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Identification of Maximum Sensitivity of Developing Apple Fruits to Naphthaleneacetic Acid[1]

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Abstract. Naphthaleneacetic acid (NAA) thinning sprays applied at appropriate intervals and dosage levels to 3 apple cultivars, verified the existence of a critical stage during which developing fruitlets were maximally sensitive. Average fruit diameter accurately identified NAA-sensitivity, but the index varied among cultivars. Polynomial regression analyses revealed a direct relationship between diameters of individual fruit samples and thinning response for each experimental unit. NAA-induced fruit abscission was usually maximal 2 to 3 days prior to the onset of cytokinesis in the endosperm. Cell wall formation did not invariably signify an end to the induction of significant abscission.

The selective removal of excess apple fruits to improve size and quality of those remaining and to encourage annual production is a long standing horticultural practice. Interest in chemicals to accomplish this task began in the 1930's with the introduction of dinitro compounds as blossom thinning agents. Greater interest was aroused by the later discoveries of bloom and post-bloom thinning properties of the sodium salt of naphthaleneacetic acid (NAA), and other related chemicals (1, 4, 5, 16).

Research efforts with NAA were initially devoted to determining correct dosage levels and timing of treatments for various cultivars (6, 7, 10, 18). Despite the suggestions (14, 15, 17) that developing apple fruitlets may reach a stage of maximum sensitivity to NAA, recommendations to growers suggested applying NAA within a recommended dosage range in accordance with a range in number of days elapsed after full bloom (AFB) or after petal fall (APF) (2, 9, 20). Some reports (2, 9) indicated a uniform response of developing apples to variously timed NAA thinning sprays, apparently negating the existence of a stage of maximum sensitivity in this multi-seeded fruit. By contrast, Tukey (19) demonstrated that an average fruit diameter of 10 to 11 mm for Rome Beauty apples accounted for environmentally induced, seasonal differences in fruit development rates and thus provided an index to identify an NAA-sensitive stage. Similarly, Donoho (8) suggested application of NAA thinning sprays to 'Jonathan' coincident with an average fruit length of 15-18 mm for maximum response. Meanwhile Batjer, Forshey, and Hoffman (3) applied thinning sprays to several apple cultivars in Washington and New York states during 1966. They reported no apparent relationship between thinning response and average fruit diameter for that single season.

Our work was initiated to determine whether or not a stage of maximum sensitivity of developing apples to NAA existed, to compare common parameters identifying that proposed stage, and to examine the relationship between embryo and endosperm development in seeds, and NAA-induced fruit abscission.

Materials and Methods

Dilute sprays of NAA were applied with a hand gun (400 psi) spraying uniform mature trees to the drip point (ca 6 to 8 gallons per tree). Dosages were selected which normally overthin (10 ppm) the 'Delicious' and 'Spy', and slightly underthin (12.5 ppm) the 'McIntosh' trees growing at the Smithfield Station. Treatments, applied at size dependant intervals, usually 2 to 3 days, were replicated 6 times and repeated for 4 seasons to compare response within and between cultivars. Trees were selected annually for uniformly abundant bloom, and treatments were randomized annually. Abscission response was assessed by taking appropriate before and after cluster and fruit counts. Initial counts consisted of a minimum of 125 flower clusters per branch, 4 representative branches per tree. Two

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abscission patterns were examined (one pattern in 1966), namely percent of flowering clusters from which all fruits abscised, and fruit set per 100 flowering clusters. Control represented natural abscission in each instance. Abundance of bloom varied among cultivars and seasons from moderate, but requiring thinning, to extremely heavy as reflected by fruit set on control trees. Strong colonies of honeybees were provided at approximately 1 colony per acre, except in 1966. Each year the weather during bloom was conducive to good bee activity.

Treatment times were identified by elapsed days AFB and APF, as well as on the basis of average diameter of fruit samples determined with vernier calipers. Samples, collected in the morning, consisted of 60 fruits, 10 from each of 6 trees; the 10 were selected as the 2 largest, obviously persisting fruits in each of 5 clusters, taken at random circumferentially at 120 to 180 cm (4 to 6 ft) above ground level.

Polynomial regression analyses (third to fifth order) were conducted to clarify the proposed relationship between fruit diameter and NAA-induced abscission. Regression analyses were performed on cluster thinning percentages for each experimental branch unit against individual fruit diameter values for the same tree.

To determine the relationship between thinning response, fruit diameter, and embryo and endosperm development seeds were excised from measured fruit samples and stored in formaldehyde:acetic acid:alcohol (FAA). Usually the 3 largest seeds from each of 30 fruits per treatment, were selected for histological examination. Seeds were dehydrated and infiltrated with tetrahydrofuran (11), embedded in paraffin, and sectioned at 10 μ prior to mounting as permanent slides.

Results

The existence of a stage of maximum sensitivity of developing apples to NAA, and the practical value of its accurate identification was emphasized during 3 of 4 seasons. All cultivars were significantly thinned by most NAA treatments in 1966, a season of very heavy bloom and heavy natural abscission (Tables 1, 2, 3). Only 1 treatment induced significant abscission of 'Delicious' fruits in 1967 and 1968, while 2 were effective in 1969 (Table 1). Of 6 annual NAA applications to 'McIntosh', only 1 in each of 1968 and 1969, elicited a significant response (Table 2). In 1967, 2 treatments induced significant 'McIntosh' cluster abscission, whereas 4 reduced fruit set. The easily thinned cultivar 'Spy' responded with significant cluster abscission to only 2 treatments in 1967, to 1 in 1969, but to 4 in 1968 (Table 3). Assessing 'Spy' response on the basis of fruit set showed significant fruit abscission from 3 treatments in each of 1967 and 1968 but no thinning in 1969.

Assessment of abscission on the bases of fruit set per 100 flowering clusters and percent cluster abscission resulted in closely parallel measures of fruit abscission, though differences in cultivar bearing patterns were emphasized. Results with 'Delicious' were virtually identical irrespective of method of thinning assessment, reflecting the tendency of this cultivar to mature only 1 or 2 fruits per productive cluster (Table 1). Similarly, 'McIntosh' responses in 1968 and 1969 were not changed by method of assessment. Responses for 'Spy' in all seasons and 'McIntosh' in 1967 were directly parallel irrespective of assessment method, but levels of significance varied.

Examination of records of temperatures and drying conditions at the times of treatment revealed no definitive influence on response (Tables 1, 2 and 3). Sprays were normally applied in late morning and early afternoon. In 1967 one treatment was applied in the evening under very slow drying conditions, to 'McIntosh' and 'Spy' at 13 and 10 days APF respectively: significant (not maximal) reductions in fruit set ensued, but cluster abscission did not differ from control levels.

The indices, days AFB and APF, and average fruit diameter were compared for accuracy in identifying maximum response

Table 1. The relationship between mean fruit diameter, days APF[z] and NAA-induced abscission of 'Delicious' apples.

Means fruit diameter (mm)	Days APF	Clusters abscised (%)	Fruit set per 100 flowering clusters	Weather conditions: Temp °F High	Weather conditions: Temp °F Low	Weather conditions: Drying conditions
6.8	5	87ab[y]	1966	63	49	Fast
9.9	10	85b		71	52	Moderate
11.0	12	93a		71	48	Fast
13.6	15	92ab		79	55	Fast
15.6	17	92ab		74	44	Fast
Control	–	75c		–	–	–
			1967			
7.8	6	85a	17A	79	59	Moderate
11.1	9	61bc	45B	83	66	Moderate
14.0	12	64b	40B	71	53	Moderate
18.4	15	50c	59B	80	63	Fast
23.0	19	54bc	55B	77	54	Fast
Control	–	52bc	56B	–	–	–
			1968			
4.9	6	44ab	79AB	71	45	Fast
7.5	9	49a	70A	82	56	Fast
8.9	11	34abc	88AB	78	59	Fast
11.6	13	20c	102B	68	54	Moderate
14.2	15	26c	98B	76	58	Fast
Control	–	30bc	102B	–	–	–
			1969			
6.5	8	88a	15A	74	43	Fast
8.3	10	82a	20AB	83	60	Fast
10.6	12	64b	38BC	76	59	Fast
12.0	14	55b	55C	68	48	Fast
14.6	17	60b	43C	69	56	Moderate
Control	–	62b	44C	–	–	–

[z]APF = after petal fall.

[y]Mean separation, within columns and years, by Duncan's multiple range test, at 5% level by lower case, at 1% by capitals.

Table 2. The relationship between mean fruit diameter, days APF[z] and NAA-induced abscission of 'McIntosh' apples.

Mean fruit diameter (mm)	Days APF	Clusters abscised (%)	Fruit set per 100 flowering clusters	Weather conditions		
				Temp °F		Drying conditions
				High	Low	
			1966			
7.3	6	74ab[y]		63	49	Fast
9.2	10	84a		67	63	Moderate
10.9	11	80a		71	52	Fast
12.1	13	83a		71	48	Fast
15.8	16	83a		79	55	Fast
19.6	18	83a		74	44	Fast
Control	–	69b		–	–	–
			1967			
10.3	8	52a	62a	79	59	Moderate
12.0	10	47a	65ab	82	61	Moderate
15.6	13	33b	85bc	72	57	Slow
19.4	16	25b	108de	78	52	Fast
22.2	19	24b	119de	78	57	Slow
27.1	23	32b	102cd	80	50	Fast
Control	–	21b	129e	–	–	–
			1968			
5.4	10	21ab	152ab	71	45	Fast
8.7	13	30a	134a	82	56	Fast
11.7	15	22ab	161ab	78	59	Fast
14.4	17	20ab	153ab	68	54	Moderate
17.7	20	22ab	140ab	62	52	Moderate
22.9	26	24ab	158ab	70	55	Fast
Control	–	14b	175b	–	–	–
			1969			
7.8	10	35a	83a	74	43	Fast
11.3	12	27ab	106ab	83	60	Fast
12.7	14	27ab	112b	76	59	Fast
15.6	16	27ab	123b	68	48	Fast
18.4	19	24b	110b	69	56	Moderate
21.7	25	27ab	103ab	70	51	Moderate
Control	–	23b	114b	–	–	–

[z]APF = after petal fall.

[y]Mean separation, within columns and years, by Duncan's multiple range test, at 5% level.

to NAA during the 3 seasons of differential response. Coefficients of variability indicated that average fruit diameter provided a markedly improved index for a given cultivar (Table 4). Significant (and usually maximum) abscission invariably resulted from NAA sprays applied to 'Delicious', 'McIntosh', and 'Spy' when fruit diameters averaged approximately 6.5 to 8.0 mm, 8 to 10 mm, and 10 to 11 mm, respectively. By contrast, sprays applied within the commonly accepted range of 7 to 10 days APF failed to induce abscission at least 25% of the years for each cultivar (Tables 1, 2, and 3), and when 10 days APF was used as the exclusive index of NAA sensitivity for 'Spy', the total failure rate increased to 50% of the years (Table 3).

Tukey (19) reported that 10 to 11 mm average diameter provided an accurate index of the NAA-sensitive stage for 'Rome Beauty'. This value accurately identified NAA-sensitivity in 'Spy' (Table 3), but exhibited a failure rate of 75% with the easily thinned cultivar 'Delicious' (Table 1). Results with 'McIntosh' appeared similar in that NAA applied when fruits averaged 11.3 and 11.7 mm failed to induce significant fruit abscission (Table 2).

Polynomial regression equations were calculated annually for 3 seasons to clarify the relationship between diameters of individual fruit samples and cluster thinning response for each experimental branch unit within a given cultivar. Third power regression curves and superimposed histograms demonstrated a direct relationship between average fruit diameter and sensitivity to NAA (Fig. 1). At the times of maximum response average fruit diameter varied among cultivars. For a given cultivar, thinning response illustrated by the regression curves was remarkably similar between seasons: curves closely paralleled their associated histograms, and seasonal variation was largely in magnitude rather than shape. Between cultivars for any given season, regression curves varied in shape, magnitude, and position of peaks (Fig. 1).

The relationship between NAA-induced abscission and endosperm development was not well defined. Maximum, significant response usually resulted from NAA treatments applied 2 to 3 days prior to cytokinesis and invariably occurred when seed endosperm was free nuclear (Table 5); however, the free nuclear condition at the time of NAA treatment did not necessarily guarantee significant fruit abscission. For example, 'McIntosh' fruits were significantly thinned at 8.7 mm but not at 5.4 mm average diameter in 1968, although endosperm in seed samples was free nuclear on both occasions (Table 5). Similarly the onset of cytokinesis in seed endosperm usually coincided with the end of significant fruit abscission; but in 1966, 68% of 'Spy' fruit samples which averaged over 17 mm contained cellular endosperm, yet significant (but not maximal) abscission was induced.

Cytokinesis in the endosperm of 'McIntosh' and 'Spy' seeds showed no direct relationship with average diameter of developing fruits (Table 5). Further, average size of 'McIntosh' embryos bore no apparent, direct relationship with either cytokinesis in the endosperm or abscission response.

Discussion

Data reported herein clearly supported the contention that developing apple fruits reach a critical stage during which they are maximally sensitive to NAA. Response to differentially

Table 3. The relationship between mean fruit diameter, days APF[z] and NAA-induced abscission of 'Spy' apples.

Mean fruit diameter (mm)	Days APF	Clusters abscised (%)	Fruit set per 100 flowering clusters	Weather conditions: Temp °F High	Weather conditions: Temp °F Low	Weather conditions: Drying conditions
			1966			
7.9	8	91a[y]		71	52	Fast
8.3	10	91a		71	48	Fast
10.8	13	97a		79	55	Fast
12.9	15	88ab		74	44	Fast
17.3	17	90a		89	67	Fast
Control	–	82b		–	–	–
			1967			
8.9	5	54a	75AB	79	59	Moderate
12.3	7	55a	64A	82	61	Moderate
15.5	10	34b	93AB	72	57	Slow
22.2	16	29b	110BC	78	57	Slow
Control	–	23b	146C	–	–	–
			1968			
7.7	4	56ab	50A	82	56	Fast
10.0	6	61a	49A	78	59	Fast
12.6	8	52abc	59A	68	54	Moderate
15.1	10	43bcd	70AB	76	58	Fast
19.8	15	38cde	78AB	69	44	Fast
22.9	17	35de	80AB	70	55	Fast
Control	–	27e	100B	–	–	–
			1969			
7.0	8	71ab	31ab	74	43	Fast
9.0	10	73ab	29ab	83	60	Fast
10.6	12	76a	26a	76	59	Fast
12.1	14	71ab	32ab	68	48	Fast
15.9	17	56c	43b	69	56	Moderate
Control	–	59bc	42ab	–	–	–

[z]APF = After petal fall.

[y]Mean separation, within columns and years, by Duncan's multiple range test, at 5% by lower case and 1% by capitals.

timed NAA treatments did not vary markedly in 1966, paralleling that reported by Batjer et al. for the same season (3). Honeybee colonies were absent from test blocks at Trenton during 1966; while fruit set was more than adequate, possibly, improved pollination and seed set during subsequent seasons rendered developing fruitlets less sensitive to NAA. The uniform response observed in 1966 implied that slightly inadequate seed set could mask the stage of maximum sensitivity to NAA thus offering one possible explanation for conflicting reports concerning its existence.

Significant abscission frequently resulted from only a single NAA treatment during subsequent seasons. This was particularly evident with 'Delicious' in 1967. Hot and fairly humid conditions prevailed when the first 2 sprays were applied, yet only the first induced significant abscission. Further, in 1968 sprays applied (from the same tank) to 'Delicious' and 'Spy' at 11 and 6 days APF respectively, induced significant abscission from 'Spy' only (Tables 1 and 3). 'McIntosh' also failed to respond on that date (Table 2). Examination of Station weather records at, and prior to, the times of other treatments similarly failed to account for the differential responses observed. These results emphasized the practical value of an accurate means to identify the sensitive stage to avoid periodic thinning failure, or to obtain maximum response annually.

NAA sprays applied in accordance with the 7 to 10 days APF index, induced significant fruit abscission during 3 of 4 seasons and maximum response in 6 of 12 experiments. Treatments applied according to mean fruit diameter invariably caused significant, and usually maximum, abscission: however different cultivars responded maximally at different mean diameters, (6.5 to 8 mm, 8 to 10 mm, and 10 to 11 mm for 'Delicious', 'McIntosh', and 'Spy', respectively), paralleling the response afforded by developing peach fruits (12). Sensitivity of peaches coincided with cytokinesis in the endosperm and was identified by mean pericarp length. By contrast, early cytokinesis in endosperm of apple seeds coincided with non-significant thinning and bore no definitive relationship with mean fruit diameter. Rather, maximum response to NAA usually occurred

Table 4. Comparative accuracy of indices to identify the stage of maximum sensitivity of 3 apple cultivars to NAA thinning sprays.

Date of maximum response	Days elapsed[z] AFB	Days elapsed[z] APF	Mean diameter of fruits (mm)
	Delicious		
6-13-67	10	6	7.8
6-6-68	17	9	7.5
6-10-69	12	8	6.5
Mean	13.00	7.67	7.27
Coef. of Var. (%)	28	20	9
	McIntosh		
6-13-67	11	8	10.3
6-6-68	20	13	8.7
6-10-69	14	10	7.8
Mean	15.00	10.33	8.93
Coef. of Var. (%)	31	24	14
	Spy		
6-15-67	12	7	12.3
6-8-68	16	6	10.0
6-14-69	16	12	10.6
Mean	14.67	8.33	10.97
Coef. of Var. (%)	16	39	11

[z]AFB and APF mean after full bloom and after petal fall, respectively.

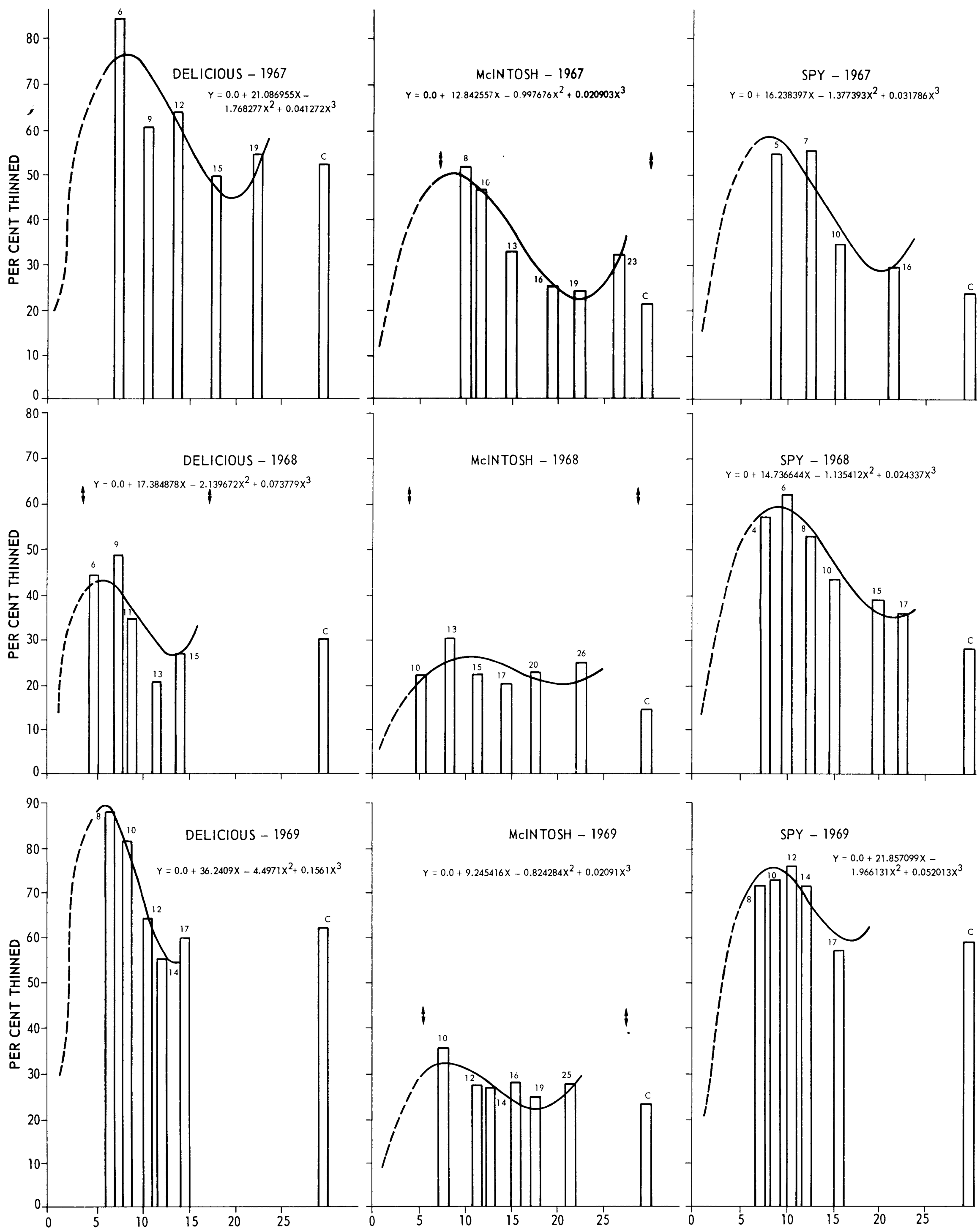

Fig. 1. The relationships between NAA-induced abscission and fruit diameters of developing 'Delicious', 'McIntosh', and 'Spy' apples. Histogram superscripts identify treatment times as days APF (numerals) or no treatment (C).

2 to 3 days prior to the identification of early cytokinesis and may thus provide a means for determining peak sensitivity in other cultivars.

Maximum fruit abscission invariably (and significant abscission usually) occurred when NAA was applied prior to the onset of cytokinesis in the endosperm of samples examined. Polynomial regression curves showed major primary peaks relating maximum abscission to well defined, but narrow, fruit diameter ranges for each cultivar; but each curve showed an upward tailing effect suggesting the possibility of a secondary period of reduced sensitivity to NAA following cytokinesis.

Luckwill (13) reported 2 peaks of endogenous hormonal stimuli in apple seeds and postulated a third; the peaks coincided with fertilization (postulated), cytokinesis, and completion of embryo growth in the cultivars 'Beauty of Bath', 'Crawley Beauty', and 'Lane's Prince Albert'. During the intervals between peaks little or no hormonal stimuli were detected. If 'Delicious', 'McIntosh', and 'Spy' correspond to these cultivars in physiological development of seeds, the observed maximum responses to NAA could be associated with

Table 5. NAA-induced abscission of apples in relation to fruit diameter, endosperm condition, and embryo size.

Clusters abscised[z] (%)	Days APF	Mean diameter of fruit (mm)	Percent of fruits with seed endosperm undergoing cytokinesis	Embryo Length (μ)	Embryo Width (μ)
		Delicious 1967			
85a	6	7.8	0	67	27
61bc	9	11.1	2	75	36
52bc	–	Control	–	–	–
		McIntosh 1967			
52a	8	10.3	0	75	31
47a	10	12.0	0	94	45
33b	13	15.6	63	119	59
21b	–	Control	–	–	–
		McIntosh 1968			
21ab	10	5.4	0	60	30
30a	13	8.7	0	76	31
22ab	15	11.7	17	94	40
14b	–	Control	–	–	–
		Spy 1966			
91a	10	8.3	0	–	–
97a	13	10.8	0	65	30
88ab	15	12.9	28	–	–
90a	17	17.3	68	–	–
82b	–	Control	–	–	–
		Spy 1967			
54a	5	8.9	0	–	–
55a	7	12.3	0	71	30
34b	10	15.5	12	87	38
23b	–	Control	–	–	–

[z]Mean separation by Duncan's multiple range test, at 5% level.

the initial minimum levels of endogenous growth substances in seeds shortly before the onset of cytokinesis. If true, one would expect a second period of reduced sensitivity to NAA following cytokinesis when endogenous auxin levels were decreasing (13). Regression curves tended to support the suggestion of a second period of reduced sensitivity of apples to NAA.

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