tauschii* (DD), have led to the establishment of tetraploid emmer (*T. turgidum*) and hexaploid bread (*T. aestivum*) wheats. Similarly, multiple rounds of polyploidy followed by domestication have resulted in another distinct wheat lineage comprising *T. monococcum*, *T. timopheevii*, and *T. zhukovskyi* (Dvorak et al., 2012; Dvořák, Terlizzi, Zhang, & Resta, 1993; Dvorak & Zhang, 1990; Nishikawa, 1983; Sarkar & Stebbins, 1956).

In general, three major traits are involved in the occurrence of the nonshattering wheat phenotype, namely nonfragile rachis, soft glumes, and free-threshing seed (Faris, Zhang, & Chao, 2014). Like barley, all wild wheat species have a brittle rachis that causes the spikelet to disarticulate and then fall to the ground upon maturity. In contrast, the first cultivated wheat is thought to have had nonbrittle spikes but with tough glumes and hulled seed (Li & Gill, 2006). Indeed, the earliest cultivated wheat, einkorn (*T. monococcum*), carries a tough rachis, which has been derived from the brittle rachis of *Triticum boeoticum* through human selection (Harlan & Zohary, 1966; Salamini, Özkan, Brandolini, Schäfer-Pregl, & Martin, 2002; Sharma & Waines, 1980; van Zeist, Wasylikowa, Behre, & Entjes-Nieborg, 1991). An independent transition from the shattering to nonshattering phenotype occurred in wild emmer wheat (*T. turgidum*, BBAA) and subsequently underwent human selection, allowing cultivated emmer wheat to acquire a nonbrittle rachis (Nesbitt, Hillman, Peña-Chocarro, Samuel, & Szabo, 1996). Two types of spikelet disarticulation occur in wheat, namely barrel-shaped (B) and wedge-shaped (W) (Fig. 3E and F) (Li & Gill, 2006). B-type disarticulation mainly occurs in the wheat species containing the D genome. With this type, the breakage emerges at the lower side of the junction of the rachis and spikelet base, and the adjacent rachis fragment is attached behind each spikelet (Kimber & Feldman, 1987; Li & Gill, 2006). By contrast, the W-type is widely found in A, B, G, S, and T genome species and results from the breakage at the upper side of the junction of the rachis and spikelet base (Kimber & Feldman, 1987; Li & Gill, 2006).

The chromosomal locations of the genes controlling W-type spikelet shattering in einkorn wheat are undetermined, but in emmer wheat (BBAA) shattering is identified by the *brittle rachis 1* (*Br1*) loci on chromosomes 3A and 3B (Feldman, 2001; Joppa & Cantrell, 1990; Nalam, Vales, Watson, Johnson, & Riera-Lizarazu, 2007). Cultivated emmer wheat carries

two codominant genes *Br-A1* and *Br-B1*, both of which are functional, whereas only *Br-A1* is expressed in cultivated *T. timopheevii* (GGAA) (Li & Gill, 2006). B-type disarticulation is controlled by the gene *Br2* and is restricted in the D genome species *Ae. tauschii* and D genome-carrying polyploid wheats such as *Aegilops cylindrica* (DDCC) and *Aegilops ventricosa* (DDNN). In hexaploid wheat, only European spelt wheat (AABBDD) carries the B-type disarticulation, where it is governed by the gene *Br2* (Li & Gill, 2006).

Apart from the nonbrittle rachis, the emergence of free-threshing grains has also contributed to the increased wheat harvest efficiency (Simons et al., 2006), as it removes the need for mechanical hulling. It is well established that the *Q* gene, which encodes a member of the AP2 family of transcription factors and arose through a spontaneous mutation from its wild-type *q*, confers the free-threshing character and square-headed inflorescence phenotype to domesticated wheat (Muramatsu, 1986). All nonfree-threshing wheats have the recessive *q* allele, whereas the free-threshing polyploid wheats harbor the dominant *Q* allele (Jantasuriyarat, Vales, Watson, & Riera-Lizarazu, 2004). Several molecular genetic studies placed the *Q*/*q* gene on the long arm of wheat chromosome 5 (Faris, Fellers, Brooks, & Gill, 2003; Faris & Gill, 2002; Simons et al., 2006). In the hexaploid common wheat, for example, three orthologs of *Q*/*q* gene, *5AQ*, *5Bq*, and *5Dq*, occur in each of the three subgenomes (Zhang et al., 2011). Physical locations and gene structures of these three orthologs suggest that an ancient duplication event occurred before the divergence of the three subgenomes. Thereafter, selective loss of one of the copies emerged in the A genome species and the other copy was lost from the B and D genome species (Zhang et al., 2011). The *5AQ* and *5Aq* alleles differ from each other by a single nonsynonymous substitution at amino acid position 329 (Simons et al., 2006) (Table 1). The wild wheat species containing an A genome all carry the *5Aq* allele. The recent mutation that gave rise to the *5AQ* allele occurred in the cultivated polyploid wheat during the domestication process (Simons et al., 2006; Zhang et al., 2011). The *5Bq* homoeoalleles function normally in wild diploid species but became pseudogenized after allotetraploidization. Further expression analysis from the hexaploid common wheat revealed that *5AQ* plays a crucial role in determining the domestication trait and that the *Q* allele is expressed at a higher level than the *q* allele, while *5Bq* contributes indirectly and *5Dq* contributes directly to suppression of the domestication trait (Simons et al., 2006; Zhang et al., 2011). Recent work based on transcriptome profiling further demonstrated that the *5Aq* shows an obviously higher expression level than *5Bq* in the wild emmer

wheat; this trend was enhanced during the domestication of cultivated emmer and common wheats (Wang & Adams, 2015).

The third trait that contributes to the free-threshing habit in cultivated wheat is the loss of tough glumes (Dubcovsky & Dvorak, 2007). The tenacious glumes (*Tg*) trait was first defined by Kerber and Dyck (1969) and is now designated as *Tg-D1* (Faris et al., 2014). Mapping analyses from several studies have revealed that *Tg-D1* is localized on the chromosome 2D of hexaploid wheat, which is epistatic to *5AQ*, and that both are required for free-threshing (Dvorak et al., 2012; Jantasuriyarat et al., 2004; Nalam et al., 2007; Rowland & Kerber, 1974; Sood, Kuraparthy, Bai, & Gill, 2009). The first hexaploid wheat is inferred to have been a nonfree-threshing form because it carried *Tg-D1* from the wild parent, *Ae. tauschii*, although it harbored a *5AQ* gene (Faris et al., 2014). Subsequently, the gene *Tg-D1* underwent mutation to *Tg-D1* which led to the occurrence of a fully free-threshing hexaploid bread wheat. Similarly, comparative mapping based on recombinant inbred lines between wild and domesticated tetraploid wheat revealed that the *Tg-B1* is the candidate gene inhibiting threshability in wild emmer wheat (Faris et al., 2014). In the case of einkorn wheat, however, the soft glume trait is conferred by the *Sog* gene which was mapped to the short arm of chromosome 2 (Sood et al., 2009; Taenzler et al., 2002). Physical locations from comparative mapping analysis revealed that the *Tg-D1* and *Sog* genes are not homeologous, suggesting that they might be involved in distinct genetic pathways (Sood et al., 2009). Taken together, these findings indicate that a series of distinct genes involved in the loss of seed dispersal and different genetic pathways have conferred the nonshattering phenotypes to diploid, tetraploid, and hexaploid wheats.

3.1.7 Cases from Maize and Other Cereal Crops

During domestication, almost all grass crops went through dramatic genetic and phenotypic changes, of which the nonshattering of seeds at maturity is regarded as the most important domestication trait of cereals (Glémin & Bataillon, 2009). In some cases, comparisons of syntenic QTLs and/or orthologous genes across cereals have revealed evidence for convergent selection on the same gene in different crop species. In the case of *OsSh1*, for example, parallel selection acting on the same ortholog has also conferred nonshattering phenotype to sorghum and maize (*Z. mays*), respectively (Lin et al., 2012) (see earlier). In the case of maize, a recent study has shown that two loci, *ZmSh1–1* and *ZmSh1–5*, explained 3.5% and 23.1% of the phenotypic variation in shattering (Lin et al., 2012) (Table 1). Similarly,

selection on *qSH1* in foxtail millet (*S. italica*) contributed to the evolution of nonshattering phenotype in that crop species (Jia et al., 2013). In buckwheat (*Fagopyrum esculentum*), two complementary dominant loci, *Sht1* and *Sht2*, are thought to control the weak pedicel (Matsui et al., 2004; Matsui, Tetsuka, & Hara, 2003), and these may be homologous to genes controlling the brittle rachis phenotype in barley and wheat. Given the high collinearity of grass genomes, it is tempting to predict that the repeated occurrences of nonshattering phenotype in cereal crops might have often resulted from the convergent selection acting on the same targets that are orthologous or homeologous genes among grass species.

3.2 Fabaceae

The Fabaceae is the third largest family of angiosperms, comprising more than 800 genera and 20,000 species (Lewis, Schrire, Mackinder, & Lock, 2005) and possessing the greatest number of domesticated crops of any plant family (41 species) (Harlan, 1992). Economically, domesticated legumes are the second most important family of crop plants after the grass family. Pulses (grain legumes) constitute ~27% of the world crop production and provide 33% of the dietary protein consumed by humans and livestock (Smýkal et al., 2015). The legume crops were domesticated worldwide in parallel with local cereal crops. For example, archeological evidence dates the domestication of pea (*Pisum sativum*) back to 10,000 YA in the Near East and Central Asia (Baldev, 1988; Riehl, Zeidi, & Conard, 2013; Zohary & Hopf, 2000), which coincides with the cultivation of wheat and barley. Similarly, the origin of soybean (*G. max*) occurred with the domestication of Asian rice (*O. sativa*) in China (Harlan, 1975; Hymowitz, 1970). While both pulses and cereals underwent selection for a loss of shattering, anatomical differences in the legume fruit create an abscission system that is altogether distinct from mechanisms of seed shattering in cereals (see Section 2).

3.2.1 *Soybean* (G. max)

Soybean was domesticated from its wild progenitor *Glycine soja* in East Asia about 3000–5000 YA (Harlan, 1975; Hymowitz, 1970; Larson et al., 2014). During domestication, cultivated soybean underwent dramatic morphological and physiological modifications, including loss of pod dehiscence; this change is thought to have been essential for the domestication of cultivated soybean. The wild soybean can scatter its seeds very effectively through pod dehiscence in response to drying after maturity (Funatsuki et al., 2012). In contrast, although there is genetic variation in the degree of pod dehiscence

in cultivated soybean, all cultivated varieties are more resistant to shattering than the wild soybean (Funatsuki et al., 2014).

The first soybean QTL for pod dehiscence was identified by Bailey, Mian, Carter, Ashley, and Boerma (1997) who used a recombinant inbred population, derived from a cross between a shattering-resistant cultivar young and a shattering-susceptible accession PI416937, to map the QTL, designated as *qPDH1*, onto linkage group J of chromosome 16. They found that *qPDH1* can account for about 50% of the phenotypic variation in shattering observed in their mapping lines. Thereafter, fine mapping narrowed down the *qPDH1* locus to within a 134 kb genomic region (29,547–29,681 kb) containing 10 predicted candidate genes (Suzuki, Fujino, Nakamoto, Ishimoto, & Funatsuki, 2010). None of these genes showed significant sequence homology with *Arabidopsis* genes associated with pod dehiscence. Further, fine mapping delimited the *qPDH1* within a 47 kb genomic region (29,621–29,668 kb) where two putative genes, Gm16g25600 and Gm16g25610, are present (Gao & Zhu, 2013). Of the two genes, Gm16g25600 encodes a bZIP-type transcription factor, and a 113 bp insertion/deletion (INDEL) polymorphism at the promoter region was initially thought to confer the shattering resistant to the cultivated soybean. However, this hypothesis was refuted by a more recent study which found that percentages of dehisced pods are not necessarily associated with the INDEL (Funatsuki et al., 2014). Instead, a candidate gene *Phd1* (Gm16g25580) located ~20 kb upstream of the 47 kb genomic region is now thought to be responsible for the shattering-resistant phenotype in cultivated soybean. The *Pdh1* gene encodes a dirigent-like protein and shows high expression level in the lignin-rich inner sclerenchyma of pod walls. Results from near-isogenic lines further revealed that the *Pdh1* gene can promote pod dehiscence through increasing the torsion of dried pod walls. In contrast, the shattering-resistant allele, *pdh1*, possesses a single-nucleotide mutation (A to T) that leads to the occurrence of a premature stop codon and then regulates the magnitude of dehiscing force (Table 1). Notably, the shattering-resistant allele was not fixed in cultivated soybean accessions. In the case of Chinese landraces, for example, only about 62% of accessions carry the shattering-resistant allele. These attributes suggest that pod shattering is likely under the control of multiple genes, each with moderate or minor phenotypic effects.

While *Phd1* is not orthologous to *Arabidopsis* pod dehiscence genes, anatomical analyses showed that the fiber cap cells with a lower AL in soybean pods are similar to the lignified valve margin cells with a lateral AL in

Arabidopsis siliques (Christiansen, Dal Degan, Ulvskov, & Borkhardt, 2002; Østergaard, 2009; Tiwari & Bhatia, 1995). To examine the importance of orthologous shattering loci between soybean and *Arabidopsis*, Dong et al. (2014) cloned a total of 11 soybean genes whose orthologs are associated with pod shattering resistance in *Arabidopsis*. In comparisons of nucleotide diversity between wild and cultivated soybean, two of these genes, Gm04g39210 and Gm16g02200, showed obvious reductions in nucleotide diversity consistent with strong selection during domestication. Moreover, cultivated soybean accessions exhibit no genetic variation in the two candidate genes, and one of the genes, Gm16g02200, overlaps with a QTL associated with the soybean pod dehiscence (Grant, Nelson, Cannon, & Shoemaker, 2009). Genetic and functional analyses demonstrated that Gm16g02200, designated as *SHATTERING1–5* (*SHAT1–5*), is the ortholog of *AtNST1/2* in *Arabidopsis* and encodes a NAC domain transcription factor (Table 1). Evidence from gene expression and transgenic complementation analyses confirmed that *SHAT1–5* controls the shattering-resistant phenotype in cultivated soybean by increasing its own expression in fiber cap cells. Population genetic analysis further revealed that a 116 kb genomic region around *SHAT1–5* has undergone a selective sweep during soybean domestication. As discussed in Section 3.1, it is likely that in Asian rice, multiple genes constitute a regulatory network that controls the loss of seed dispersal in the crop. Similarly, it is possible that both *SHAT1–5* and *Pdh1* might be involved in similar genetic pathways in soybean, and that they together regulate the secondary cell wall thickening and shattering resistance found in crop varieties (Dong et al., 2014).

3.2.2 *Common Bean* (P. vulgaris)

Common bean (*P. vulgaris*) is one of the most important legume crops, providing as much as 15% of total daily calories and 36% of total daily protein in parts of Africa and the America (Schmutz et al., 2014). Population genetic analyses revealed that wild common bean consists of two geographically isolated and genetically differentiated gene pools, Mesoamerican and Andean, which diverged about 100,000 YA (Mamidi et al., 2013). The cultivated common bean was domesticated from the two gene pools independently about 8000 YA and then underwent local adaptation that has led to distinct phenotypic characteristics among different cultivars (Bitocchi et al., 2013, 2012; Mamidi et al., 2011).

Like soybean, loss or reduction in pod shattering is a critical trait of domesticated common bean. The wild common bean possesses fibers in

the sutures and pod walls, and loss of these fibers results in the indehiscence of the pods at maturity (Koinange, Singh, & Gepts, 1996). QTL mapping based on a recombinant inbred population between the cultivar Midas and a wild accession G12873 identified two tightly linked QTLs or possibly a single QTL, designated as *St*, on chromosome 2 (Koinange et al., 1996). Recently, Gioia, Logozzo, Kami, Zeuli, and Gepts (2013) cloned an ortholog of *Arabidopsis INDEHISCENT* (*IND*) gene from common bean, *PvIND*. Linkage mapping in an inbred population mapped *PvIND* to chromosome 2, where the *St* QTL also occurs. However, no cosegregation was found between *PvIND* and *St*, and no polymorphisms at the *PvIND* locus are correlated with the dehiscent/indehiscent phenotype, suggesting that *PvIND* is not the candidate gene controlling the pod shattering in common bean.

Recent population genomic analyses based on the whole genomes of 60 wild accessions and 100 landraces have identified ~2500 putative domestication-related genes in the two common bean gene pools (Schmutz et al., 2014). Surprisingly, only 59 candidate genes were shared between the two pools, and pod shattering genes remain undetermined. In an extension of this analysis, we used the DNA sequence of the *Arabidopsis AtIND* gene (At4g00120) to search against the common bean genome on the Phytozome database (http://phytozome.jgi.doe.gov/pz/portal.html); this allowed us to place the ortholog of *AtIND* at a location of 43.63 Mb on chromosome 2. Although the common bean ortholog, *PvIND*, is not among the genes identified by Schmutz et al. as showing a signature of selection during domestication, several putative domestication candidate genes are localized around the *St* locus in the two gene pools. We propose that further genetic analyses could benefit by focusing on the nucleotide variation pattern within this region as a potential source of functional variation.

3.2.3 *Pea* (P. sativum)

Pea is one of the earliest domesticated crops and is mainly cultivated in temperate and subtropical regions (Redden, Leonforte, Ford, Croser, & Slattery, 2005; Riehl et al., 2013). Wild pea exhibits full pod dehiscence upon maturity, while cultivated pea has indehiscent pods that allow all the seeds to be retained at maturity (Abbo et al., 2014). Despite its long history as a genetic model system, dating to Mendel's famous early studies, surprisingly little is known about pea domestication genes. More than 40 YA, the *Dpo1* locus was identified as a major QTL controlling the pod dehiscence in wild pea (Blixt, 1972). However, progress has been slow since then in the

identification of additional QTL associated with the pea pod dehiscence. Most recently, Weeden (2007) detected four pod indehiscence QTLs, *Dpo1*, *Dpo2*, *Np*, and *Gp*, using two different recombinant inbred populations (Weeden, 2007). Of the two mapping populations, all four QTLs were detected in one population; only *Dpo1* and *Np* were detected in the other, and they map to the same linkage group in the two populations. Unfortunately, the actual genes underlying pod indehiscence in cultivated pea are still unknown.

3.2.4 Pod Dehiscence-Related Genes from Other Legumes

In addition to the soybean, common bean, and pea, loss of pod dehiscence has been studied to some extent in lupin (*Lupinus angustifolius*), chickpea (*Cicer arietinum*), and pigeonpea (*Cajanus cajan*) (Abbo et al., 2009; Ladizinsky, 1979; Muehlbauer, Summerfield, & Kaiser, 1998). In the lupin, for example, two QTLs, *Tardus* and *Lentus*, are responsible for the loss of pod shattering in cultivars (Boersma, Buirchell, Sivasithamparam, & Yang, 2007; Boersma, Nelson, Sivasithamparam, & Yang, 2009). In addition, it has recently been documented that the NOOT-BOP-COCH-like genes are conserved among legume species, which together regulate the abscission of process (Couzigou et al., 2016). However, although more than 40 legume crops were domesticated and cultivated worldwide, studies of the identification of pod shattering genes lag far behind those of the cereal crops. It should be noted that both macro- and microsynteny are frequent and widespread among the legume genomes (Choi et al., 2004; Young, Mudge, & Ellis, 2003). These observations suggest that at least some of the genes underlying the pod indehiscence might well be shared among the legume crops. With the recent publication of several legume crop reference genomes, including chickpea, pigeonpea, adzuki bean, and common bean (Kang et al., 2015; Schmutz et al., 2014; Varshney et al., 2012, 2013), we are hopeful that comparative mapping may have considerable utility for future identification and functional characterization of the legume pod shattering-related genes.

3.3 Brassicaceae

The Brassicaceae is a large angiosperm family that contains 338 genera and ~3700 species (Al-Shehbaz, Beilstein, & Kellogg, 2006; Warwick, Mummenhoff, Sauder, Koch, & Al-Shehbaz, 2010), including the model plant *Arabidopsis thaliana*. More than 10 economically important ornamental and crop species in this family were domesticated and are grown throughout

the world (Al-Shehbaz et al., 2006; Meyer et al., 2012; Meyer & Purugganan, 2013). While loss of pod indehiscence is not universally selected for in Brassicaceae crops, it is a feature of many crops, including those within the economically important *Brassica* genus. Brassicaceae fruits develop as siliques which split open upon maturity along a specialized tissue called the valve margin (Balanzá, Navarrete, Trigueros, & Ferrándiz, 2006; Girin, Sorefan & Østergaard, 2009; Girin et al., 2010; Østergaard, 2009; Roberts et al., 2002). Lines of *Arabidopsis* with indehiscent pods as well as indehiscent crop varieties have been studied to identify the underlying pod dehiscence genes. In *Brassica*, both dehiscent and indehiscent phenotypes occur in the diploid species, *Brassica rapa* (AA genome), *Brassica oleracea* (CC), and *Brassica nigra* (BB), as well as in their resulting tetraploids, *Brassica napus* (AACC), *Brassica juncea* (BBCC), and *Brassica carinata* (AABB) (Kadkol, Halloran, & Macmillan, 1985; Meakin & Roberts, 1990b; Morgan, Bruce, Child, Ladbrooke, & Arthur, 1998; Prakash & Chopra, 1988; Spence, Vercher, Gates, & Harris, 1996; Wang, Ripley, & Rakow, 2007; Wei et al., 2010).

3.3.1 *Inferences from* Arabidopsis *for Mustard and Legume Crops*

A. thaliana is the most important plant model system for identifying genes and determining their functions (The *Arabidopsis* Genome Initiative, 2000). The developmental basis and genetic regulatory network underlying pod shattering has been well documented in *Arabidopsis* (Dinneny, Weigel, & Yanofsky, 2005; Dong & Wang, 2015; Ferrándiz, 2002; Lewis et al., 2006; Østergaard, 2009). Here, we focus on the application of these *Arabidopsis* genes to study crop species.

The *Arabidopsis IND* gene plays crucial roles in the development and differentiation of the DZ (Liljegren et al., 2000, 2004). Similarly, *ALCATRAZ* (*ALC*) is another regulatory gene which is specifically expressed together with *IND* in the dehiscence zone during late fruit development (Rajani & Sundaresan, 2001). In contrast, *SHATTERPROOF1* (*SHP1*) and *SHATTERPROOF2* (*SHP2*) are two MADS-box transcription factors that act redundantly to control the pod dehiscence, as neither single mutant displays a detectable phenotype from wild type (Liljegren et al., 2000). Molecular genetic and regulatory network analyses showed that *SHP1/2* are specifically expressed in the DZ and function upstream of *IND* and *ALC* (Colombo et al., 2010; Ferrándiz, 2002; Lewis et al., 2006; Liljegren et al., 2000). Likewise, the *FRUITFULL* (*FUL*) MADS-box gene is expressed in the carpel primordia at early stages of flower development and

negatively regulates *SHP1/2* expression (Ferrándiz et al., 1999). In addition, expression of *SHP1/2* is also regulated by the *REPLUMLESS* (*RPL*) gene which encodes a homeodomain transcription factor and acts on the specification of replum identity (Roeder, Ferrándiz, & Yanofsky, 2003). After the establishment of distinct cell types in the DZ, *NAC* transcription factors (*NST1* and *NST3*) and *SECONDARY WALL-ASSOCIATED NAC DOMAIN PROTEIN1* (*SDN1*) regulate the secondary cell wall thickening and final separation of distinct cell types in dehiscence zone (Mitsuda & Ohme-Takagi, 2008; Zhong, Lee, & Ye, 2010).

Orthologs of these genes have been detected in diverse crop species, and some also show correlations with the pod dehiscence (Arnaud, Lawrenson, Østergaard, & Sablowski, 2011; Boss, Vivier, Matsumoto, Dry, & Thomas, 2001; Dhakate, Shivaraj, & Singh, 2014; Dong et al., 2014; Gioia et al., 2013; Girin et al., 2010; Hua et al., 2009; Mühlhausen, Lenser, Mummenhoff, & Theißen, 2013; Nanni et al., 2011; Peng et al., 2015). For example, the same point mutation at the orthologs of *cis*-element *RPL* is correlated with reduced seed dispersal across the Brassicaceae and even in rice (Arnaud et al., 2011; Konishi et al., 2006). These features strongly suggest that orthologs of these *Arabidopsis* genes have similar functions in a number of crops. To this end, isolation and identification of orthologs of these genes might be an efficient avenue to obtain the phenotypic-related genes in the other crops.

3.3.2 *Rapeseed* (B. napus)

Rapeseed (*B. napus*) is one of the most important oilseed crops and provides more than 13% of the world's supply of vegetable oil (Amar, Becker, & Möllers, 2008; Hajduch et al., 2006). It has been documented that rapeseed ($2n = 38$) is an amphidiploid species that originated from the spontaneous hybridization between *B. oleracea* ($2n = 18$) and *B. rapa* ($2n = 20$) at least 10,000 YA (Hasan et al., 2008; Nagaharu, 1935). Wild forms of *B. napus* have been reported to occur in both Europe and (as a naturalized introduction) New Zealand, where both the diploid species *B. oleracea* and *B. rapa* grow wild (McNaughton, 1976; Shahzadi et al., 2015). The cultivated rapeseed was domesticated in Europe about 400–500 YA and spread from there to the other regions (Gómez-Campo & Prakash, 1999). Unlike the other crops, pod dehiscence has not been eliminated during the domestication of cultivated rapeseed (Kadkol et al., 1985; Meakin & Roberts, 1990a; Morgan et al., 1998; Prakash & Chopra, 1988; Spence et al., 1996; Wang et al., 2007; Wei et al., 2010). Therefore, premature dehiscence before

and during harvest is one of the significant problems for commercial production of rapeseed, which could account for as much as 50% of yield loss if harvesting is delayed (MacLeod, 1981; Price, Hobson, Neale, & Bruce, 1996).

The anatomy and cytology of rapeseed pod dehiscence have been well characterized (Ferrándiz, 2002; Kadkol, 2009; Meakin & Roberts, 1990b; Spence et al., 1996). To identify the genes underlying pod dehiscence, Mongkolporn, Kadkol, Pang, and Taylor (2003) employed randomly amplified polymorphism DNA markers to investigate an F_2 population derived from two shattering-resistant lines. Two markers, RAC-3_{900} and RX-7_{1000}, are linked with the recessive major genes *Sh1* and *Sh2*, respectively. However, neither marker could be mapped onto the *B. napus* linkage map. Hu et al. (2012) identified 70 single-nucleotide polymorphisms (SNPs) which are associated with rapeseed pod shatter resistance. In particular, 14 of these SNPs are localized within a 396-kb genomic region on the chromosome A09. Similarly, several QTLs were also detected from the different rapeseed chromosomes, which together account for more than 38.6–49% (Wen et al., 2013) and 57% (Raman et al., 2014) of the genotypic variations, respectively. However, the candidate genes controlling pod dehiscence remain to be identified. Given that several orthologs of the *Arabidopsis* pod dehiscence-related genes have been identified in *Brassica*, and that ectopic expression of the *Arabidopsis FUL* gene in *B. juncea* can produce pod shatter-resistant *Brassica* fruit (Østergaard, Kempin, Bies, Klee, & Yanofsky, 2006), we propose that, in addition to the QTL mapping approach, these orthologs might provide another strategy to detect pod dehiscence genes in rapeseed.

4. MOLECULAR GENETIC BASIS OF FRUIT RETENTION IN FRUIT CROPS

The dry seed crops, including cereals and legumes, provide the staple food for the world's population. In contrast, fleshy-fruited crops are mainly cultivated as the sources of vegetables and fruits. Fruit crops have been domesticated from a diverse array of plant families, and control of fruit abscission is a common agricultural concern across many of them. Selection for ripe fruit retention can pose special challenges, as many fruit species must shed some of their immature fruits during the growing season in order to allow a subset to fully develop into mature, full-sized fruits (Bangerth, 2000; Sun, Bukovac, Forsline, and van Nocker, 2009). Here, we summarize

our current understanding of the shedding mechanisms in three representative fruit crops, namely tomato, apple, and orange. The three crops were domesticated from the families Solanaceae, Rosaceae, and Rutaceae, respectively, all three of which include a large number of domesticated fruit species that are cultivated throughout the world.

Tomato (*Solanum esculentum* var. *esculentum*) is one of the most important vegetables in the world and was domesticated from the wild species *S. esculentum* var. *cerasiforme* in South America (Blanca et al., 2012; Lin et al., 2014; Peralta, Spooner, & Knapp, 2008; Zuriaga, Blanca, & Nuez, 2009). Compared to the wild species, the domesticated tomato possesses several distinct traits such as a more compact growth habit, larger fruit size, and suppression of fruit shedding (abscission) (reviewed in Bai & Lindhout, 2007). Of these traits, molecular genetic of the fruit abscission has been well documented in previous studies (Budiman et al., 2004; Mao et al., 2000; Nakano et al., 2012; Yang et al., 2005). For example, a MADS-box gene *JOINTLESS* was identified on chromosome 11 in the *jointless* mutant tomato line (Butler, 1936; Mao et al., 2000; Rick & Yoder, 1988) (Table 1). Molecular genetic and transgenic complementation experiments revealed that a deletion in *JOINTLESS* results in the failed development of the pedicel AZ in the mutant. Similarly, the mutant *jointless*-2 was found in the wild tomato *Lycopersicon cheesmanii* and then introduced into the cultivated tomato (Budiman et al., 2004; Rick, 1956). QTL mapping and sequence analyses placed the candidates within a 326-kb genomic region on chromosome 12, where five putative genes were identified (Budiman et al., 2004; Yang et al., 2005). However, the exact candidate genes underlying AZ development are still not determined. In contrast, another MADS-box gene, *MACROCALYX* (*MC*), is thought to play crucial roles in the development of the tomato pedicel AZ (Nakano et al., 2012). Molecular genetic and functional analyses have revealed that *MC* gene shows significant sequence similarity to the *Arabidopsis FUL* gene and interacts physically with the *JOINTLESS* gene. The two genes are specifically expressed in the AZ and regulate the expression of downstream genes, which together contribute to the pedicel development during the abscission.

Within the Rosaceae, apple (*Malus domestica*) is a major fruit crop in temperate regions and has hundreds of varieties throughout the world (Cornille, Giraud, Smulders, Roldán-Ruiz, & Gladieux, 2014). The wild Central Asian species *Malus sieversii* is thought to be the main contributor in the ancestry of the cultivated apple (Coart, Van Glabeke, De Loose, Larsen, & Roldan-Ruiz, 2006; Harris, Robinson, & Juniper, 2002;

Robinson, Harris, & Juniper, 2001; Velasco et al., 2010), although the European crabapple (*Malus sylvestris*) also appears to have made large contributions to the genomic composition of the domesticated species (Cornille et al., 2012).

To reveal the mechanisms underlying the abscission or retention of ripening fruit, Dal Cin, Danesin, Boschetti, Dorigoni, and Ramina (2005) compared the expression pattern of two ethylene biosynthesis genes (*MdACS5B* and *MdACO*) and three hormone receptor/signal transduction genes (*MdERT1*, *MdERS1*, and *MdCTR1*) between nonabscising fruitlet and abscising fruitlet populations. They found that *MdACS5B* and *MdACO* transcripts accumulated during the experimental period in the abscising fruitlet population, whereas the expression patterns of *MdERT1*, *MdERS1*, and *MdCTR1* are dependent on tissue and genetic background. These features suggest that apple fruitlet drop is preceded by a stimulation of ethylene biosynthesis and a gain in sensitivity to the hormone. Thereafter, Sun et al. (2009) investigated 144 accessions representing wild, domesticated, and their hybrids for abscission-related traits. Unexpectedly, although the internal ethylene concentration at the time of abscission varied by over three orders of magnitude, there are no significant differences in seasonal timing of fruit abscission among wild, domesticated apples, and their hybrids.

As described in Section 2, abscission involves four major developmental steps (Fig. 2). Of these steps, regulation of steps 2 and 3 has been investigated most extensively in shedding organs (Botton et al., 2011; Meir et al., 2010; Roberts et al., 2002). Genes involved in ethylene and auxin biosynthesis are especially important in these steps; these are highly conserved among diverse crops and have complex regulatory network interactions. Given the importance of step 1 genes for loss of shattering in grains and legumes (eg, rice *sh4* and soybean *SHAT1–5*; see Section 3), examination of this first developmental step in fruit crops might help to provide new insights into the genetic basis of fruit retention. With the availability of a reference genome for apple (Velasco et al., 2010), it should become increasingly feasible to detect candidate genes controlling the fruit shedding in future.

In the Rutaceae, domesticated citrus (*Citrus* spp.) are cultivated worldwide for juice and fresh fruit; they provide important sources of vitamin C and other health promoting compounds (Wu et al., 2014). Thousands of years of cultivation and extensive interspecific hybridization have yielded about 25 species and at least 250 commercial varieties (Velasco & Licciardello, 2014). The study of abscission in citrus began in the 1950s

because of the high cost of storage after harvesting (Goren, 1993; Wilson & Coppock, 1969). To date, fruits of some citrus varieties are known for their ability to remain on the tree for long periods after ripening. Anatomical, physiological, and hormonal aspects of citrus abscission have been well discussed (Goren, 1993). For example, five AZs are identified in the citrus, of which, the AZ in the calyx is thought to control the fruit shedding of citrus (Goren, 1993) and plant hormones such as ethylene and auxin can regulate the abscission. However, little is known about the molecular mechanisms underlying the fruit shedding in citrus. A recent study has sequenced diverse mandarin, pummelo, and orange genomes, and these genomic data will undoubtedly help to provide new strategies to detect the abscission-related candidate genes in the citrus crops (Wu et al., 2014).

5. CONCLUDING REMARKS

Loss of seed and fruit dispersal mechanisms has occurred repeatedly in diverse crops through independent selection during their domestication processes. Here, we reviewed the molecular genetic and developmental bases of the evolution of nonshattering phenotypes in six major crop families. In general, QTL mapping and linkage analyses are the most common methods used, and majority of the candidate genes have been localized based on these traditional approaches. However, pedigree mapping populations are less easily developed in perennial and vegetatively propagated crops (Ross-Ibarra, Morrell, & Gaut, 2007). With advances in sequencing technologies and increasing reference genomes, population genomics provides an efficient means to detect candidate genes related to fruit/seed retention and other domestication traits. In particular, it has been well documented that orthologs from different species might have similar functions. We therefore propose that future studies should combine both traditional mapping and modern genomic strategies. Ultimately, as our knowledge of candidate genes increases, we will be able to begin to shift away from a focus on individual gene evolution toward regulatory networks and their integrated evolutionary interactions.

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