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Effects of the Phenotype and Seed Parent on the Size, Productivity and Fruit Quality in Second-Generation Seedling Apple Trees

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Abstract

First-generation seedling apple trees derived from 'McIntosh Wijcik' (*Malus* × *domestica* Borkh.) were used as putative pollen parents to generate seed using 'Cripps Pink' and 'Fuji' as seed parents. Seeds from this open pollination were stratified, germinated, grown in the greenhouse, overwintered under cover and planted in the field. During their juvenile years, the seedling trees were sorted into two phenotypic categories: 1) trees exhibiting the wild-type phenotype typical of 'Cripps Pink' and 'Fuji', and 2) trees with an apparent columnar phenotype. Trees that had been identified with the 'Wijcik-like' phenotype were smaller than wild-type trees. Although they were smaller and yielded less fruit, they were found to be more efficient. No statistically significant interactions of cultivar and phenotype were noted for either tree size or efficiency. This research demonstrates that significant scion-dwarfing can occur in 'Wijcik-type' trees with enhanced yield efficiency. Harvest date, size and length-to-diameter ratio were similar for fruit of both tree phenotypes and for both cultivars. Fruits from wild-type seedling trees were firmer, with higher soluble solids concentration (SSC) and a lower starch index than fruits from 'Wijcik-type' apple seedling trees. Apple scions with the greater height-to-spread ratio found in the 'Wijcik-type' phenotype could be applicable to the tall-spindle production system currently in vogue in North America. One of the major expenses to growers - labor - could be reduced significantly with the eventual development of scion varieties that are more efficient and naturally develop a more desirable architecture.

For the past half-century, apple growers in North America have reduced apple tree size and increased planting densities with the goal of improving fruit quality and production efficiency. The adoption of size-controlling rootstocks coupled with support systems has been a primary innovation driving this dramatic change. The current approach is to develop a narrow, cone-shaped tall-spindle tree. This system enhances precocity and productivity by stressing training over pruning in the early years (Robinson et al., 2011). While this leads to improved precocity, it also requires greater economic inputs, primarily for support systems and the hand-labor required to intensively manage young trees.

Apple tree size and structure are determined by three components: rootstock, soil and scion. Despite our knowledge that cultivar selection plays an important role in tree size, perhaps the least attention has been paid to the scion's contribution. Size control through scion selection began in earnest with the selection of spur-type cultivars (Faust and Zagaja, 1984). In some cultivars such as 'Delicious', this was effective allowing growers to plant at closer spacing even when using semi-dwarf and seedling rootstocks (Barden and Marini, 1999; Ferree, 1988; Seeley et al., 1979). In other cultivars, spur-type trees were not as successful since these had less effect on tree size or efficiency (Walsh, 1981).

Faust and Zagaja (1984) crossed 'Redspur' and 'Goldspur' with the goal of producing

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genetically dwarfed scions. While the trees were smaller, they lacked precocity, likely imparted by 'Delicious' as a pollen parent. In Italy, Sansavini and Ventura (1994) also used spur-type 'Delicious' as a parent to attempt to control vigor in a seedling population. They found fewer phenotypic differences in their progeny, with most seedling trees showing normal (non-spur-type) size and vigor.

Lapins (1969) reported that a single, dominant gene was present in the spontaneously-observed limb mutation 'McIntosh Wijcik' (Fisher, 1995; Lapins, 1969). Unlike other 'McIntosh' spur-types, this mutation transmits its habit genetically (Lapins, 1976). The *Columnar* gene (*Co*) has been suggested as a potential tool to modify tree architecture in plant breeding programs (Kelsey and Brown, 1992). In England, Tobutt had success using 'McIntosh Wijcik' as a parent in a long-term breeding effort. This compact trait was stable and heritable through two generations. Tobutt's data showed a slight deviation from the expected segregation during the F_1, but a clear 1:1 segregation in F_2 populations (Tobutt, 1994). Several columnar varieties were released including 'Maypole', 'Tuscan' and 'Telamon' (Tobutt, 1988a; 1988b; 1988c). The genetic basis of the columnar habit in Wijcik has been researched further with newer methods. It is now thought that there is one dominant gene (*Co*) on chromosome 10 and several modifying genes that explain the deviations from a 1-to-1 ratio of inheritance (Baldi et al., 2013).

Researchers at the Geisenheim Research Institute in Germany also used 'McIntosh Wijcik' as a parent. Their work was based on coupling the *Co* gene with immunity to apple scab to create high yielding, low maintenance orchards with natural resistance to apple scab, mildew, drought and frost damage. They developed a series of commercial cultivars, which are adapted to ultra-high density planting systems where fruit are borne on a single axis of growth, with few or no side branches. This system is currently being marketed commercially to growers facing high land and labor costs as CATS (Jacob, 2008; Khanizadeh et al., 2002).

Canadian researchers sought to breed fruit tolerant to apple scab and cold weather. They also used 'McIntosh Wijcik' as a pollen parent. It was hybridized to O-522 a breeding selection containing the *Rvi6* gene for scab resistance derived from *Malus floribunda 821*(Bus et al., 2011). From this cross, they released 'MacExcel', a compact scab-resistant cultivar (Khanizadeh et al., 2002). While that particular cultivar did not yield commercial-quality fruit, it could be useful in breeding to produce commercial spur-type scab resistant cultivars adapted to cool climates. In many of the studies cited above, the goal was to develop columnar trees that are adapted to an ultra-high density planting system (Kelsey and Brown, 1992).

To test the possibility of developing high-quality, precocious, genetic dwarf apple trees for warm-temperate climates we began screening second generation seedlings thought to contain the *Co* gene. Our preliminary results at the end of the fourth leaf, showed that unpruned seedling apple trees with the columnar phenotype were less vigorous than wild-type seedling trees (Harshman et al., 2008). This paper builds on our initial report, detailing the effects of the apparent Wijcik phenotype on tree size, productivity, efficiency and fruit size and fruit quality over four cropping seasons.

Materials and Methods

Field Hybridization: Open Pollination of 'McIntosh Wijcik'. Two 'McIntosh Wijcik' apple trees were used as seed parents. In 1991, fruit were harvested from open pollinated 'McIntosh Wijcik' trees that had been planted in an isolated block of 'Gala (Kidd's D-8)', their seeds removed and stratified. We sought to follow the open-pollination approach with two isolated cultivars, pioneered by AJ Heinecke, that eventually led to the development of the 'Empire' apple (Derkacz et al., 1993). Since these trees were located in an isolated research plot, 'Gala' served as the putative pollen parent. Seeds were germinated and grown for six months in the greenhouse in College Park, MD. Two hundred seedlings showing short-internodes were identified and planted at Western Maryland Research and Education Center (WMREC) at Keedysville, MD. Trees exhibiting fire blight symptoms, aerial rooting or woolly apple aphid susceptibility were removed. Precocity and annual productivity were also noted. Trees that had not bloomed by the sixth leaf, or that showed a tendency toward biennial bearing were also discarded. In 1998, these 'McIntosh' seedling trees were further culled to 30 trees displaying the best horticultural characteristics and were identified as CompactGalaMac (CGMx) selections.

Field Hybridization: Crosses of CGMx to 'Cripps Pink' and 'Fuji'. CGMx trees were used as pollen parents to attempt to introduce traits from 'McIntosh Wijcik' and 'Gala' into late-season commercial cultivars. After transplanting the CGMx trees at 13 by 13 m spacing with a Vermeer tree spade, nursery trees were set 2 m from the trunk of each transplanted CGMx tree. These included 'Fuji' and 'Cripps Pink' on M.9 rootstock (ACN, Aspers, PA). These commercial cultivars were used as the open-pollinated seed parents to develop a second-generation of apple seedlings.

Seeds were removed from the fruit, stratified, germinated and held in the greenhouse until they could be moved to the field. During that time, seedlings exhibiting visible powdery mildew (*Podosphaera leucotricha)* symptoms or in apparent poor health were discarded. Over 900 seedlings were transplanted in 2002. Trees were planted in staggered two-row beds; the in-row spacing was 2 m and the center-to-center row spacing was 5 m.

Field Maintenance. The planting was established at the Western Maryland Research and Education Center in Keedysville, MD. Soil at that location is typed as Hagerstown Loam, which is a deep, productive well-drained limestone-derived soil that is well-suited to apple tree growth and fruit production. This land had previously been planted with apple and pear trees for fruit research. Prior to the planting of second generation seedlings, the ground was planted to field corn for three years to reduce weeds and nematodes, and build soil fertility. The field was not fumigated. Seedlings were planted into bare ground and the field was disked the first season. Drip irrigation was used until plants were established. A permanent cover crop of hard fescue was established six months after planting. After their initial establishment, the seedlings were not fertilized as the site had high residual fertility from the previous corn crops. Trees were managed using an IPM/preventative schedule developed for this region (Halbrendt, 2012). To highlight each tree's natural architecture, leaders were headed only once and then singled in the third leaf. No additional pruning was made to any of these trees. Although pesticide treatments were applied, no chemical thinning materials were used.

Field Evaluation of Second-Generation Seedling Trees. While it is relatively easy to identify the columnar trait in a controlled cross F_1 population (Lee and Looney, 1976), the phenotype was not apparent in the greenhouse-grown F_2 seedlings. Consequently all trees were taken to the field and phenotyped prior to the onset of bearing. The two phenotypic categories identified were: 1) trees with wild-type phenotype, and 2) trees with columnar phenotype. All columnar trees were originally retained for this study, while only ten percent of the wild-type trees were retained to serve as a control population.

During four fruiting seasons, bloom data and fruit set were recorded. Each tree received either a 0 (no fruit) or a 1 (visible fruit) rating (data not shown). Since this also served as a breeding block, trees showing susceptibility to fire blight and aerial roots were removed annually. The number of visible fire blight strikes was also recorded when there were outbreaks. Any tree with more than ten strikes was discarded. Aerial roots were evaluated in the winter of 2009 and trees with obvious and numerous aerial roots were also discarded. About ninety percent of the original trees had been removed prior to the completion of this study. The final number of trees analyzed in this report was: 13 Wijcik-type 'Cripps Pink' seedlings, 16 wild-type 'Cripps Pink' seedlings, 56 Wijcik-type 'Fuji' seedlings and 19 wild-type 'Fuji' seedlings.

Fruit Analysis. Fruit was harvested weekly from early August until the middle of October, approximately 110 to 170 days after full bloom. All fruits were harvested from each tree when the fruit on that tree had reached its apparent commercial maturity. Maturity was assessed subjectively once a week by the authors. Fruit maturity was based on fruit size, surface color, ground color and ease of attachment. This was followed by a taste-test that focused on starchiness and tannin development. Fruits not meeting the expected criteria were not harvested until judged to be commercially mature. The fruit were weighed and counted, and mean fruit weight calculated. The apples were arranged from largest to smallest, and five median fruit were chosen as a subsample for fruit quality analyses. When the number of apples exceeded one picking container, then one median sample was taken for every harvest container.

Fruit height and diameter were measured using calipers. Fruit firmness was determined using a FT 327 Fruit Penetrometer (Wagner Instruments, Greenwich, CT). A small apple disc from each apple was juiced using a garlic press to create a composite sample. Soluble solids concentration (SSC) was measured as °Brix using a Leica Mark II Plus Abbe Refractometer (Leica Microsystems Inc, Buffalo Grove, IL). The apple fruits were cut in half at the equator and the stem-end of the fruit was placed into a potassium-iodide solution to determine the qualitative level of starch present (Blanpied and Silsby, 1992).

Statistical Analysis. To determine the effects of tree phenotype and seed parent variety on tree vigor and fruit quality variables, an analysis of variance was conducted using the Mixed procedure (SAS, version 9.2, SAS Institute Inc., Cary, NC, USA). Data were analyzed on a tree by year basis. The model statement was y = variety | phenotype | year and non-significant interaction terms were removed. Means reported were calculated using the LSMeans statement. As a novel way to measure the tree's overall yield efficiency, we calculated canopy volume efficiency. Canopy volume was calculated using recommended canopy volume equations (Westwood, 1993) - if the tree was wider than it was tall we used one equation and if the tree was taller than it was wide, we used the second equation.

Results

Rather than focusing on the small number of single-stem, columnar trees that would require planting at ultra-high densities, we chose to test whether second-generation trees from this cross could be developed with size control and tree-architecture benefits through the scion, that might be applicable to the current apple management system advocated in North America. We chose to focus on vegetative vigor, using seedlings grown on their own roots. These were derived from a second generation of seedling trees that were bred using 'McIntosh Wijcik' as a grandparent. We chose to test whether a measurable difference in tree vigor, productivity and efficiency occurred in seedlings that showed a range of characteristics that we identified as the 'Wijcik-type' phenotype.

Phenotype significantly affected measures of tree vigor. For all measures of tree stature (height, spread, trunk cross sectional area, cumulative yield efficiency and canopy volume efficiency) the 'Wijcik-type' trees were smaller (Table 1). These values confirm the relative dwarfing that 'McIntosh Wijcik' imparts on its progeny. For cumulative yield efficiency, 'Wijcik-type' trees were significantly more efficient than were the wild-type trees. Canopy volume efficiency was also calculated; 'Wijcik-type' progeny were twice as efficient as wild-type trees. Seed parent cultivar and the interaction between seed parent and phenotype were not statistically significant. While the wild-type trees were more productive, they had not yet reached their ultimate size. Due to their

Table 1. Effect of phenotype and seed parent on the size, yield and efficiency of seedling apple trees measured from 2008-2011.

Variable	Tree size				Cumulative yield (kg)	Efficiency	
	Height (m)	Spread (m)	TCA (cm^2)	Canopy (m^3)		Cumulative yield ($kg \cdot cm^{-2}$)	Canopy volume ($kg \cdot m^{-3}$)
Phenotype							
Columnar	3.87	2.23	18.82	10.80	24.31	1.65	3.37
Wild-type	4.21	4.52	65.66	43.52	73.21	1.13	1.68
p-value	0.0045	0.0001	0.0001	0.0001	0.0001	0.0285	0.0156
Seed Parent							
Fuji	4.03	2.86	31.50	28.87	35.30	1.37	1.98
Cripps Pink	3.89	3.34	42.55	25.45	55.28	1.74	3.06
p-value	0.1090	0.3606	0.5908	0.3325	0.3901	0.1262	0.1200
Phenotype x Seed Parent							
p-value	0.4082	0.1669	0.2606	0.6697	0.2087	0.3877	0.2535

lower efficiency, the wild-type trees were still growing rapidly and would be expected to reach heights and spreads of 10 m. Since the columnar trees were more efficient, they put more of the available substrates into cropping. They are not expected to grow larger due to their greater yield and canopy efficiencies. The smaller tree size is an advantage for growers looking to reduce costs involved in pruning, thinning and harvesting, while the higher yield efficiency and canopy volume efficiency infer that this could be an alternate approach to improving future orchard efficiency.

Various fruit quality measures were analyzed in order to compare the effect of seed parent cultivar and phenotype. In every case except weight of the largest fruit and the fruit length-to-diameter ratio, year was significant. The year by phenotype interaction, however, was not significant for any of the fruit quality variables measured (not shown). Since the trees were not irrigated and some showed biennial bearing, the significance of year was not surprising. Neither cultivar nor phenotype had a significant effect on harvest date, largest fruit weight or length-to-diameter ratios.

While not statistically significant, it is interesting to note that the 'Wijcik-type' progeny had a slightly larger fruit size, which may have been due to maturing slightly earlier. Interestingly, the later-maturing wild-type fruit had greater SSC despite also retaining more starch (Table 2). Firmness, SSC and starch index were significantly different between phenotypes (Table 2). Fruits from wild-type trees were firmer and had higher SSC than their Wijcik-type counterparts. This may be related to differences in canopy shading or, alternately, traceable to the inherent earlier ripening of these fruit. Fruit harvested from the 'Cripps Pink' progeny were firmer and had a lower SSC than fruits harvested from the 'Fuji' progeny which may have reflected the difference in maturity and quality between these two long-season cultivars. Although the starch-iodine test showed a slight, but statistically significant, difference among treatments, fruits from both phenotypes were typically harvested at a similar storage maturity (Blanpied and Silsby, 1992).

This project started as a classical breeding project 20 years ago. Since then, many advances have been made in apple breeding - the apple genome has been sequenced (Velasco et al., 2010), marker assisted seedling selection is being adopted (Moriya et al., 2009), and the first genetically modified apple could be available to growers in the US very soon (Carter, 2012). Several projects are dedicated to increasing marker avail-

Table 2. Effect of phenotype and seed parent on the harvest date and fruit quality of fruits harvested from seedling apple trees measured from 2008-2011.

Variable	Harvest date (Julian)	Mean fruit wt. (g)	Largest fruit (g)	Length/ diameter ratio	Firmness (N)	SSC (°Brix)	Starch index (No.)
Phenotype							
Columnar	262	120.23	166.04	0.8507	41.68	14.67	4.86
Wild-type	268	116.48	153.17	0.8486	47.14	15.29	3.89
p-value	0.0744	0.5526	0.2059	0.9970	0.0001	0.0052	0.0002
Seed Parent							
Fuji	262	122.07	164.99	0.8494	42.83	15.33	4.65
Cripps Pink	267	114.65	153.43	0.8498	45.99	14.63	4.10
p-value	0.8338	0.2988	0.2883	0.5255	0.0586	0.4629	0.0527
Phenotype x Seed Parent x Year							
p-value	0.0075	0.0001	0.2059	0.3080	0.0001	0.0001	0.0001

ability and increased efficiency of cultivar development specifically in Rosaceous crops (Iezzoni et al., 2010; Laurens et al., 2010; Patocchi et al., 2009). In future generations, the cycle time could be greatly reduced by incorporating these technologies and thus, the incorporation of this grower-friendly architecture into new cultivars could be done more rapidly.

This research demonstrates that additional progress can be made using the columnar trees beyond those with a single axis of growth. In this second-generation population, we found that a number of trees developed "grower-friendly" architecture. With the natural shape of a narrow cone (Table 1) and their need for less pruning than wild-type apple trees, second-generation columnar trees could fit nicely into the tall-spindle production system currently in vogue in North America. One of the major expenses to growers - labor - could be reduced significantly through the development and use of scions that are more efficient than wild-type cultivars and require less pruning labor to develop the desired architecture.

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