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Xylem vessel element structure explains why columnar apple trees flower early and have higher yield

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The vessel elements of secondary xylem in branches of columnar and normal apple trees were studied by isolation method and micrograph. The lengths and diameters were measured and the type of side wall (reticulate or pitted) was noted. Most of the perforation plates were simple. Normal apples had more abnormal vessel element cells than columnar apples. The average diameter of the xylem vessel elements of columnar apples was 43.27 µm, which was significantly greater than that of normal apples (32.64 µm). The lengths of the vessel elements did not differ significantly between columnar and normal apples. The results provided a theoretical basis for explaining the early flowering and fruiting of columnar apple trees and their higher fruit yield.

Key words: Columnar apple, isolation method, vessel element.

INTRODUCTION

The xylem vessel is a major component of plant vasculature, and the structure of vessel elements, the cells that make up xylem vessels, can affect growth and development of plants by affecting the rate of water and mineral transport. Columnar apple trees originated from the 'Weisai Ke Xu' mutant of the cultivar 'Asahi' and have many advantages over normal apple trees, such as very short internodes, high germination rates, weak branching, and generally short lateral branches from the trunk (Zhang et al., 2003). In particular, columnar apples flower and fruit earlier than normal apples, making columnar apples valuable resources for the genetic improvement of apples.

Previous research has investigated various aspects of columnar apples, including cultivar breeding (Dai et al., 2003), leaf anatomy (Liang et al., 2009), photosynthetic characteristics (Zhang et al., 2010), and vessel element biology based on element marker-based (Wang et al., 2002; Tian et al., 2005). Vessel element structure and the evolution of secondary xylem vessels has been reported in peach (Guo et al., 2008), mango (Chen and Tang, 2005), Grevillea (Chen and Tang, 2004a), Aquilaria (Chen and Tang, 2004b), Manilkara (Chen, 2007), but apple, especially columnar apple, has been little studied. In this study, the general internal structure of secondary xylem vessels of columnar apples was compared with that of normal apples using the segregation method and micro-photography to provide a theoretical basis for understanding the earlier flowering and fruiting phenology of columnar apples.

MATERIALS AND METHODS

Test material was collected in March 2011 from apple trees growing at the Qingdao Laixi Toyozane horticultural farm. South-facing branches were sampled from 2-year-old trees that were 1.5 m high and showed consistent growth.

The cultivars were as follows: Cultivar 1, Normal hybrid offspring of '*Fuji*' × '*Telamon*'; Cultivar 2, Normal hybrid offspring of '*Gala*' × '*Telamon*'; Cultivar 3, '*Fuji*'; Cultivar 4, Columnar hybrid offspring of '*Fuji*' × '*Telamon*'; Cultivar 5, Columnar hybrid offspring of '*Gala*' × '*Telamon*'; Cultivar 6, '*Telamon*'. Cultivars 1, 2 and 3 were normal

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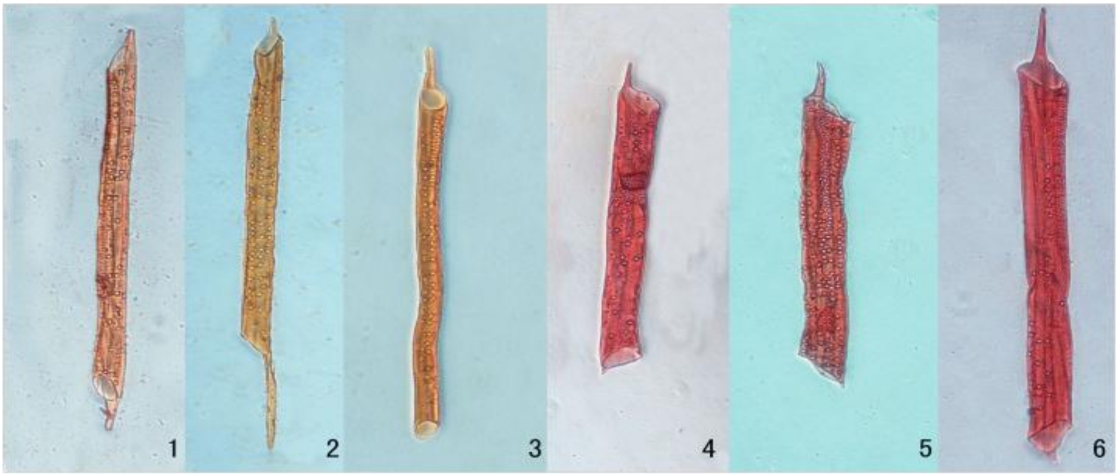

Figure 1. The pitted vessel element shape of xylem of branches from different cultivars:1, '*Fuji*'×'*Telamon*' normal apple; 2, '*Gala*'×'*Telamon*' normal apple; 3,'*Fuji*'. 4, '*Fuji*'×'*Telamon*' columnar apple; 5, '*Gala*'×'*Telamon*' columnar apple; 6, '*Telamon*'.

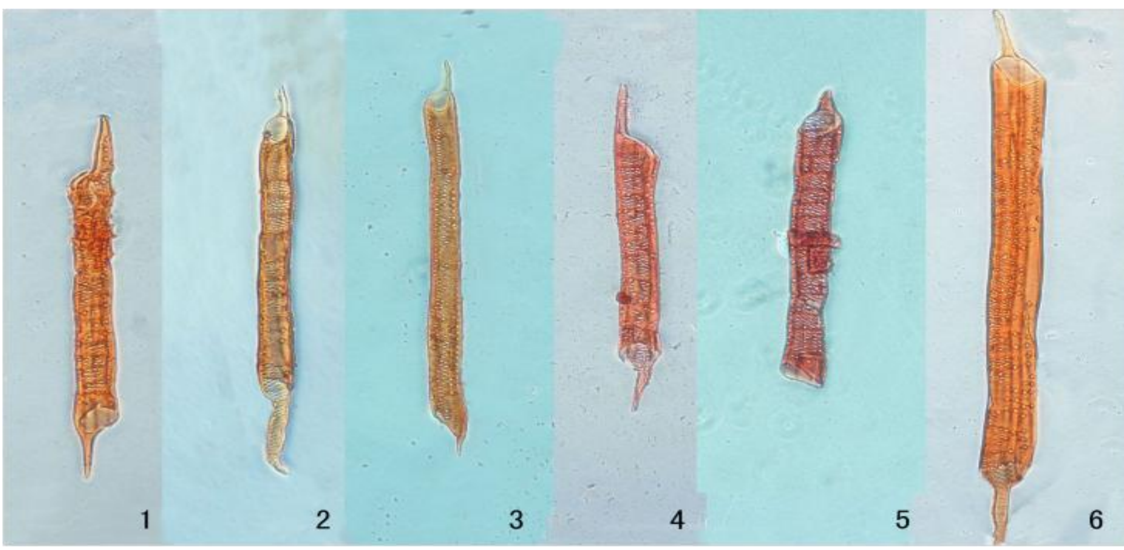

Figure 2. The reticulate vessel element shape of xylem of branches from different cultivars: 1, '*Fuji*'×'*Telamon*' normal apple; 2, '*Gala*'×'*Telamon*' normal apple; 3, '*Fuji*'. 4, '*Fuji*'×'*Telamon*' columnar apple; 5, '*Gala*'×'*Telamon*' columnar apple; 6, '*Telamon*'.

cultivars, and cultivars 4, 5 and 6 were columnar cultivars.

Experimental methods

Cut branches were washed and approximately 1 cm pieces cut from the same positions on each branch. These pieces were vertically sliced into cross-sectional strips 2 to 3 mm wide and dried for 3 to 4 days at 30 to 40°C in an incubator (Chen and Xie, 2003). Each piece was made into a temporary slide by staining with 0.5% Safranin dye, then observed and its vessel elements microscopically photographed with a Nikon E80i biological microscope. One hundred samples of each cultivar were randomly observed. We measured vessel length (excluding tail) and diameter with Image-Pro Plus 6.0, then averaged and statistically analyzed the data using the DPSv7.05 software.

RESULTS AND ANALYSIS

Morphology of xylem vessel elements of apple branches

Xylem contains two types of vessel elements: pitted and reticulate. The type of xylem vessels found in shoots of columnar apple trees was not significantly different from those of normal apple trees under light microscopy (Figures 1 and 2). In normal apple trees,

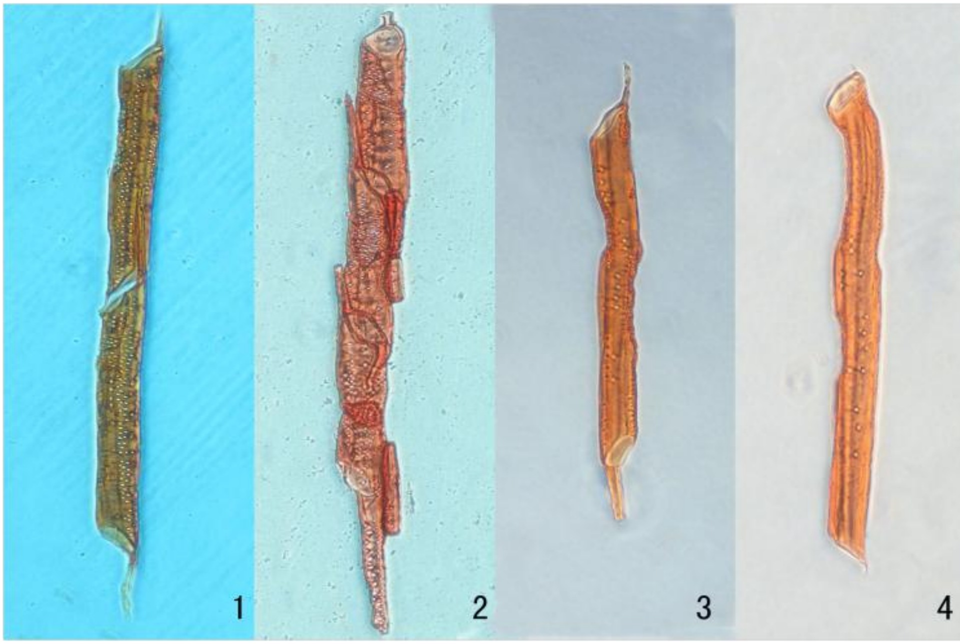

Figure 3. The connection of vessel element in vertical and abnormal cells: 1 and 2 are the connection of vessel element in vertical; 3 and 4 are the abnormal cells.

69.7% of the vessel elements were reticulate, compared with 75.7% in columnar apple trees. The perforation plates that serve as the vertical connections between vessel elements were also observed when possible. There were some abnormal vessel elements (vessel elements of uneven diameter) (Figure 3). The columnar apples had fewer deformities of their vessel elements (a 5.75% malformation rate) than normal apples (9.66%).

Vessel element length in two types of apple branches

The average lengths of the vessel elements were 243.359, 253.875, 260.776, 240.747, 218.674 and 293.383 µm for cultivars 1 to 6, respectively. There were no significant differences in average vessel element length between columnar and normal apple branches (Table 1).

Vessel element diameter in two types of apple branches

The average diameters of the vessel elements of cultivars 1 to 6 were 35.345, 32.255, 30.318, 43.830, 41.638 and 44.345 µm, respectively. The vessels of columnar apples were significantly wider than those of normal apples ($P < 0.01$), and the diameters of different cultivars in the same types had significant difference ($P < 0.05$) (Table 2).

DISCUSSION

The main function of xylem vessels is to transport water and minerals from the roots to other parts of the plant to support transpiration and photosynthesis. Columnar apples had more reticulate vessel elements, less secondary wall thickening, and fewer abnormal vessel elements in their xylem than normal apples. These anatomical differences would enhance the transport rate of water and minerals in both horizontal and vertical directions. Vessel element structure explains why columnar apples have a higher transport efficiency of water and minerals and a photosynthetic efficiency than normal apples (Zhang et al., 2010), and also explains why columnar apples have the physiological characteristics of earlier flowering and fruiting and higher yield.

Physiological anatomist Zimmermann (1983) proved that the diameter of xylem vessels was directly related to the transport rate. That is, the larger the diameter of a xylem vessel, the higher its transport efficiency. The average diameter of xylem vessel elements of columnar apples was significantly greater than that of normal apples. The larger vessel diameter enhances the transport efficiency of water and minerals. Columnar apples thus have more efficient and rapid transport to the leaves, which benefits photosynthesis. The data presented here has provided an anatomical explanation for early flowering and fruiting in columnar apple trees (Zhang et al., 2010).

The relationship between the lengths of vessel elements and water transport is still debated. Bass et al. (1983) believed that the lengths of individual vessel elements were not directly related to water transport efficiency but that the total length of the xylem vessel was directly correlated to water transport efficiency. Carlquist (1975) pointed out that the longer the xylem vessel, the smaller the resistance of water transport. The relationship

Table 1. Comparison of the length of the vessel elements of xylem of branches between columnar and normal apple.

Number	Variety (Combination)	Type	Length of the vessel element(μm)		
			Average	Max	Min
1	*Fuji* × *Telamon*	Normal	243.359^{bBC}	482.485	111.691
2	*Gala* × *Telamon*	Normal	253.875^{bB}	518.067	105.897
3	*Fuji*	Normal	260.776^{bB}	443.888	110.093
4	*Fuji* × *Telamon*	Columnar	240.747^{bBC}	384.116	101.233
5	*Gala* × *Telamon*	Columnar	218.674^{cC}	470.394	103.748
6	*Telamon*	Columnar	293.383^{aA}	485.454	116.505

Note: Different letters of A, B, C and D represent significant difference at α = 0.01 level. Different letters of a, b, c and d represent significant difference at α = 0.05 level. Material 1 was '*Fuji*'×'*Telamon*' normal apple, Material 2 was '*Gala*'×'*Telamon*' normal apple, Material 3 was '*Fuji*', Material 4 was '*Fuji*'×'*Telamon*' columnar apple, Material 5 was '*Gala*'×'*Telamon*' columnar apple, Material 6 was '*Telamon*'.

Table 2. Comparison of the dimension of the vessel element of xylem of branches between columnar apple and normal apple.

Number	Variety (Combination)	Type	Dimension of the vessel element (μm)		
			Average	Max	Min
1	*Fuji* × *Telamon*	Normal	35.345^{cC}	51.712	17.476
2	*Gala* × *Telamon*	Normal	32.255^{dD}	53.886	11.989
3	*Fuji*	Normal	30.318^{eD}	46.078	13.062
4	*Fuji* × *Telamon*	Columnar	43.830^{aA}	57.226	22.230
5	*Gala* × *Telamon*	Columnar	41.638^{bB}	59.653	26.096
6	*Telamon*	Columnar	44.345^{aA}	66.021	22.862

Note: Different letters of A, B, C and D represent significant difference at α = 0.01 level. Different letters of a, b, c and d represent significant difference at α = 0.05 level. Material 1 was '*Fuji*'×'*Telamon*' normal apple, Material 2 was '*Gala*'×'*Telamon*' normal apple, Material 3 was '*Fuji*', Material 4 was '*Fuji*'×'*Telamon*' columnar apple, Material 5 was '*Gala*'×'*Telamon*' columnar apple, Material 6 was '*Telamon*'.

between vessel element length and apple type still needs further study.

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