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## Involvement of cell proliferation and cell enlargement in increasing the fruit size of *Malus* species

Takeo Harada<sup>a,\*</sup>, Wakako Kurahashi<sup>a</sup>, Masumi Yanai<sup>b</sup>,  
Yuhya Wakasa<sup>c</sup>, Takashi Satoh<sup>d</sup>

<sup>a</sup> Department of Agriculture and Life Science, Hirosaki University, Hirosaki 036-8561, Japan

<sup>b</sup> Institute for Environmental Science, Rokkasho 039-3212, Japan

<sup>c</sup> National Institute of Agrobiological Science, Tsukuba 305-8602, Japan

<sup>d</sup> Division of Breeding, Aomori Apple Experimental Station, Kuroishi 036-0332, Japan

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### Abstract

Cell number and cell size in the fruit flesh of five *Malus* cultivars (two crabapples and three domesticated apples) were analyzed from soon after blossom until maturity. *M. floribunda*, whose fruit size is one of the smallest among *Malus*, exhibited absence of cell proliferation throughout fruit ontogeny. Furthermore, the rate of cell enlargement, which was almost uniform until the mature stage in other species, slowed down from about 45 days after full blossom (DAFB), resulting in a cell size approximately half that of the other cultivars. The fruit of *M. coronaria*, which is of medium size, possessed approximately half the cell number of *M. domestica* cv. ‘Fuji’, due to a slower proliferation rate. The cv. ‘Sekaiichi’ of *M. domestica* had the largest fruit among the cultivars investigated, and showed a faster increase in cell number. These results indicate that a combination of greater cell division capacity and an enhanced degree of cell enlargement are involved in the increase of *Malus* fruit size.

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**Keywords:** *Malus*; Apple; Fruit size; Domestication; Cell size; Cell number

\* Corresponding author. Tel.: +81 172 39 3777; fax: +81 172 39 3750.

E-mail address: [tharada@cc.hirosaki-u.ac.jp](mailto:tharada@cc.hirosaki-u.ac.jp) (T. Harada).

## 1. Introduction

In addition to the factors that define apple fruit quality, such as color, firmness, and flavor, size is also an economically important characteristic. Many reports have described the effect of environmental factors on size (Skene, 1966; Westwood et al., 1967; Atkinson et al., 2001; Stanley et al., 2001). Fruit thinning leads to an increase in the final size of remaining fruit due an increase in the leaf:fruit ratio (Magness and Overley, 1929; Batjer et al., 1957; Forshey and Elfving, 1977). However, when grown under the same conditions, some cultivars have large fruit, while others have small fruit, so that conspicuous differences in fruit size among cultivars appear to be of genetic origin.

Intrinsically, there is a great difference in fruit size among *Malus* species. For example, crabapples are seldom larger than 5 cm in diameter, whereas some cultivated apples are often larger than 10 cm. Recent DNA analyses have suggested that the domesticated apple originated from *M. sieversii*, a ‘wild apple’ of Central Asia, whose fruit is only about 4 cm in diameter (Harris et al., 2002). Ataxonomic study by Robinson et al. (2001) also favored the hypothesis that *M. sieversii* and its close relatives are the progenitors of *M. domestica*. It has been considered that throughout a period of several million years, more large fruit have been selected by mammals such as bears that have acted as distribution vehicles. In addition, selection by humans might also have contributed to increasing the fruit size and widening the area of distribution. However, recent investigations do not support the concept of human involvement, because large-scale collection of *M. sieversii* from Central Asia has revealed that some trees have a fruit size exceeding 6 cm, thus approaching that of many commercial cultivars (Luby et al., 2001). Aside from theorization, little is known about how apples have increased their fruit size.

It is a matter of course that disparity in the size of apple fruit between species is the result of differences in cell number and/or cell size (Bain and Robertson, 1951). Cell number is generally determined in the first 35–50 days after full blossom (DAFB) (Denne, 1960). After this cell division phase, the increase in fruit size depends on enlargement of the cells. Several studies have shown a very close relationship between cell number and ultimate fruit size (Smith, 1950; Bain and Robertson, 1951; Skene, 1966; Westwood et al., 1967). However, this evidence was obtained from only a few domesticated apple species. There have been no data from the tiny fruit of crabapples or huge fruit such as that of cv. ‘Twenty Ounce’ (Beach et al., 1905). It would be of considerable interest to determine whether cell proliferation and/or cell enlargement is reduced in the small crabapple or conversely increased in the case of very large fruit. In order to know which cell event has contributed to the increase of fruit size during the course of *Malus* domestication, we measured the cell size and cell number of fruits of two crabapple and three domesticated apple cultivars during their fruit ontogeny.

## 2. Materials and methods

### 2.1. Plant materials

Two crabapples and three domesticated apple cultivars differing markedly in fruit size were used in this study (Table 1). The latter cultivars were thinned conventionally by hand

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