Fruit Varieties Journal 46(2):83-87 1992

American Pomological Society U.P. Hedrick Award for Research Paper by a Student: (1990 First Place Award)

'McIntosh Wijcik': A Columnar Mutation of 'McIntosh' Apple Proving Useful in Physiology and Breeding Research

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'McIntosh' is one of the leading cultivars in the apple industry, and its popularity with consumers indicates that it will remain an important cultivar in the future (21). Like many widely grown cultivars, 'McIntosh' has given rise to a number of spur-type mutants characterized by increased spur production and reduced vegetative growth. These strains include 'Macspur,' 'Morspur' (Raikes strain), 'Starkspur McIntosh' (Gatzke strain), 'Starkspur UltraMac' (Dewar strain), 'Starkspur Compact Mac' (Wijcik strain) (4), and 'Chick-A-Dee McIntosh' (19). The most distinct of these strains is 'McIntosh Wijcik' (Fig. 1), a columnar mutation discovered in Canada (4, 5). Stark Bro's Nurseries, Louisiana, Mo, holds the U.S. plant patent for 'McIntosh Wijcik,' marketing it as 'Starkspur^{R} Compact Mac'^{TM}.

'McIntosh Wijcik' is characterized by compaction of the internodes, reduced lateral shoot growth, and increased spurriness (11). The fruit quality and tree growth habit of this strain were initially described as horticulturally unsuitable (5), yet others have since characterized fruit quality as similar to 'McIntosh' with good color (16).

Unlike other spur-type mutants of 'McIntosh,' the columnar mutation genetically transmits its habit (11, 13). Therefore, 'McIntosh Wijcik' is serving as an important genetic resource for plant breeders seeking to develop compact cultivars for high density orchards, as well as a model system for plant physiologists seeking to understand hormonal interactions and their effects on plant habit. This review summarizes what is known about 'McIntosh Wijcik' columnar apple and explores its future role in research and industry.

Genetic Studies

Determination of the inheritance of plant form in apple has been elusive, with the transfer of desirable habit to the progeny often under polygenic control (1, 12, 13, 18, 32). The discovery of 'McIntosh Wijcik' and its distinct columnar habit interested apple breeders searching for a dependable mechanism of introducing spur-type habit into their breeding programs. Lapins (11, 13) reported that 'McIntosh Wijcik' was unique because it transmitted its habit to about 45% of its progeny, indicating control by a single dominant gene, *Co*. However, Lapins (13) speculated that there may be one or more modifiers of the *Co* gene because the percentage of compact offspring in the test crosses was consistently less than that expected. Since dominant genes controlling plant form are rare in apple, the discovery that 'McIntosh Wijcik' is heterozygous for the gene for columnar habit is of great significance.

Roles in Plant Breeding

Spur-type scion cultivars and dwarfing rootstocks have enabled apple

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growers to increase orchard productivity (2). Spur-type trees will continue to grow in importance as economic pressures necessitate the development of cultivars suitable for high density plantings. The *Co* gene for columnar habit present in 'McIntosh Wijcik' provides plant breeders with a means to produce columnar, spur-type cultivars. Tobutt (27) has used 'McIntosh Wijcik' in breeding at the East Malling Research Station, and thus far one ornamental ('Maypole'), and three dessert types ('Telamon,' 'Trajan,' and 'Tuscan') have been released from this program (28). A long term goal of this breeding research is to eliminate the use of expensive grafted trees by developing own-rooted columnar cultivars that are easily propagated and resistant to collar rot (27). Breeding programs in Sweden, Canada, and the United States are also incorporating the *Co* gene (29). Research underway at Cornell University's New York State Agricultural Experiment Station is aimed at combining the columnar habit with commercial fruit quality and multiple disease resistance (S. K. Brown, unpublished).

The *Co* gene is being examined for its potential use in molecular biology. James (7) suggested its use in tissue culture screening for mutations. Cloning the gene for compact habit has been listed as a desirable goal for future transfer to other fruit species. However, physiological and biochemical means of identifying and manipulating the gene are required.

Hormonal Studies

Plant physiologists have studied endogenous hormone levels in 'McIntosh Wijcik' in hopes of uncovering the cause of its unique habit. The *Co* gene was thought to regulate the level of a specific growth substance, but several hormones have been implicated in the control of the columnar habit.

Abscisic Acid

Research with dwarfing rootstocks (23, 31) and with compact mutants of

'Cortland' and 'Golden Delicious' (8) indicated that high levels of abscisic acid (ABA) may play a role in determining compact habit, while other studies found no such correlation (3). Lee and Looney (15) examined levels of free abscisic acid in seedlings from crosses of 'McIntosh Wijcik' with 'Summerred,' 'Golden Delicious,' and 'Alkmene' and found free abscisic acid levels were lower in compact progeny when reported on a per shoot tip or per gram fresh weight basis. They postulated that the contradiction between these results and previous work was due to the use of different bio-

assay techniques. It is also possible that the conflicting results between compact genotypes and columnar material in these experiments may indicate that a different mechanism is responsible for compaction in apples containing the *Co* gene.

When the level of free and conjugated ABA was measured in spur buds from 'McIntosh' and 'McIntosh Wijcik' trees, free ABA expressed on a tissue fresh weight basis was lower in the 'McIntosh Wijcik' buds, but total ABA per bud was greater in 'McIntosh Wijcik' spurs due to their larger size (16). While the precise influence of abscisic acid on the columnar habit remains uncertain, elevated levels of free ABA do not appear to be a factor.

Gibberellins

Gibberellins are known to play a role in expansion growth (20, 22, 23) and may be involved in determining the compact habit of 'McIntosh Wijcik.' Gibberellin levels were measured in seedlings from a 'McIntosh Wijcik' x 'Golden Delicious' cross, and compact seedlings were found to have less gibberellin activity than standard seedlings. When exogenous GA_3 was applied to both groups, the compact seedlings responded with a greater percentage increase in growth, with little effect on apical dominance (15). 'McIntosh Wijcik' was also found to have significantly lower polar gibberellin levels than three other 'McIntosh' strains (17). Low endogenous levels of gibberellin are thought to be responsible for the compaction of internodes in the columnar mutant (16).

Auxin

Auxin (IAA) is involved in stimulating cell enlargement (30) and maintaining apical dominance (26). The reduced lateral branching exhibited by 'McIntosh Wijcik' suggests high levels of physiologically active auxin, yet research to test this hypothesis has yielded conflicting results. When free and total IAA were measured in spur buds of 'McIntosh' and 'McIntosh Wijcik,' overall auxin levels were not significantly different, but the ratio of free to total IAA was much greater in 'McIntosh Wijcik' non-fruiting spurs, suggesting that auxin has a role in determining the columnar habit (16). However, exogenous application of an auxin synthesis and transport inhibitor, 2, 3, 5-triiodobenzoic acid (TIBA), actually increased apical dominance of compact seedlings from a 'McIntosh Wijcik' x 'Golden Delicious' cross, indicating auxin has a minor role in regulating columnar habit (15).

Cytokinins

Cytokinins are known to interact with auxin in controlling lateral bud development (24, 25). Looney et al. (17) found that endogenous levels of zeatin-like substances were significantly higher in 'McIntosh Wijcik' extracts as compared to 'Summerland Red McIntosh,' 'Macspur,' and 'Morspur McIntosh' when reported on a per gram dry weight basis. Tissue culture experiments showed 'McIntosh Wijcik' had a much greater tolerance to excess benzyladenine (BA) than 'Macspur' or standard 'McIntosh,' as shoot proliferation rates for these varieties were 90%, 20% and 0%, respectively, at 10 uM BA (10). Jones (9) speculated that 'McIntosh Wijcik' may have the ability to metabolize excess cytokinin to levels required for its growth and development. Thus, it appears that cytokinins may play a substantial role in determining the spurry, columnar habit.

Hormonal Summary and Prospects for the Future

How plant hormones interact to influence columnar growth is unclear, yet the distinct differences in the level of these substances between 'McIntosh Wijcik' and other 'McIntosh' strains suggests their interaction in the physiological basis of the columnar habit. Looney et al. (17) proposed that high cytokinin levels may inhibit gibberellin

synthesis. It is possible that developing lateral buds fail to elongate and form spurs instead of shoots.

The presence of an inhibitor other than ABA has been reported in 'McIntosh Wijcik,' but the activity of this substance remains unknown (14). Inhibitory substances have also been reported in compact spur strains of other cultivars (6). A clarification of the role of these substances and their physiological effects on growth and development remains a goal of future research in determining the precise mechanism by which the *Co* gene modifies plant habit in apples.

Concluding Remarks: Columnar Habit and the Apple Industry

The discovery of 'Starkrimson,' a spur-type mutation of 'Delicious,' dramatically changed the apple industry (2). 'Starkrimson' became very popular due to its enhanced red fruit color, and the reduced vegetative growth associated with its spur-type habit was soon recognized as a highly beneficial characteristic. The benefits of growing trees of reduced stature are now well known, as overall orchard efficiency has increased with the advent of spur-type scions, dwarfing rootstocks, growth regulators, and cultural practices designed to reduce vegetative growth (2).

The introduction of commercially suitable columnar apple varieties could lead to a further refinement of the apple industry similar to that which occurred with the introduction of 'Starkrimson.' The benefits of traditional spur-type strains are enhanced in the columnar habit transmitted by 'McIntosh Wijcik.' These trees are like a single spurry branch, and they may be planted very close together to give excellent yields per acre. It is likely that minimal pruning and training would be required as excess vegetative growth is avoided, and cultural practices should be easier due to the reduced size of the columnar trees.

Rising land prices and production costs will force growers to seek new methods of maximizing productivity, thus columnar apple varieties with superior fruit quality are likely to grow in acceptance and importance in the future. Research is underway to design an orchard system for very high density plantings of columnar cultivars (28). The use of the *Co* gene from 'McIntosh Wijcik' will play a critical role in the creation of new columnar apple varieties, and the development of a series of high quality, disease resistant columnar cultivars could revolutionize future apple production.

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Fruit Varieties Journal 46(2):87-92 1992

Postharvest Quality of 'Virginia Gold' Apple Fruit

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Abstract

'Virginia Gold' (*Malus domestica* Borkh.) is cross between 'Golden Delicious' and 'Yellow Newtown' (Albamarle Pippin). 'Virginia Gold' fruit matures approximately 160 days from full bloom and, unlike 'Golden Delicious' fruit, it is not susceptible to russett except in the stem cavity. At maturity, soluble solids concentration (SS) is lower, while flesh firmness and starch index are similar to 'Golden Delicious.' In addition, titratable acidity (TA) and TA/SS ratio are higher in 'Virginia Gold' than in 'Golden Delicious.' 'Virginia Gold' fruit stored in a commercial controlled atmosphere storage were firmer than fruit held at regular cold storage, and the fruit did not shrivel even when stored for up to 8 months without polyethylene box liners.

'Virginia Gold' fruit is susceptible to soft scald (ribbon scald) when stored at low temperature. In 1988 and in 1990, 37% and 46% of the fruit developed soft scald when stored at -1.1°C, respectively. Soft scald was eliminated by storing the fruit at 2.2°C or by controlled atmosphere storage and was significantly reduced by dipping the fruit postharvest in a combination of diphenylamine and ethoxyquin.

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