

The Effect of NAA and BA on Carbon Dioxide Assimilation by Shoot Leaves of Spur-type 'Delicious' and 'Empire' Apple Trees

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ABSTRACT. The effects of NAA, BA, or Accel on CO₂ assimilation of shoot leaves of mature bearing Redchief 'Delicious' and 'Empire' apple (*Malus ×domestica* Borkh.) trees were evaluated over two seasons. BA at 50 mg·L⁻¹ did not significantly affect any of the gas-exchange parameters measured. NAA (15 mg·L⁻¹) consistently suppressed CO₂ assimilation rate (from ≈10% to 24% below that of the control). This suppression was NAA-concentration dependent, continued for >15 days after treatment, and was completely overcome in 'Empire', but only partially or not at all in 'Delicious' when BA was combined with NAA. These results are discussed in relation to fruit thinning and NAA-induced inhibition of fruit growth in spur-type 'Delicious'. Chemical names used: 2-(1-naphthyl) acetic acid (NAA); N-(phenyl)-1H-purine-6-amine (BA); BA + gibberellin A (GA)₄₊₇ (Accel).

NAA is widely used for thinning apples. Although the fruit thinning activity of NAA has been known for some time (Burkholder and McCown, 1941), its mechanism of action is not well understood. Several hypotheses have been proposed, namely, induced seed abortion (Luckwill, 1953), reduced seed function (Weinbaum and Simons, 1974), induced ethylene production (Curry, 1991), and photoassimilate deficiency due to reduced sucrose and sorbitol translocation (Schneider, 1978). Physical shading or applying photosynthetic inhibitors (Byers et al., 1990b) during or shortly after bloom reduces fruit set similarly to NAA; this may be viewed as further evidence for the photoassimilate-limitation hypothesis (Schneider, 1977, 1978).

Postbloom application of NAA may, in addition to causing fruit abscission, reduce growth of persisting fruit (Greene, 1943). This effect on fruit growth can occasionally be severe, particularly in spur-type strains of 'Delicious', for which fruit size at harvest often is smaller than expected based on crop load. A similar, but less pronounced, effect on fruit size has also been observed in the less-sensitive 'Empire' (Bukovac et al., 1994).

Recently, Accel has been introduced for thinning apples based on the activity of BA (Elfving and Cline, 1993; Greene, et al., 1990). In contrast to NAA, BA applications may result in a fruit size larger than expected for a given crop load, particularly in small-fruited cultivars such as 'Empire' and 'Jonathan' (M. Bukovac, unpublished data). In view of these contrasting effects of NAA and BA on apple fruit growth and the renewed interest on the role of photosynthates in fruit abscission (Byers et al., 1990b; Grappadelli et al., 1994), we investigated whether NAA and BA affected photosynthesis in apple leaves.

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Materials and Methods

PRELIMINARY EXPERIMENTS, 1993. Five-year-old Redchief 'Delicious' and 'Empire' apple trees on MM.106 rootstock at the Horticultural Teaching and Research Center (East Lansing, Mich.) were selected for uniformity of tree size and crop load. 'Delicious' trees were blocked by row (four replications) within the orchard and the following four whole-tree treatments were randomly assigned within each block: 1) control (no treatment), 2) NAA (Fruitone N; Amvac Chemical Corp., Los Angeles) at 15 mg·L⁻¹, 3) BA (Abbott Laboratories, Long Grove, Ill.) at 50 mg·L⁻¹, and 4) NAA at 15 mg·L⁻¹ plus BA at 50 mg·L⁻¹ (tank mixed). Whole trees were sprayed to runoff with a handgun (2.4 MPa) at 20-mm king fruit diameter (KFD).

Five terminal shoots with good light exposure were selected 2 d after treatment from the periphery of the canopy of each tree, and gas exchange was measured on the fourth or fifth fully expanded leaf from the shoot apex. All gas-exchange measurements were made at saturating light levels (10 AM to 1 PM, ≥1200 μmol·m⁻²·s⁻¹) using a portable infrared gas analyzer (ADC LCA 2; Analytical Development Co., Hoddesdon, England) equipped with a Parkinson broadleaf chamber (6.25 cm² leaf area). Leaves were enclosed in the chamber and allowed to equilibrate for 30 to 60 s, after which CO₂ and relative humidity differences, leaf temperature, and flow rate were recorded. From these values, net CO₂ assimilation rate (*A*), transpiration rate (*T*), stomatal CO₂ conductance (*g_s*), mesophyll CO₂ conductance (*g_m*), and internal CO₂ concentration (*C_i*) were calculated using the program of Moon and Flore (1986) adapted to Statistical Analysis System (SAS) language (M.A. Longstroth, unpublished). Values for the five shoots were averaged and analyzed as a randomized complete-block design with factorial treatment structure. All statistical analyses were performed using SAS's general linear model procedure (SAS Institute, Cary, N.C.).

The same experimental design was used for the 'Empire' study. Chemical treatments were applied at 27 mm KFD, gas exchange was measured 2 d after treatment, and photosynthetic parameters were calculated as described above.

TIME COURSE. In 1994, Redchief 'Delicious' trees were selected from the same planting used in 1993, and blocked by rows (six blocks). The same treatments were applied as described in the preliminary experiments except that Accel containing 1.8% (w/w) BA and 0.18% (w/w) GA₄₊₇ was used as the source of BA since no

Table 1. Effect of NAA and BA on gas exchange in Redchief 'Delicious' apple shoot leaves 2 d after treatment.

Treatment ^y	Parameter ^z									
	A ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		T ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		g_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		g_m ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		C_i ($\mu\text{mol}\cdot\text{mol}^{-1}$)	
	Mean	% of control	Mean	% of control	Mean	% of control	Mean	% of control	Mean	% of control
Control	12.3	100	6.45	100	148	100	53.0	100	233	100
NAA	9.3	76	5.34	83	109	73	41.2	78	228	98
BA	11.0	90	6.36	99	137	93	47.5	90	232	100
NAA + BA	10.6	86	6.45	100	137	93	45.0	85	236	101
<i>P</i> values for planned treatment comparisons										
Control vs. NAA	0.005		0.057		0.020		0.007		0.331	
Control vs. BA	0.151		0.868		0.448		0.142		0.910	
Control vs. NAA + BA	0.064		0.999		0.458		0.044		0.552	
NAA vs. NAA + BA	0.143		0.057		0.070		0.290		0.134	

^zA = net CO₂ assimilation rate, T = transpiration rate, g_s = stomatal CO₂ conductance, g_m = mesophyll CO₂ conductance, and C_i = internal CO₂ concentration.

^yNAA at 15 mg·L⁻¹ and BA at 50 mg·L⁻¹.

differences in thinning response were observed between the two formulations (M.J. Bukovac, unpublished data). All treatments were made at 28.5 mm KFD. Gas exchange was measured and photosynthetic parameters were calculated as previously described. Measurements were taken 2, 6, 10, 22, and 28 d after treatment on leaves eight to nine nodes from the shoot base (i.e., the fourth or fifth fully expanded leaf from the shoot apex at time of first measurement) to establish duration of response in treated leaves. The experiment was analyzed as described above, except repeated measurements were treated as split-plot treatments (Little and Hills, 1978). Means within a given measurement date were compared by LSD calculated from a corrected error mean square (Gill, 1986).

CONCENTRATION RESPONSE. Thirteen-year-old Redchief 'Delicious'/MM.111 trees growing at the Clarksville Horticultural Experiment Station, Clarksville Mich., were selected for uniformity of tree size and crop load. NAA was applied at 7.5, 15, and 30 mg·L⁻¹ on 10 July (≈48 mm KFD). Treatments were assigned randomly within each of six replications. Measurements were made 1, 3, 8, 15, and 23 d after treatment. Leaves were selected as described for the time-course study and measurements and calculations were performed as previously described. Statistical analy-

sis was conducted as with the time-course study, and response for NAA concentration was determined by orthogonal contrast.

Results

PRELIMINARY EXPERIMENTS, 1993. NAA applied to Redchief 'Delicious' at 20 mm KFD reduced A by 24% 2 d after application (Table 1). BA had no significant effect on A, while the combination of NAA and BA reduced A by 14%. Although NAA significantly reduced g_s , the calculated value for C_i did not differ from that of the control. This suggested that the effect of NAA was not on g_s , but due to reduced g_m (Farquhar and Sharkey, 1982). NAA reduced g_m by 22% (Table 1). This effect on g_m and, consequently, A was partially attenuated when BA was combined with NAA.

The effect of NAA and BA on 'Empire' shoot leaves was similar to that observed for 'Delicious'. NAA reduced A by 20% 2 d after treatment with a corresponding reduction in calculated g_m (Table 2). As with 'Delicious', g_s was reduced, but C_i was not significantly different from that of the control. BA had no effect on A or g_m but significantly increased g_s and C_i . NAA plus BA did not significantly affect gas exchange.

TIME COURSE. The following season, NAA applied to 'Deli-

Table 2. Effect of NAA and BA on gas exchange in 'Empire' apple shoot leaves 2 d after treatment.

Treatment ^y	Parameter ^z									
	A ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		T ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		g_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		g_m ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		C_i ($\mu\text{mol}\cdot\text{mol}^{-1}$)	
	Mean	% of control	Mean	% of control	Mean	% of control	Mean	% of control	Mean	% of control
Control	12.7	100	5.21	100	151	100	53.1	100	239	100
NAA	10.1	80	4.63	89	119	79	42.4	80	237	99
BA	12.9	102	5.94	114	176	117	51.6	97	251	105
NAA + BA	12.1	96	5.32	102	150	100	50.1	94	242	101
<i>P</i> values for planned treatment comparisons										
Control vs. NAA	0.001		0.186		0.013		0.002		0.647	
Control vs. BA	0.659		0.107		0.035		0.556		0.020	
Control vs. NAA + BA	0.364		0.790		0.947		0.257		0.507	
NAA vs. NAA + BA	0.005		0.122		0.015		0.011		0.274	

^zA = net CO₂ assimilation rate, T = transpiration rate, g_s = stomatal CO₂ conductance, g_m = mesophyll CO₂ conductance, and C_i = internal CO₂ concentration.

^yNAA at 15 mg·L⁻¹ and BA at 50 mg·L⁻¹.

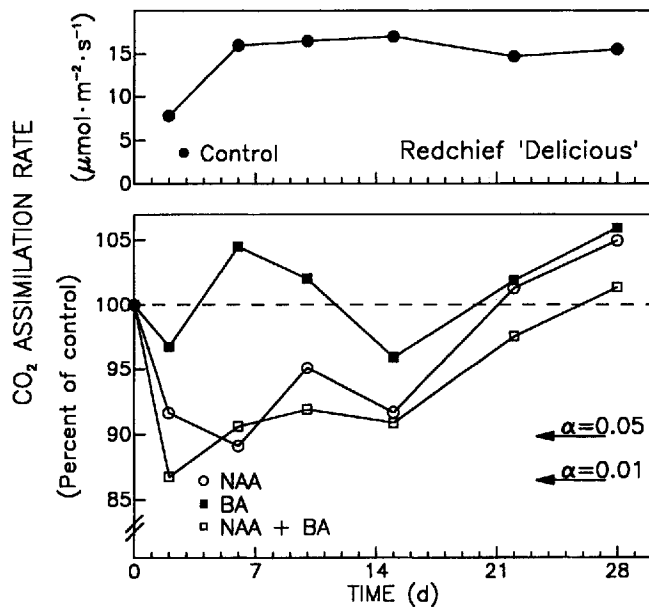


Fig. 1. Effects of NAA ($15 \text{ mg}\cdot\text{L}^{-1}$) and BA ($50 \text{ mg}\cdot\text{L}^{-1}$) on CO_2 assimilation rate (A) of shoot leaves of Redchief 'Delicious' at 2, 6, 10, 22, and 28 d after treatment. A is given for the control in the top panel and for chemical treatments, expressed as a percent of control, in the bottom panel. Arrows denote values signifying differences from control at $\alpha=0.05$ or 0.01 based on LSD calculated with adjusted error mean square for chemical treatments within a measurement date.

cious' trees had similar effects on photosynthetic parameters of shoot leaves. NAA decreased A 2, 6, 10, and 15 d after treatment, with recovery by day 22 (Fig. 1). Again, the reduced A was associated with a significant reduction in g_m and slight reduction in g_s (data not shown). BA did not significantly affect A at any of the dates measured. A tank mix of NAA and BA reduced A similarly to NAA alone.

CONCENTRATION RESPONSE. NAA at $7.5 \text{ mg}\cdot\text{L}^{-1}$ significantly reduced A 3 d after treatment. At higher NAA concentrations (15 and $30 \text{ mg}\cdot\text{L}^{-1}$), A was significantly lower than the control's for up to 15 d after treatment (Fig. 2), with complete recovery after 3 weeks. There was a significant negative linear relationship between NAA concentration and A for all times of measurement except 23 d after treatment. Data for 8 d after treatment are illustrated in Fig. 3.

Discussion

Foliar application of NAA resulted in a concentration-dependent reduction in net CO_2 assimilation. At rates recommended for postbloom fruit thinning ($15 \text{ mg}\cdot\text{L}^{-1}$) (Hull, 1993), this reduction ranged from 15% to 20% and persisted for >2 weeks after treatment. It should be noted that NAA applications for these studies were made generally later than recommended for thinning because of our need for adequate foliage for time-course and related studies. In preliminary observations (data not presented), we found that sensitivity to NAA tended to decrease with leaf age, suggesting that the NAA effect may have been greater if applied earlier to younger foliage (e.g., equivalent to time of thinning). To compensate for this, gas exchange was measured on comparable young newly expanded shoot leaves. Schumacher et al. (1993), using 'Golden Delicious', reported slight reductions in A from a related compound, naphthaleneacetamide, at $100 \text{ mg}\cdot\text{L}^{-1}$. Grochowska and Lubinska (1973) found significantly reduced spur-leaf respiration of 'Landsberger Reinette' following NAA application.

However, we are unaware of published reports showing NAA suppression of CO_2 assimilation in apple leaves at concentrations commonly used for fruit thinning.

The site of action for NAA-induced reduction in A cannot be determined conclusively from our data. However, the calculated value for C_i did not vary with treatment, suggesting that suppression of A is not due to a stomatal limitation, rather to reduced g_m . Schneider (1978) showed that NAA significantly reduced phloem transport of photoassimilates from apple leaves. Thus, accumulation of photoassimilates in the leaves could result in feedback inhibition of A . However, the effect of NAA on phloem transport dissipated by 3 or 4 d and, thus, cannot totally explain the extended reduction in A we observed. Feedback inhibition could explain the reduction in A if NAA alters regulation of assimilate partitioning. A decrease in seed hormones (Crowe, 1965; Ebert and Bangerth, 1982) could cause such reduced sink activity (Brenner et al., 1989; Weinbaum and Simons, 1974). However, it should be noted that, for these studies, NAA was applied after peak sensitivity of the fruit to NAA (Black et al., 1995; Leuty, 1973). This could be indirect evidence of an effect of NAA on the source leaf, either directly on the photosynthetic process or by altering source-regulated partitioning (Daie, 1989). Such an effect on carbon partitioning has been shown in citrus, where NAA reduced ^{14}C export from $^{14}\text{CO}_2$ -treated leaves and inhibited fruit growth (Mauk et al., 1986).

Based on data presented here, reduced A resulting from an effect of NAA on g_s can not be ruled out. Gas-exchange data may overestimate C_i when stomatal closure is not uniform (Beckman et al., 1992; Downton et al., 1988). This patchy stomatal closure was observed when abscisic acid was applied through the transpiration stream of crabapple (*Malus 'Dolgo'*) leaves (Mott, 1995). A similar patchy reduction in g_s by foliarly applied NAA may obscure a stomatal limitation.

BA did not significantly affect A in 'Delicious' and only partially overcame (Table 1) or did not (Fig. 1) overcome the effect

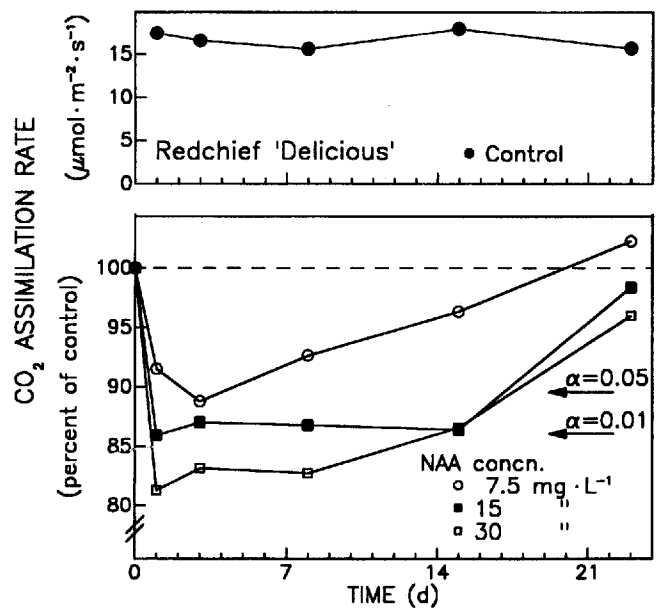


Fig. 2. Effects of NAA concentration on CO_2 assimilation rate (A) of Redchief 'Delicious' shoot leaves at 1, 3, 8, 15, and 23 d after treatment. A for control is given in the top panel and for NAA expressed as a percent of control in the bottom panel. Arrows denote values signifying differences from control at $\alpha=0.05$ or 0.01 based on LSD calculated with adjusted error mean square for chemical treatments within a measurement date.

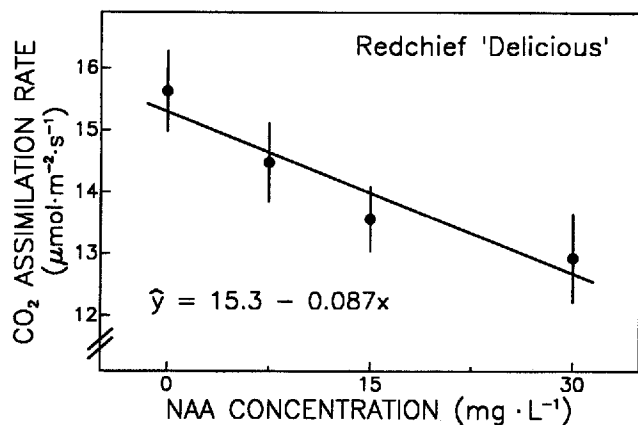


Fig. 3. Response curve illustrating the relationship between NAA concentration and CO₂ assimilation rate in shoot leaves of Redchief 'Delicious' 8 d after treatment. By orthogonal contrast, $P = 0.002$ for linear and $P = 0.234$ for quadratic.

of NAA. However, NAA-suppressed *A* in 'Empire' was completely overcome by BA (Table 2). The basis for the failure of BA to attenuate NAA-suppressed *A* in 'Delicious' in the second season (Fig. 1, 1994) is not clear. However, the source of BA for the 1994 season was Accel, which contained 0.18% (w/w) GA₄₊₇. Although we found no differences in the thinning or fruit growth effects between Accel and BA, the presence of the GA₄₊₇ may have been a factor. In citrus, however, BA enhanced assimilation of ¹⁴CO₂ and its translocation to developing fruit (Mauk et al., 1986). Perhaps in apple, the primary effect of BA is to increase the sink strength of the fruit by enhancing cell division in the young fruitlets (Wismer, et al., 1995), particularly in small-fruited cultivars.

Regardless of the biochemical mode of action, the observed reduction in *A* may play an important role in the fruit thinning and fruit size responses following foliar applications of NAA. Reducing the availability of photoassimilates is known to reduce fruit set. Schneider (1978) used shade cloth to reduce light interception of 'Delicious' trees by 25% for 3 d and observed a >50% reduction in fruit set compared to nonshaded controls. Byers et al. (1990a, 1990b) found that either physical shading (for 10 d at a fruit diameter of 8 to 33 mm) or applying photosynthetic-inhibiting herbicides caused significant thinning. Based on these reports, it is not unreasonable to assume that a 20% reduction in available photoassimilates following NAA application, sustained over several days, may be an important factor in the abscission and early growth of apples. This significant reduction in photoassimilates available to developing fruitlets during the critical cell-division phase of fruit growth (Grappadelli et al., 1994; Hansen, 1971) may be a key factor in the occasional negative effect of NAA on fruit size.

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