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Classification of Apple Genetic Resources Using Early Fruit Abscission Pattern

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Abstract

Apple trees generally have heavy bloom and fruit set, producing a surplus of fruit that cannot be supported to maturity. Fruit thinning is necessary for improving fruit size and quality, but chemical thinning can be inconsistent in effectiveness and hand thinning is very laborious and expensive. Therefore, self-abscising cultivars in which fruits abscise themselves within a cluster can be useful for time- and labor-saving commercial production. Based on the fruit abscission pattern from full bloom to 30 days after full bloom, 48 apple genetic resources were classified into three groups: 1) a non-abscising group, in which no fruits were abscised; 2) a June drop group, in which the abscission process occurred non-selectively in clusters; and 3) a self-abscising group, in which only the central or the last fruit in a cluster remained to grow, and the others were abscised. Most cultivars in the self-abscising group showed a fruit abscission pattern, in which the central fruit dominated over lateral fruits in a cluster, inducing their growth inhibition and final abscission. Exceptionally, in *Malus coronaria* 'Charlottae', the central fruit did not dominate the lateral fruits, but was abscised first within a cluster. The date of full bloom and fruit weight were significantly related to fruit abscission – fruit abscission was delayed with early dates of full bloom and smaller fruit size.

Apple trees generally produce excess fruitlets to the extent that trees are not able to maintain the full initial fruit load. Fruit thinning is an essential practice for producing apples of commercial size and quality (Dennis, 2000). However, chemical thinning results in considerable variability in efficacy depending on environmental conditions (Wertheim, 2000). Furthermore, thinning chemicals sometimes have harmful side effects including tree vigor and yield reduction (Black et al., 1995; Marini, 1996), fruit malformation and russeting (Bound et al., 1993), and reduction of pollinating insect populations (Dennis, 2000). In small-scale cultivation, hand thinning is often practiced to obtain bigger, higher-quality fruit, but it is labor- and time-intensive. Self-abscising cultivars would be an effective alternative and be well suited to modern apple production and, consequently, the development of cultivars with this characteristic has recently been included in breeding programs.

Early fruit abscission is characterized by the survival of only one fruit in a cluster, while the other fruits are abscised within 30 days after full bloom (DAFB). Early fruit abscission is induced by competition occurring among fruitlets in a cluster (intra-fruitlet), among fruitlets throughout the entire tree (inter-fruitlet), and between fruitlets and bourse shoots (Bangerth, 2000). Although many factors are associated with the induction of fruit abscission, the interplay between auxin and ethylene has long been thought to trigger fruit abscission (Abebie et al., 2008; Abeles

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and Rubinstein, 1964; Sexton, 1997; Taylor and Whitelaw, 2001). Ethylene production is reported to activate abscission by increasing the expression of hydrolytic enzymes and by decreasing auxin transport according to the model of senescence-triggered abscission based on leaf explants (Bonghi et al., 1993; Suttle and Hultstrand, 1991). However, this model cannot be applied to the abscission of young apple fruit, because no increase in ethylene production is observed during the early stages of abscission (Bangerth, 2000; Sun et al., 2009). Bangerth (2000) proposed a correlative inhibition model, suggesting that the central fruit, which blooms first in a cluster, dominates auxin export by repressing transport from adjacent lateral fruits. The growth of dominated fruits is inhibited and their abscission is initiated, resulting in programmed organ shedding.

Carbohydrate competition among inter-fruitlets or intra-fruitlets could lead to sugar starvation in abscising fruitlets, because fruitlets having lower sink strength were abscised more readily (Botton et al., 2011; Iwanami et al., 2012; Lakso et al., 2006). Apple microarray experiments have suggested that sugar starvation, rather than auxin transport, is a more important trigger of fruit abscission. Sugar starvation mediates reactive oxygen species accumulation, and abscisic acid (ABA) and ethylene signaling, resulting in activation of the abscission process (Botton et al., 2011). Furthermore, the abscission process accompanies an increase in ABA content (Giulia et al., 2013).

To investigate abscission-related characteristics during early fruit development and ultimately introduce these characteristics into breeding programs, the abscission patterns of 48 representative apple cultivars (*Malus* × *domestica* Borkh.) and *Malus* species were evaluated. The apple genetic resources were classified according to their fruit abscission pattern based on the numbers of fruits persisting from full bloom (FB) to 30 DAFB, and they were examined in terms of the date of FB and fruit weight.

Materials and Methods

Forty-eight apple genotypes were grown at the orchard of the National Institute of Horticultural and Herbal Science, Suwon, Korea. Their early fruit abscission patterns were evaluated from FB until 30 DAFB by counting the persisting fruits. The numbers of remaining fruits were counted from 100 fruitlet clusters of the different cultivars or species. Five to ten trees of each cultivar or species were used to evaluate the early fruit abscission patterns over the 2004 to 2013 period. Data collected in 2013 are presented in this study. Although the data presented were collected in only one year, observations across a number of growing seasons indicate that the patterns of flowering, abscission and fruit set that are reported here were consistent from year-to-year. The dates of FB were recorded following the examination references of fruit trees in the Rural Development Administration, Korea. The date was defined as the observation date when at least 90% of the flowers throughout the tree bloomed. Fruits were weighed at 30 DAFB. All flowers were hand-pollinated with mixed pollens collected from various cultivars to avoid self-incompatibility resulting from the same S-genotypes.

Results and Discussion

According to the patterns of fruit abscission within 30 DAFB, the 48 apple genetic resources could be categorized into three groups (Table 1): 1) a non-abscising group, in which no fruits were abscised; 2) a June drop group, in which the abscission process occurred non-selectively in clusters; and 3) a self-abscising group, in which only the central or last fruit in a cluster remained to grow and the others were abscised. Most crabapples belonged to the non-abscising group, and non-abscised fruits even adhered to the peduncles in their dried form until the following year. No abscission occurred in this group, suggesting either that the abscission mechanism is absent or that it is disrupted in the course of abscission. For example, few

Table 1. Classification of apple genetic resources used to study the early fruit abscission pattern from full bloom to 30 days after full bloom. The parentage information was from Kitahara et al. (2005) and http://www.orangepippin.com.

Abscission pattern type	Cultivar	Parentage
Non-abscising	Flower of Kent	Unknown
	M.9	Seedling of Paradise
	M.26	Seedling of Paradise
	M.27	Seedling of Paradise
	MM.106	Northern Spy × M.1
	M. baccata Manchurian	Unknown
	M. floribunda 821	Unknown
	M. asiatica	Unknown
	M. sieboldii	Unknown
	M. gloriosa	Unknown
	M. arnoldiana	Unknown
	M. macromalus	Unknown
	M. sargentii	Unknown
	M. prunifolia	Unknown
	Ottawa 322	Unknown
	P.14	Unknown
June drop	Chukwang	Fuji × Mollie's Delicious
	Discovery	Seedling of Worcester Pearmain
	Earliblaze	Unknown
	Fuji	Ralls Janet × Delicious
	Gala	Kidd's Orange × Golden Delicious
	Gamhong	Earliblaze × Unknown
	Golden Delicious	Unknown
	Hongro	Earliblaze × Golden Delicious
	Jonagold	Golden Delicious × Jonathan
	Ralls Janet	Unknown
	Red Delicious	A sport of Delicious
	Saenara	Earliblaze × Golden Delicious
	Sekaiichi	Red Delicious × Yellow Delicious
	Shinano Sweet	Fuji × Tsugaru
	Tsugaru	Golden Delicious × Jonathan
Self-abscising	Arlet	Golden Delicious × Idared
	Akane	Jonathan × Worcester Pearmain
	Belle de Boskoop	Unknown
	Caravel	Melba × Crimson
	Carroll	Moscow Pear seedling × Melba
	Hokuto	Fuji × Mutsu
	Hwahong	Fuji × Sekaiichi
	Kizashi	Unknown
	Kougetsu	Golden Delicious × Jonathan
	M. coronaria Charlottae	Unknown
	Mutsu	Golden Delicious × Unknown
	Saika	Akane × Orin
	Sansa	Gala × Akane
	Suntan	Cox's Orange Pippin × Court Pendu Plat
	Virginia Gold	Newton Pippin × Golden Delicious
	X3191	Idared × Prima
	Yoko	Golden Delicious × Jonathan

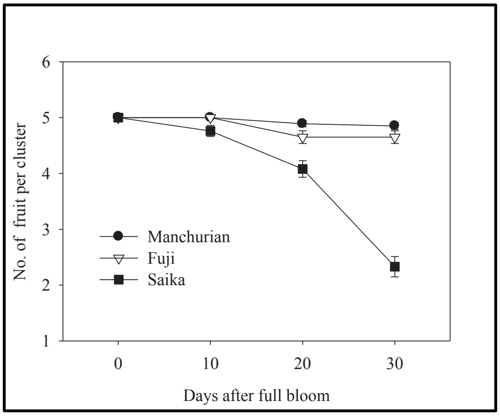

Fig. 1. Early fruit abscission from full bloom to 30 days after full bloom in *Malus baccata* 'Manchurian', 'Fuji', and 'Saika', representing the non-abscising, June drop, and self-abscising groups, respectively. Fruit abscission was evaluated in 100 flower clusters from at least five trees. Vertical bars are the standard errors of the means.

fruits were abscised in the non-abscising cultivar *M. baccata* 'Manchurian' (Fig. 1). The majority of commercial cultivars were included in the June drop group. Within this group, the abscission process occurred non-selectively throughout the entire tree; as a result, either all of the fruits in a cluster were abscised, or all of the fruits survived. In the June drop group, 'Fuji' sometimes maintained almost five fruits per cluster until 30 DAFB, while in other instances entire clusters were detached beginning at 10 DAFB (Fig. 1). The self-abscising group showed a selective abscission pattern. Typically only the central fruit persisted in a cluster and four lateral fruits were shed within 30 DAFB. In the self-abscising group, with 'Saika', for example, the lateral fruits were dropped, and only one fruit persisted in a cluster when abscission occurred. However, the average number of remaining fruits was counted as 2.3 on the basis of the entire tree, because no abscission occurred in some clusters (Fig. 1). Consequently, less additional fruit thinning is required for the cultivars in this self-abscising group.

Based on the date of FB, most *Malus* species that belonged to the non-abscising group (88.2%) bloomed at early dates (Fig. 2A). The majority of commercial cultivars that belonged to the June drop or self-abscising group had a later date of FB than the non-abscising group (Fig. 2). Hence, it appeared that the earlier that the date of FB occurred, the lower was the amount of early fruit abscission that took place.

Fruit weight was significantly related to fruit abscission, with smaller fruit among the abscission groups being associated with a lower amount of early abscission (Fig. 3). *Malus* species in the non-abscising group weighed less than 30 g, a distinctive feature of crabapples, whereas the rest weighed more than 50 g. Crabapples may evade intra-fruitlet competition in a cluster or inter-fruitlet competition throughout the entire tree due to their small fruit size. For most commercial cultivars, however, competition for carbohydrates may be a main factor because their fruits are big enough to trigger early abscission. Considering carbohydrate competition among inter-fruitlets or intra-fruitlets, limited allocation of photosynthates causing sugar starvation would likely occur in abscising fruitlets as sink strength is reported to be an important factor in driving early abscission (Botton et al., 2011; Celton et al., 2014; Giulia et al., 2013; Iwanami et al., 2012; Lakso et al., 2006).

Most cultivars in the self-abscising group, like 'Saika', showed a fruit abscission pattern in which the central fruit dominated over lateral fruits in a cluster, inducing their growth inhibition and final abscission (Fig. 4A). There was one exception; in *M. coronaria* 'Charlottae', the central fruit did not dominate the lateral fruits, but was abscised first in a cluster (Fig. 4B). The fruit nearest the peduncle survived, although it had bloomed last. Therefore, its pollination and fertilization were likely the most delayed. Although the apical flower bloomed earlier, it abscised first from a cluster. Fruits were shed sequentially from the distal fruit toward the peduncle. Finally, only the proximal fruit in

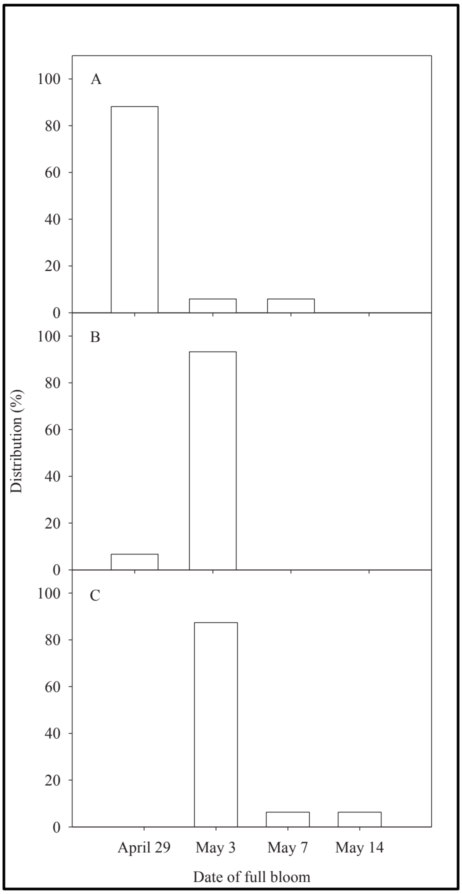

Fig. 2. Distribution of apple genetic resources with regard to the date of full bloom in the different fruit abscission groups. A, non-abscising group; B, June drop group; C, self-abscising group.

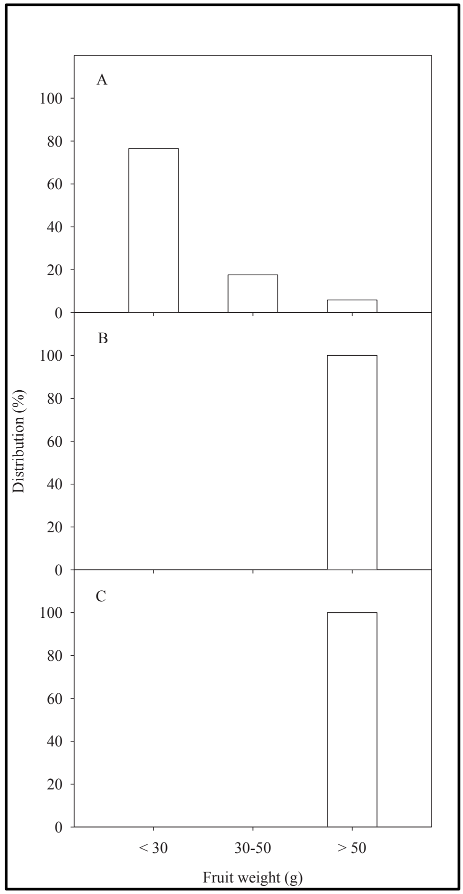

Fig. 3. Distribution of apple genetic resources with regard to fruit weight in the different fruit abscission groups. A, non-abscising group; B, June drop group; C, self-abscising group.

a cluster survived. The apical fruit might be prevented from exporting auxin by the lateral fruits and consequently eventually be abscised. Then, the second flower is dominated by the third flower, the third by the fourth, and so on sequentially due to the lack of pedicel clustering. In *M. coronaria* 'Charlottae', pedicels are not clustered at a peduncle (Fig. 5B); rather, they separate independently, rotating along the apical pedicel from the central axis, so they look like lateral shoots emerging from a primary shoot, forming a counter-clockwise whorl. Accordingly, the first flower (apical fruit) is most hampered, and the fifth flower (proximal fruit) has a high possibility of surviving, because it is disturbed the least. These observations show that the factors inducing abscission in 'Saika' may be transported basipetally through fruit pedicels, prioritizing interconnection with the main vasculature of the stem (Fig. 5A), whereas in *M. coronaria* 'Charlottae', other factors may be transported acropetally toward the apical fruit (Fig. 5B). The fruit ab-

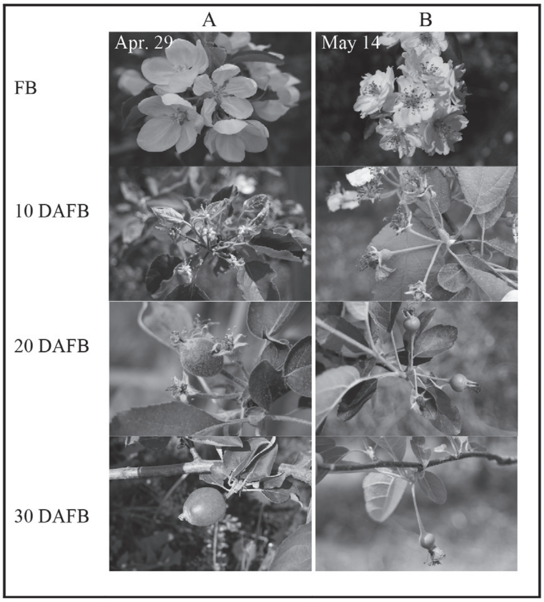

Fig. 4. Abscission patterns of young fruits within a cluster in self-abscising apple cultivars. A, 'Saika'; B, *Malus coronaria* 'Charlottae'.

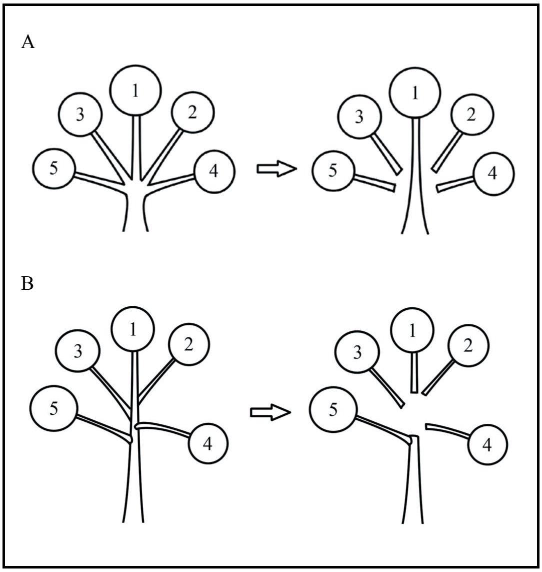

Fig. 5. Self-abscission patterns in apple genetic resources. A, 'Saika'. The central fruit dominates the lateral fruits and causes most of the lateral fruits to be abscised; B, *Malus coronaria* 'Charlottae'. Fruits are abscised successively from the central one in a cluster and the last one to flower survives to grow and ripen. Numbers represent the flowering order.

scission in 'Saika' could be explained by a correlative inhibition model, in which inhibition of auxin transport is considered the main signal inducing the early fruit abscission (Bangerth, 2000). The central fruit, which is connected to the main vasculature of the auxin stream in a stem, predominates in auxin transport, strengthening its comparative advantage over lateral fruits, whereas the lateral fruits cannot join this vasculature as directly and are easily abscised.

In this study, we classified apple genetic resources using the early fruit abscission pattern. The main factor inducing fruit abscission may be sugar starvation associated with a source-sink relationship (Botton et al., 2011; Celton et al., 2014; Guilia et al., 2013; Iwanami et al., 2012; Lakso et al., 2006) or genes related to auxin signaling (Dal Cin et al., 2009). The mechanisms of early fruit abscission should be examined in more detail.

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