Frequency of Vascular Nodules in the Fruit of 'Gala' x 'Splendour' Hybrids and Other Apple Cultivars

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Abstract. The new apple (*Malus × domestica* Borkh.) cultivar Sciros™, resulting from a cross of 'Gala' with 'Splendour', is marketed internationally from New Zealand. A characteristic of this cultivar is the presence of dense, dark green or black nodules in the fruit cortex, located in close proximity to the five sepal vascular bundles. Nodules are visible as green spots beginning about 40 days after bloom and they continue to develop, reaching a length of up to 8 mm at fruit maturity, although there is considerable variation in their size. Large vascular nodules often develop dark brown centers and reduce the visual quality of the fruit flesh. The frequencies of vascular nodules in 61 'Gala' x 'Splendour' hybrids from New Zealand and British Columbia, Canada, were examined. These ranged from a mean of 0 to 12.1, depending on the hybrid. Thirteen hybrids were in the high frequency class (2.76–12.1), 28 in the low frequency (0.04–1.86), and 20 were without nodules. The mean nodule frequency in Sciros™ was 12.1 nodules per fruit, the highest of all hybrids examined. Our survey of 44 other cultivars confirmed the occurrence of vascular nodules in 'Gala' and 'Splendour', with mean vascular nodule frequency of 1.9 and 0.5 nodules per fruit, respectively. Nodules were also found in 'Newtown Pippin' (frequency 0.8), and in a 'Newtown Pippin' x 'Granny Smith' hybrid (frequency 0.1).

The frequent occurrence of small green vascular nodules consisting of aggregations of small cells, often with a lignified central cavity, in the cortex of 'Gala' x 'Splendour' hybrids was reported by Lane et al. (2000). Their presence in the hybrids and in both parents at low frequency, but not in most other cultivars, suggested a genetic predisposition to nodule development. Nitrogen nutrition, geographical location, fruit position within the tree, tree age, and endophytic bacteria in the cortex and nodules did not explain the presence of the nodules, although deficit irrigation was reported to promote nodule frequency in 'Gala' (Lane et al., 2000).

Vascular nodules in apple fruit cortex are closely associated with the large vascular bundles, and they increase in size and change color from pale green to dark green or black and sometimes red during growth and development. As vascular nodules enlarge in mature

fruit, the center of the nodules often becomes brown. This appears to be the result of the death of some of the cells in the central part of the nodule and formation of a lignin shell. When the nodule is bisected, a brown central cavity surrounded by lignin is apparent. The nodules are not conspicuous in freshly picked fruit, but they become more noticeable after storage and the appeal of the fruit to the consumer is reduced, especially if the fruit is sliced longitudinally.

Our report details the presence or absence and frequency of vascular nodules in 61 'Gala' x 'Splendour' hybrids originating and grown in both New Zealand and British Columbia, Canada. In addition, 44 apple cultivars, including 'Gala' and 'Splendour', grown in one or both locations were examined for nodules. We provide further information on the vascular nodule frequency distribution of 'Gala' x 'Splendour' breeding selections.

Materials and Methods

Apples (*Malus × domestica* Borkh.) used in this investigation were from samples collected from the repository orchard located at the HortResearch Hawkes Bay Research Centre at Havelock North, Hawkes Bay, New Zealand, and from breeding and cultivar plots at the Pa-

cific Agri-Food Research Centre, Summerland, British Columbia, Canada. At Hawkes Bay, fruit of 41 'Gala' x 'Splendour' hybrids were picked from 13-year-old trees. This fruit was stored at 1 °C and nodules examined within 3 weeks of picking. The Summerland fruit was from trees 7–9 years old of 20 'Gala' x 'Splendour' hybrids. This fruit was stored at 5 °C and examined within 5 d of picking. Several of the 'Gala' x 'Splendour' hybrids have been released as named cultivars (Table 1). Sample sizes were 25 fruit for the fruit collected at Hawkes Bay and a lesser number (indicated in Table 1) for some Summerland samples.

In addition to the 'Gala' x 'Splendour' hybrids, fruit of 29 cultivars ('Albany Beauty', 'Braeburn', 'Coromandel Red', 'Count Oratia', 'Cox's Orange Pippin', 'Delicious', 'Democrat', 'Early Red', 'Ellison's Orange', 'Emergo', 'Fiesta', 'Fuji', 'Gala', 'Golden Harvest', 'Golden Delicious', 'Granny Smith', 'Hawkes Bay Red', 'Jonalicious', 'Kidd's Orange', 'Northern Spy', 'Oregon Spur', 'Red Dougherty', 'Rome Beauty', 'Shizuka', 'Spartan', 'Splendour', 'Sturmer', 'Summerland', and 'Newton Pippin') were collected from the Hawkes Bay cultivar repository orchard. At Summerland, fruit of 15 additional cultivars ('Belle De Boskoop', 'Discovery', 'Elstra', 'Empire', 'Garland', 'Gloster', 'Gravenstein', 'Idared', 'Jester', 'Jonadel', 'Jonathan', 'McIntosh', 'Mutsu', 'SummerRed', and 'Tydemans') and a 'Newton Pippin' x 'Granny Smith' hybrid (8C-31-110) were collected and examined. Fruit of the named cultivars were stored and examined in the same way as the 'Gala' x 'Splendour' hybrids.

The technique used to count the vascular nodules in individual apples was based on preliminary experiments that established that the nodules were most frequently associated with the sepal and, to a much lesser extent, the petal vascular bundles within the apple flesh. The sepal vascular bundles can be seen opposite the locules in apples cut laterally. Frequency of nodules associated with the sepal bundles was 12 times greater than with petal bundles. Therefore, only vascular nodules associated with the sepal bundle were recorded. Nodules do occasionally appear in the cortex, away from the large sepal and petal vascular bundles, but their frequency was less than 1% of the sepal bundle-associated vascular nodules. To determine nodule frequency, the apple fruit was cut in half laterally using a thin, sharp knife.

Each half of the fruit was then cut longitudinally into five sections with the cut made alongside the sepal bundle. The nodules were much darker in color than the cortex and were easily seen even if the cut was not in exact alignment with the sepal bundle. Nodules were counted in initial experiments using a stereo microscope, but this was later found to be unnecessary as we became more practised at identifying the nodules. Since nodules were frequently bisected when sectioning the fruit, the cut surfaces were matched to avoid counting a nodule twice. The number and location of nodules were recorded for each fruit.

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Table 1. Frequency of vascular nodules in 'Gala' x 'Splendour' hybrids originating in British Columbia (BC) or New Zealand (NZ). Nodule frequency class, clone number or cultivar name, frequency of nodules, and standard deviation (SD), are given. n = 25 unless otherwise indicated.

Nodule frequency distribution of the 'Gala' x 'Splendour' hybrids				
Absent	Low		High	
Origin/clone	Origin/clone	Frequency (SD)	Origin/clone	Frequency (SD)
NZ 68	NZ 2862	0.04 (0.2)	BC 8S 26-50	2.76 (1.9)
NZ 472	NZ 854	0.04 (0.2)	NZ 1815	3.00 (2.0)
NZ 494	NZ 48	0.08 (0.4)	NZ 1785	3.24 (2.3)
NZ 584	NZ 1286	0.08 (0.3)	NZ 921	5.40 (3.8)
NZ 863	BC 8S 28-6 (n = 10)	0.10 (0.3)	NZ 274	5.60 (4.1)
NZ 1016	NZ 2623	0.12 (0.3)	NZ 758	6.16 (3.3)
NZ 1302	BC 8S 69-23	0.12 (0.4)	NZ 1487	7.12 (4.8)
NZ 1699	BC 8S 29-18	0.12 (0.3)	NZ 2160	7.56 (4.1)
NZ 2045	BC SPA 441 (n = 10)	0.20 (0.4)	BC 8S 31-17 (n = 10)	8.50 (4.2)
NZ 2245	BC SPA 493	0.20 (0.4)	NZ 20	8.60 (4.5)
NZ 2405	NZ 1208	0.24 (0.5)	BC 8S 27-2	9.76 (7.2)
NZ 2429	NZ 1302	0.24 (0.8)	NZ 1419	11.72 (3.6)
NZ 3020	NZ 447	0.32 (0.6)	NZ 2085	12.12 (4.4)
BC 8S-26-58	BC 8S 27-43	0.36 (0.7)		
BC 8S-29-46	BC SPA 505	0.40 (0.6)		
BC 8S 26-52	NZ 1190	0.64 (0.9)		
BC 8S 31-56	NZ 2184	0.68 (0.8)		
BC Chinook	NZ 1372	0.68 (1.1)		
BC 8S 28-14 (n = 10)	NZ 330	0.76 (0.8)		
BC 8S 70-33 (n = 13)	NZ 58	0.92 (1.0)		
	NZ 150	0.92 (0.9)		
	BC 8S 69-5 (N = 12)	1.00 (1.5)		
	NZ 1620	1.12 (1.0)		
	NZ 1945	1.12 (1.5)		
	NZ 109	1.29 (1.1)		
	BC 8S 61-22	1.5 (1.6)		
	BC SPA 440 (N = 10)	1.52 (1.3)		
	NZ 2028	1.68 (1.7)		
	NZ 2576	1.84 (1.4)		

Results

Frequency of vascular nodules in 'Gala' x 'Splendour' hybrids. The location along the sepal bundle, color, and shape of the nodules was similar irrespective of the hybrid. Nodules were most frequently observed in the stem end of the apple, usually in the area contained by the sector 30° to 60° from the fruit axis measuring from the stem. Nodule color was typically green due to chlorophyll pigment, although some nodules examined had become dark green or black. The form of nodules varied but tended to be wedge shaped with the narrow end oriented towards the core of the apple. Size distribution was from very small, barely detectable nodules to the largest, or several fused nodules, up to 8 mm long. The shape, orientation, and size of the nodules has been described previously (Lane et al., 2000).

Frequency of nodules in these hybrids was divided into three categories. Category 1: no nodules; category 2: low frequency of 0.04–1.84 nodules per fruit; and category 3: high frequency of 2.76–12.12 nodules per fruit. Of the population of 61 hybrids examined, 20 were observed to have no vascular nodules, 28 were in the low vascular nodule frequency class, and 13 were in the high frequency class.

Frequency of vascular nodules in named cultivars. Of the other cultivars listed in the Materials and Methods section, vascular nodules were only observed in 'Gala', 'Splendour',

'Newtown Pippin', and the 'Newton Pippin' x 'Granny Smith' hybrid. Fruit of 'Newtown Pippin' had a mean frequency of 0.84 nodules per fruit (21 in total from the 25 fruit), and fruit of the 'Newton Pippin' x 'Granny Smith' hybrid 0.08. Mean frequency per fruit of vascular nodules in 'Gala' was 1.9, and in 'Splendour' was 0.5.

Both 'Gala' and 'Splendour' were categorized as having a low frequency of nodules. 'Royal Gala', a strain of 'Gala', had a mean nodule frequency similar to 'Gala', 1.6 nodules per fruit. These data are similar to frequencies reported by Lane et al. (2000) for 'Royal Gala' but less than the values reported for 'Regal Gala' of 3.6 to 8.4.

Discussion

'Splendour' is a chance seedling that originated in New Zealand about 1948 (Bollard, 1983), whereas 'Gala' originated in the 1930s from a cross of 'Kidd's Orange' with 'Golden Delicious'. 'Kidd's Orange' is from a 'Cox's Orange Pippin' x 'Delicious' cross (McKenzie, 1983). Possible parents of 'Splendour' are 'Golden Delicious' and 'Delicious' as they were popular and widely grown cultivars at that time. However, vascular nodules were not observed in 'Golden Delicious' or 'Delicious', nor in 'Kidd's Orange' or 'Cox's Orange Pippin'.

The occurrence of nodules in 'Gala', 'Splendour', and many of their hybrids, plus

the occurrence of nodules in 'Newtown Pippin' and at least one of its progeny, but the absence of nodules in the other cultivars we examined, suggests that the occurrence of nodules is an inherited trait. It is tempting to consider the possibility that the nodule frequency classes (high, low, and absent) correspond to inheritance of a single gene, following the classical Mendelian inheritance pattern. We were unable to test this hypothesis because the populations of hybrids we had access to were not random. We examined two separate seedling populations that had been selected for individuals with high fruit quality while other hybrids had been discarded. Future studies with a random population of this cross could determine the answer to this interesting question. We were not able to further test our hypothesis with 'Newtown Pippin' x 'Gala' or 'Newtown Pippin' x 'Splendour' siblings, as no breeding populations with these progeny could be located, but examination of populations of these hybrids would give interesting information also.

Vascular nodules vary in location within fruits and in frequency in fruits within a tree. Several nodules may form on a single sepal bundle while other bundles in the same fruit have none. The size of nodules also varies, being larger in clones with a higher nodule frequency. This suggests other factors may influence genetic expression.

Lane et al. (2000) reported that deficit irrigation promoted nodule frequency with 'Royal Gala' and 'Regal Gala' cultivars in British Columbia, but different nitrogen nutrition levels had no effect. Unpublished reports focusing on environmental causes of nodulation in cultivar NZ 2085, 'Sciros'™, in New Zealand found tree size, fruit exposure to light or shade, crop load, or position on canopy did not correlate with nodule frequency.

The comparable nodule frequencies in cultivars and strains examined both in New Zealand and British Columbia, Canada, suggest genetic determinants are the main influences on nodule formation, and development and environmental factors are secondary.

Further studies investigating other factors that may influence nodule development would contribute to a more complete understanding of their formation.

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