

9. Cummins, M. B., E. W. Jenkins, and R. G. Dunning. 1935. Apple orcharding: winter injury; grass endurance; irrigation and nitrate; twenty-sixth to thirtieth year of a 14-variety orchard. Vermont Agr. Expt. Sta. Bul. 395:1-67.
10. Forshey, C. G. and D. C. Elfving. 1977. Fruit numbers, fruit size, and yield relationships in 'McIntosh' apples. J. Amer. Soc. Hort. Sci. 102:399-402.
11. Forshey, C. G. and D. C. Elfving. 1979. Estimating yield and fruit numbers of apple trees from branch samples. J. Amer. Soc. Hort. Sci. 104:897-900.
12. Forshey, C. G. and M. W. McKee. 1970. Production efficiency of a large and a small 'McIntosh' apple tree. HortScience 5:164-165.
13. Hoblyn, T. N., N. H. Grubb, A. C. Painter, and B. L. Bates. 1936. Studies in biennial bearing. I. J. Pomol. 14:39-76.
14. Little, T. M. 1981. Interpretation and presentation of results. HortScience 16:637-640.
15. Magness, J. R., L. P. Batjer, and L. O. Regeimbal. 1948. Apple-tree response to nitrogen applied at different seasons. J. Agr. Res. 76:1-25.
16. Mason, J. L. 1964. Yield and quality of apples grown under four nitrogen levels in uncultivated grass sod. Proc. Amer. Soc. Hort. Sci. 85:42-47.
17. Preston, A. P. 1954. Apple rootstock studies: the Malling IX crosses. Annu. Rpt. E. Malling Res. Sta. for 1953. p. 89-94.
18. Preston, A. P. 1954. Apple rootstock studies: thirty-five years' results with Lane's Prince Albert on clonal rootstocks. J. Hort. Sci. 33:29-38.
19. Quinlan, J. D. and A. P. Preston. 1968. Effects of thinning blossom and fruitlets on growth and cropping of Sunset apple. J. Hort. Sci. 43:373-381.
20. Rogers, B. L. and A. H. Thompson. 1962. Yield, fruit size and growth of York Imperial apple trees as affected by chemical thinning and differential nitrogen nutrition for 6 years. Proc. Amer. Soc. Hort. Sci. 80:50-57.
21. Rogers, W. S. and G. A. Booth. 1964. Relationship of crop and shoot growth in apple. J. Hort. Sci. 39:61-65.
22. Weeks, W. D., F. W. Southwick, M. Drake, and J. E. Steckel. 1958. The effect of varying rates of nitrogen and potassium on the mineral composition of McIntosh foliage and fruit color. Proc. Amer. Soc. Hort. Sci. 71:11-19.
23. Westwood, M. N. and A. N. Roberts. 1970. The relationship between trunk cross-sectional area and weight of apple trees. J. Amer. Soc. Hort. Sci. 95:28-30.
24. Wilcox, J. C. 1937. Field studies of apple tree growth and fruiting. II. Correlations between growth and fruiting. Sci. Agr. 17:573-586.
25. Williams, M. W. and H. D. Billingsley. 1974. Effect of nitrogen fertilizer on yield, size, and color of 'Golden Delicious' apple. J. Amer. Soc. Hort. Sci. 99:144-145.

*J. Amer. Soc. Hort. Sci.* 107(6):1097-1104. 1982.

## Relationship of Seed Number and Maturity to Berry Development, Fruit Maturation, Hormonal Changes, and Uneven Ripening of 'Concord' (*Vitis labrusca* L.) Grapes<sup>1</sup>

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**Abstract.** Fruits were collected on weekly intervals in 1980, beginning at fruit set (ovary shatter) and continuing through harvest. Additional samples collected at harvest in 1980 and veraison in 1981 were sorted into preveraison green, postveraison green, and ripening categories. Seed number per berry was directly related to accumulation of <sup>14</sup>C-photosynthate, fresh weight, and dry weight. Seed number had little relationship with berry content of indoleacetic acid (IAA), abscisic acid (ABA) or percentage of acidity. Percentage of soluble solids was not affected by seed number prior to veraison, but after veraison, percentage of soluble solids and intensity of juice color were inversely related to seed number. Nonripe fruit at the time of harvest had fewer seeds per berry, and fruit containing an immature seed did not accumulate ABA or enter veraison. IAA levels were similar in ripening and nonripening fruit. IAA declined to basal levels by about 55 days after peak bloom. ABA began to increase after 65 days from peak bloom and berry changes associated with veraison occurred after 72 days.

For production of high quality grape berries, the whole cluster should ripen at the same time. The lack of uniformity of berry ripening within a cluster is termed "uneven ripening", and is characterized by the presence of green berries in an otherwise

mature ripe cluster. Uneven ripening of 'Concord' is a major problem in the Southern United States, often prohibiting production. Northwest Arkansas is the southern boundary for commercial 'Concord' production and, even in this region, severe problems with juice quality can develop due to uneven fruit ripening.

Fruit ripening is considered to be a senescence process regulated through hormonal control (24). Ethylene evolution from grape berries remains low through the period of grape maturation (6, 13); however, changes in auxin and ABA levels appear to correlate with the initiation of ripening (veraison) (13, 22). Endogenous auxin levels are relatively high during early stages of berry development, but decline prior to initiation of ripening (5, 13, 22). Auxin applied prior to veraison delays ABA increase

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(6, 11) and fruit ripening (6, 11, 12, 26). ABA substantially increases at the time of fruit ripening (6, 9, 11, 13), and when applied prior to veraison, will initiate ripening (11, 12).

Uneven ripening is more severe when the grapevine is stressed by environmental or cultural factors. Daytime temperatures in Arkansas can approach 40°C during July and August (21) and leaves can attain temperatures up to 10° higher than ambient (15), producing an effective leaf temperature well above a photosynthetic optimum of 25 to 30° for *Vitis vinifera* (14, 15) and *V. labrusca* (25) cultivars. Water stress reduces photosynthetic activity in grapevines (15, 16). Cultural stress induced through increasing fruit loads (7, 18, 19), withholding irrigation during dry periods (20), or otherwise not maintaining an adequate leaf to fruit ratio (7, 8, 17), increases the severity of uneven ripening.

Even though stresses could promote competition among berries by reducing the available photosynthate, a need exists to identify inherent physiological differences between ripening and nonripening berries which may affect the time of veraison or rate of ripening. Seed content affects grape berry development (23, 30), although there are conflicting reports regarding the influence of seeds on uneven ripening (27, 28, 29). This study investigated relationships between seed development, berry development, fruit maturation, and hormonal changes in ripening and nonripening 'Concord' berries.

### Materials and Methods

**Fruit sampling.** Samples were collected in 1980 and 1981 from a nonirrigated, own-rooted 'Concord' vineyard established in 1957 at the Main Experiment Station, Fayetteville, Ark. Vines were trained to a single wire cordon trellis and pruned to a 30 + 10 severity (2).

In 1980, duplicate samples (about 500 berries each) were collected weekly beginning at ovary shatter (June 6) and continuing through harvest (September 2). Berries were deseeded, sorted on the basis of seed number, weighed, and frozen immediately in liquid nitrogen. After freezing, samples were subdivided for IAA, ABA, and fruit quality analysis.

At harvest in 1980 (September 2) and during veraison in 1981 (July 28), fruit samples (3 replications) were collected and sorted into 3 maturity categories: 1) preveraison green, 2) postveraison green, and 3) ripening. Pre- and postveraison green fruit were separated on the basis of firmness. Preveraison fruit showed no softening, which indicates the initial stages of fruit maturation (veraison), and required an average force of  $4.6 \pm 0.5$  kg to compress individual berries to the point of rupture using a U.C. Fruit Firmness Tester (Western Industrial Supply, Inc.) equipped with an Ametek LKG-14 gauge and an 8-mm tip. Postveraison green fruit had begun to soften ( $2.8 \pm 0.4$  kg force required to compress to the point of rupture) but had no color development. The berries were deseeded, weighed, and frozen in liquid nitrogen for later analysis. The seeds were counted and classified as mature or immature based on seed coat color.

To further investigate the influence of seed number and maturity on fruit maturation, 3 replicate fruit samples of the 3 maturity categories were collected during veraison (July 28) in 1981 and subdivided into 5 groups based upon seed content: 1-seeded berries with 0 or 1 mature seed per berry, and 2-seeded berries with 0, 1, or 2 mature seeds per berry. All berries were deseeded, weighed, and frozen in liquid nitrogen for later analysis.

**Quality analysis.** Samples were thawed and homogenized for 30 sec in a laboratory blender. A portion of the sample was removed for dry weight determination and the remainder was

heated in a water bath for one hour at 85°C. Pulp was removed by straining through cheesecloth. Soluble solids were determined using a Bausch and Lomb Abbe refractometer. Acidity was determined by titration and expressed as the percentage of tartaric acid. The intensity of the purple juice color was determined (after veraison only) spectrophotometrically at 520 nm on 5 ml of juice diluted to 100 ml with deionized water.

**Indoleacetic acid and abscisic acid analysis.** Deseeded frozen grape tissue (20 g) were homogenized in 50 ml of 100% methanol. Samples were filtered, methanol was removed by rotary evaporation, and pH was adjusted to 2.8 with 0.2 N H<sub>2</sub>SO<sub>4</sub>. The samples were clarified by centrifugation (15,000 × g) and partitioned twice against equal volumes of diethyl ether. The ether phases were dried by rotary evaporation and resuspended in 0.2 ml of methanol. Recovery of added standard IAA was 86% and ABA was 93%.

IAA and ABA concentrations were determined using a Beckman model 332 gradient high-pressure liquid chromatograph equipped with 2 Model 110A solvent metering pumps, a Model 420 system controller programmer, a Model 210 sample injection valve equipped with a 25 µl loop, a Beckman Model 155 variable wavelength detector, and a Series 5000 Fisher chart recorder.

The hormones were separated isocratically in 45% methanol and 0.2 M acetic acid (3) at a solvent flow rate of 1.0 ml/min (4000 psi) using a 4.6 mm × 25 cm Beckman Ultrasphere-ODS reversed phase column with 5 µm C-18 silica packing. Injection volume was 25 µl and the detecting wavelength was 280-nm for both compounds. Identities of IAA and ABA were determined by retention times. Retention times were 8.5 and 13.6 min for IAA and ABA, respectively (Fig. 1). Preliminary hormone quantitations were similar using these chromatography methods compared with ion exchange methods used by During (10) and suggest relative peak purity. Peak height was related linearly to concentration and was used to quantify both compounds. IAA and ABA standards were obtained from Calbiochem, San Diego, Calif.

**<sup>14</sup>C labeling.** Six representative shoots (1 per vine) were selected with 3 clusters per shoot for monitoring translocation of <sup>14</sup>C-photosynthate into berries. Treatments were applied on July 3 and Sept. 2, 1980. A vial containing 0.1 ml of <sup>14</sup>C-NaHCO<sub>3</sub> (Amersham Corp., Arlington Heights, IL 60005) with a specific activity of 50 µCi/ml was placed inside a polyethylene bag (about 400 cc internal volume) surrounding the first leaf distal to the third cluster. <sup>14</sup>CO<sub>2</sub> was liberated by addition of 0.5 ml of 1.0 N HCl. The enclosed leaf was exposed to sunlight for 3 hr, the polyethylene bag was removed, and the distal cluster was harvested 8 hr after initial leaf exposure to <sup>14</sup>CO<sub>2</sub> and frozen.

Berries from the July 3 treatments were sorted into 1-, 2-, and 3-seeded categories for radioactivity determinations. On September 2, berries were sorted into pre- and postveraison green and ripe categories prior to freezing. Liquid scintillation counting was conducted within 5 days after treatment. For counting, berries were deseeded, weighed, placed in liquid scintillation vials (1 per vial), and crushed. Cocktail (15 ml) containing 50 mg POPOP [1, 4-bis-2-(5-phenyloxazolyl)-benzene], 7 g PPO (2,5-diphenyloxazole), and 100 g naphthalene per liter dioxane was added to each sample. Samples were counted for 50 min in a Packard Tri-Carb 2650 Liquid Scintillation Counter.

### Results and Discussion

Environmental conditions during the summer of 1980 were severe and uneven ripening in 'Concord' vineyards was preva-

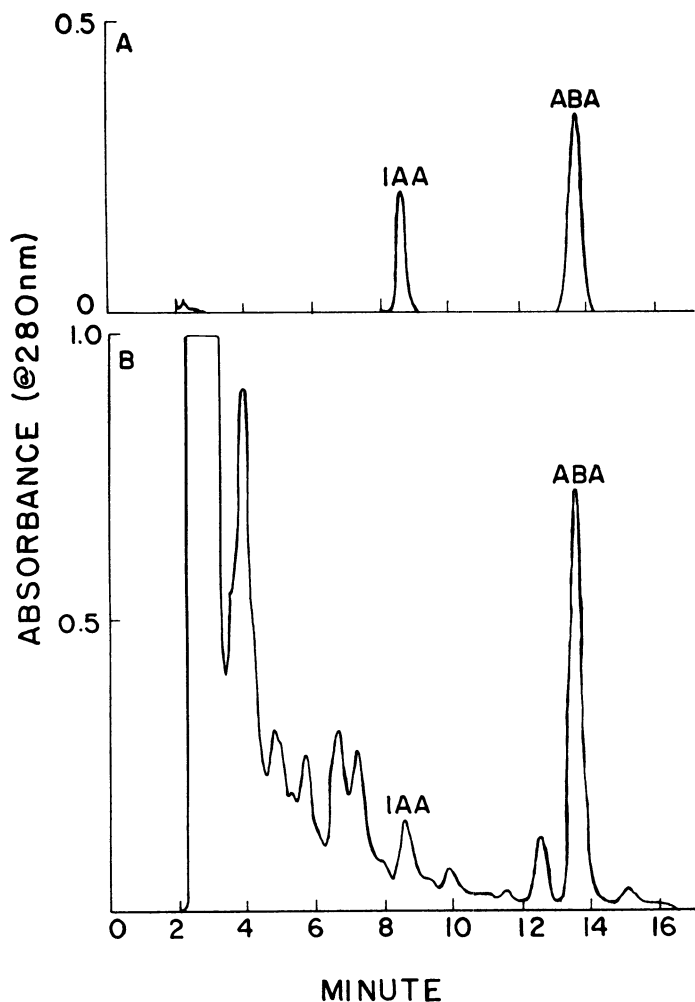


Fig. 1. Chromatograms showing separation of authentic (A) and extracted (B) indoleacetic acid (IAA) and abscisic acid (ABA) by reversed phase HPLC (AUFS = 0.2).

lent. In 1980, 45 days of the growing season between June 1 and August 31 reached or exceeded daytime temperatures of 35°C, while only 2 days exceeded 35° in 1981. Drought conditions also occurred in 1980 with only 4.6 cm of rainfall during July and August, compared to 27.7 cm during the same period in 1981. The 20-year (1960 to 1980) average rainfall during July and August in northwest Arkansas is 18.3-cm.

Changes in berry size (fresh weight) during the 1980 season (Fig. 2) illustrate the "double sigmoid" growth curve typical of *Vitis* species. However, the "lag" stage of berry development (between about 30 and 75 days from peak bloom) was considerably longer and size increase during fruit maturation was reduced as compared to 'Concord' in New York (22). These berry growth patterns may not represent Arkansas-produced 'Concord' fruit in normal years. However, the increased size due to seed number was evident throughout the growing season.

Dry weight accumulated slowly until veraison (about 72 days after peak bloom) when several-fold increases were evident; higher seed numbers contributed to higher dry weight accumulations (Fig. 3). On July 3, 1980, seed number related directly to <sup>14</sup>C-photosynthate accumulation per berry and per g fresh weight (Table 1).

Seed number had little influence on percentage of acidity through the sampling period (Fig. 4). Acidity reached a maximum of about 3.0% at 20 days after peak bloom and gradually

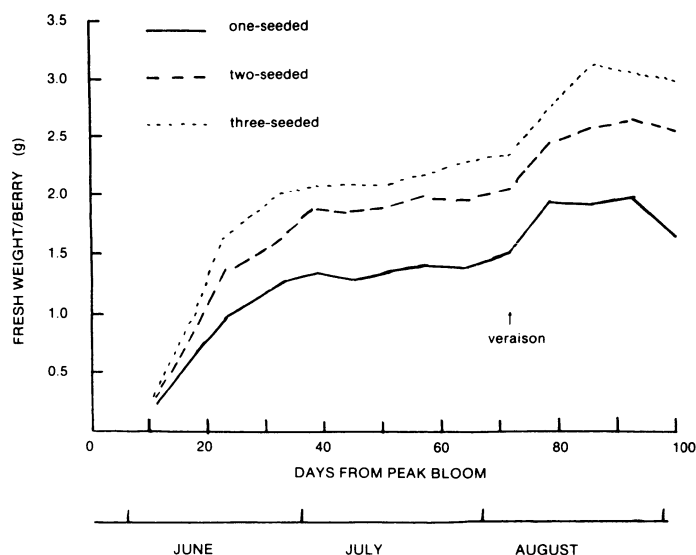


Fig. 2. Effect of seed number per berry on fresh weight of 'Concord' grapes, 1980.

declined until veraison, when acidity decreased rapidly to about 0.5%. Percentage of soluble solids remained constant at near 5% until veraison, followed by the expected rapid increase (Fig. 4). Seed number influenced percentage of soluble solids only after veraison, with an inverse relationship between seed number and percentage of soluble solids. Intensity of juice color was also inversely related to seed number (data not shown). Higher percentage of soluble solids and better color in berries with fewer seeds may have been due to dilution effects because of the higher moisture content of berries containing more seeds.

When acidity and soluble solids are expressed on a "per berry" basis, both increase with seed number (Fig. 5). Acid accumulated in the berries for about 35 days following peak bloom and subsequently declined until harvest. Soluble solids per berry slowly accumulated until veraison, followed by rapid increases. Acid and soluble solids per berry increased with seed number.

Seed number had little influence on endogenous levels of IAA and ABA (Fig. 6). IAA was highest early in the season (at berry shatter) and gradually declined to a base level at 50 to 55 days

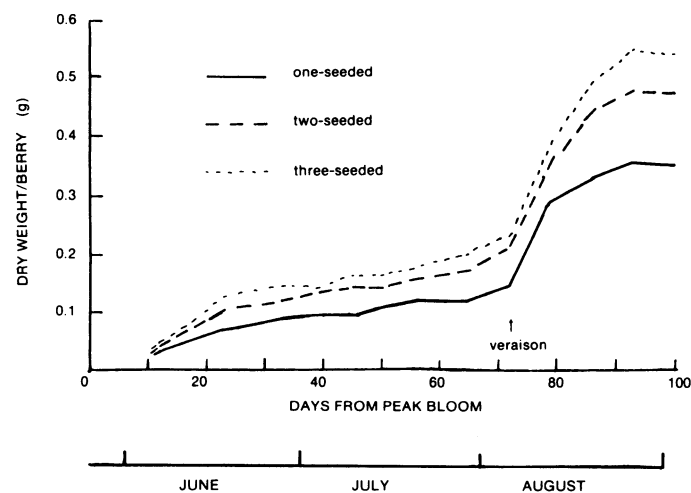


Fig. 3. Effect of seed number per berry on dry weight accumulation of 'Concord' grapes, 1980.

Table 1. Effect of seed number on berry weight and  $^{14}\text{C}$  accumulation in 'Concord' grapes, July 3, 1980.

No. of seeds	Fresh wt per berry (g)	DPM <sup>a</sup> per berry ( $\times 10^3$ )	DPM per g fresh wt ( $\times 10^3$ )
1	0.99c <sup>b</sup>	9.7c	9.8c
2	1.57b	20.8b	13.2b
3	1.96a	39.5a	20.2a

<sup>a</sup>Disintegrations per min.

<sup>b</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

after bloom. Bioassays of auxin in 'Concord' grapes in New York indicated that auxin levels increased up to the "lag" phase of berry development and then rapidly declined (22).

About 10 days after the IAA decline (65 days after bloom), ABA began increasing (Fig. 6). This initial ABA increase was about 10 days before the rapid increases in fresh weight (Fig. 2), dry weight (Fig. 3), and soluble solids (Fig. 4 and 5). ABA accumulation in the berry tissue approached 100  $\mu\text{g}/100\text{ g}$  fresh weight by 100 days after peak bloom. This value is higher than has been reported previously in cultivars of both *V. vinifera* (11) and *V. labrusca* (13).

At harvest (September 2) in 1980, differences in seed number and seed maturity were evident between different maturity categories (Table 2). Normally ripening fruit contained the highest number of seeds per berry with no difference between preveraison and post veraison green fruit. However, all the seeds in berries which had entered veraison were mature (brown seed

coat color) as compared to 26.3% immature seeds in preveraison green fruit. These same trends in seed number and maturity were apparent at the time of general veraison (July 28) in 1981 (Table 3).

Fresh weight and dry weight increased with berry maturity at harvest in 1980 (Table 2) and at veraison in 1981 (Table 3), although the differences in dry weight between pre- and post-veraison green fruit were not significant in 1980.

Soluble solids, both in percentage of and grams per berry, increased with berry maturity in both years (Tables 2 and 3). Percentage of acidity declined with increasing fruit maturity in both years; however, when expressed on a per berry basis to remove the effects of berry size, acidity showed little change between the fruit maturity categories.

$^{14}\text{C}$  accumulation in fruit of the 3 maturity categories indicated that those berries which had just entered veraison (postveraison green) were the most active sinks and were beginning to actively accumulate photosynthate in the ripening process (Table 2). Ripe fruit were not as actively accumulating photosynthetic materials as postveraison green, while preveraison green fruit were comparatively weak sinks.

IAA contents were similar among the 3 fruit maturity categories at harvest in 1980 (Table 2) and at veraison in 1981 (Table 3). These results, combined with the steady IAA decline after berry shatter and the relatively low IAA levels attained before veraison (Fig. 6), do not indicate an involvement of IAA in uneven ripening.

Nonripening fruit had low ABA content at the time of harvest in 1980 (Table 2). Once the fruit entered veraison, ABA increased, and in the ripe maturity category, ABA levels ap-

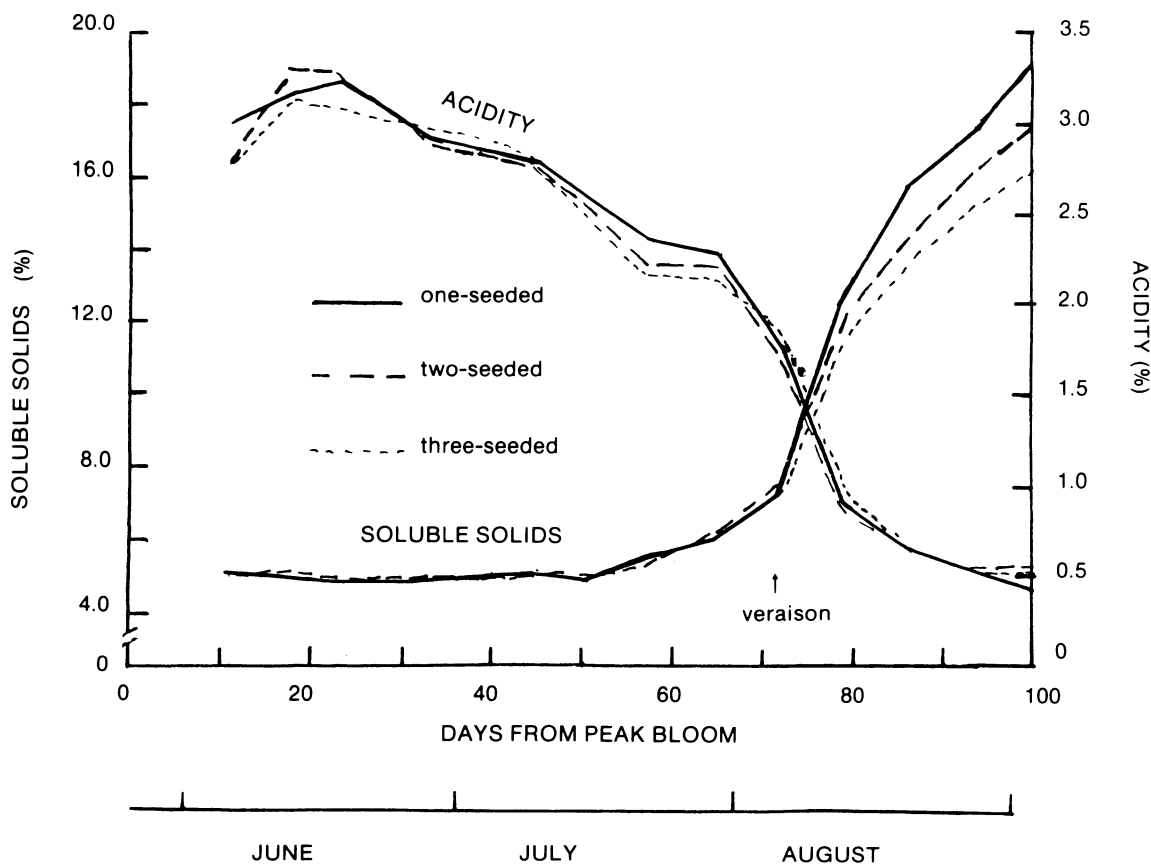


Fig. 4. Effect of seed number per berry on percentage of soluble solids and percentage of acidity in 'Concord' grapes, 1980.

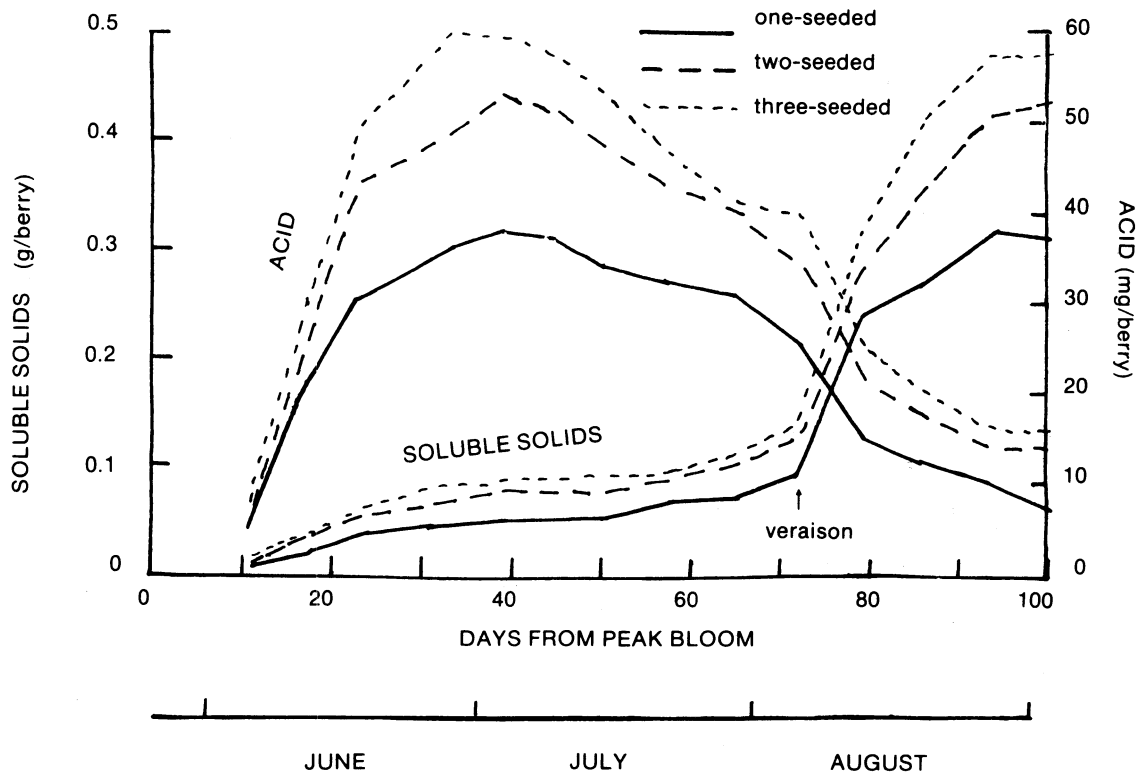


Fig. 5. Effect of seed number per berry on grams of soluble solids and mg of acid per berry in 'Concord' grapes, 1980.

proached 100  $\mu\text{g}/100\text{ g}$  fresh weight. Similar trends were evident at veraison in 1981 (Table 3), but fruit in the coloring category had not yet attained maximum ABA content.

At veraison in 1981, fruits were sorted on the basis of seed number and seed maturity. Berries containing only 1 seed were in the preveraison stage of development if that seed was immature (Table 4). However, if the seed was mature (as indicated by a dark-brown seed coat color), then fruits were distributed

through the 3 maturity categories. Some of the fruit (17%) containing 1 mature seed remained in the preveraison green category, which suggests that the seed matures prior to the onset of the berry quality changes associated with veraison.

Of the berries containing 2 seeds, those with both seeds immature or those containing 1 mature and 1 immature seed were in the preveraison green category (Table 4). All berries containing 2 mature seeds had entered veraison with none remaining

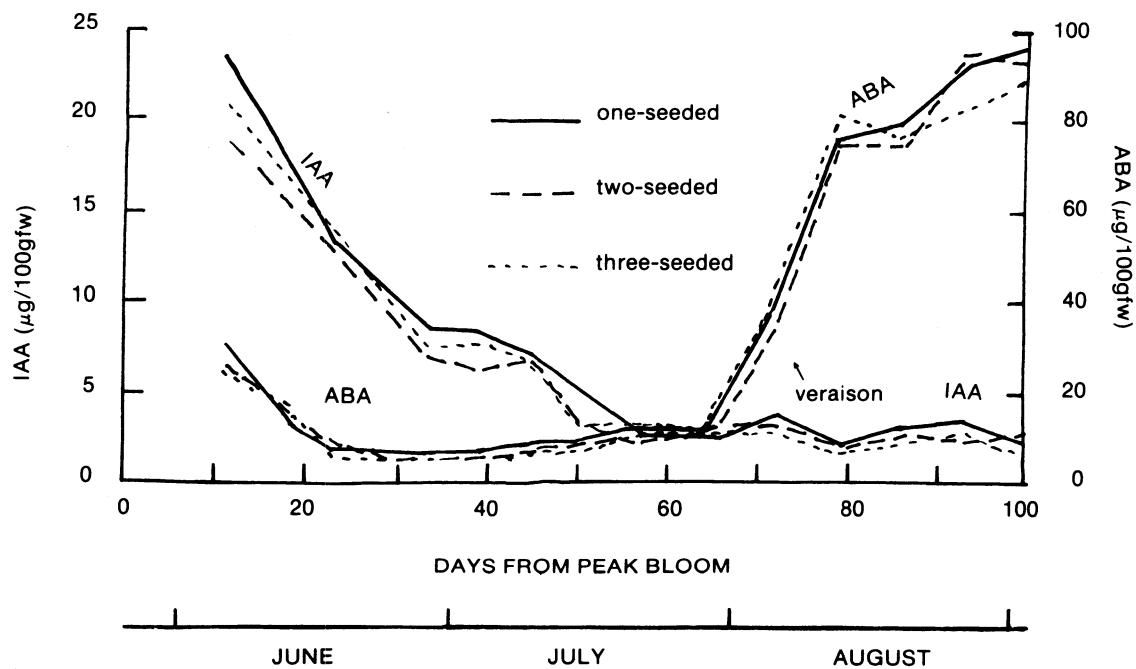


Fig. 6. Effect of seed number per berry on indoleacetic acid (IAA) and abscisic acid (ABA) content per g fresh weight of 'Concord' grapes, 1980.

Table 2. Characteristics of 'Concord' grapes in different maturity stages at the time of harvest, Sept. 2, 1980.

Fruit maturity	No. seeds per berry	Immature seeds (%)	Fresh wt (g)	Dry wt (g)	Soluble solids		Acid <sup>z</sup>		DPM <sup>y</sup> per berry ( $\times 10^3$ )	IAA $\mu\text{g}/100\text{gfw}^x$	ABA $\mu\text{g}/100\text{gfw}^x$
					%	g/berry	%	mg/berry			
Preveraison green	1.94a <sup>w</sup>	26.3b	1.91c	0.20b	8.7c	0.17c	1.16c	22.2a	3.7c	2.1a	16.5c
Postveraison green	1.96a	0.0a	2.35b	0.30b	10.5b	0.25b	0.96b	22.6a	29.0a	2.2a	31.3b
Ripe	2.25b	0.0a	3.00a	0.55a	16.7a	0.50a	0.65a	19.5a	13.3b	2.7a	96.2a

<sup>z</sup>Expressed as tartaric.

<sup>y</sup>Disintegrations per minute.

<sup>x</sup>gfw = grams fresh weight.

<sup>w</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

Table 3. Characteristics of 'Concord' grapes in different maturity stages during veraison, July 28, 1981.

Fruit maturity	No. seeds per berry	Immature seeds %	Fresh wt (g)	Dry wt (g)	Soluble solids		Acid <sup>z</sup>		IAA $\mu\text{g}/100\text{gfw}^y$	ABA $\mu\text{g}/100\text{gfw}^y$
					%	g/berry	%	mg/berry		
Preveraison green	1.32b <sup>x</sup>	66.2b	1.70c	0.16c	8.1c	0.14c	2.60a	44.2a	3.9a	18.3c
Postveraison green	1.24b	0.0a	2.07b	0.23b	10.0b	0.21b	2.17b	44.9a	3.5a	29.1b
Coloring	1.65a	0.0a	2.54a	0.32a	12.0a	0.30a	1.85c	47.0a	3.8a	64.0a

<sup>z</sup>Expressed as tartaric.

<sup>y</sup>gfw = grams fresh weight.

<sup>x</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

in the preveraison category. The fact that 100% of the 2-seeded berries containing 1 mature and 1 immature seed were present in the preveraison category suggests that both seeds must mature before the onset of veraison.

Within each fruit maturity category, 2-seeded berries were larger and generally had higher dry weights (Table 5). One-seeded berries in the preveraison green category were smaller and tended to have a lower dry weight if the seed was immature. Seed number had little influence on percentage of soluble solids of fruit in postveraison green or coloring categories, but soluble solids per berry was higher in 2-seeded berries due to the increased size. In preveraison green fruit, a slightly higher percentage of soluble solids had accumulated in 1-seeded berries if that seed was mature.

Percentage of acidity was not influenced by seed number but those berries containing an immature seed were slightly more acid than berries containing all mature seeds (Table 5). Due to berry size differences, acid content per berry was generally higher in 2-seeded than in 1-seeded berries.

IAA was not influenced by seed number or seed maturity and remained relatively constant among the fruit maturity categories (Table 5). In preveraison green fruit, ABA was relatively low; however, 1-seeded fruit containing a mature seed had begun to increase in ABA content. These data indicate that seeds mature before ABA begins to accumulate and before the berry enters veraison. Seed number had only slight influence on ABA content of postveraison green and coloring fruit, with 2-seeded berries having somewhat higher ABA levels.

In this study, fruit ripening did not commence until ABA had increased in the berry tissue. Also, ABA did not start accumulating until the seeds had matured. For 2-seeded berries, ABA did not increase until both seeds had matured, suggesting an association of immature seeds with suppression of ABA accumulation and delayed ripening. ABA may be the immediate initiator of the grape-ripening process since increases in ABA directly precede veraison, and application of ABA to berries can initiate fruit ripening (6, 9, 11, 13).

Table 4. Influence of seed number and seed maturity on the fruit maturity distribution of 'Concord' grapes during veraison, July 28, 1981.

Seed category		Maturity distribution within each seed category (%)		
No. seeds per berry	No. mature seeds	Preveraison green	Postveraison green	Coloring
1	0	100	0	0
1	1	17	54	29
2	0	100	0	0
2	1	100	0	0
2	2	0	26	74

Table 5. Influence of seed number and seed maturity on berry size, fruit quality, and hormone content of 'Concord' grapes during veraison, July 28, 1981.

Fruit maturity	No. seeds per berry	No. mature seeds	Fresh wt (g)	Dry wt (g)	Soluble solids		Acid <sup>2</sup>		IAA $\mu\text{g}/100\text{gfw}^w$	ABA $\mu\text{g}/100\text{gfw}^w$
					%	g/berry	%	mg/berry		
Preveraison green <sup>y</sup>	1	0	1.67c <sup>y</sup>	0.15b	7.8b	0.13b	2.52b	41.9b	4.5a	14.8b
	1	1	1.86b	0.19ab	8.8a	0.16ab	2.32a	43.2b	3.5a	18.7a
	2	0	2.29a	0.21a	7.7b	0.18a	2.52b	57.7a	3.6a	13.8b
	2	1	2.23a	0.21a	8.1b	0.18a	2.39a	53.3ab	4.0a	14.8b
Postveraison green <sup>x</sup>	1	1	2.08b	0.22b	9.7a	0.20b	2.14a	44.5b	3.1a	24.1b
	2	2	2.78a	0.30a	9.8a	0.27a	2.12a	58.9a	3.3a	26.2a
Coloring <sup>x</sup>	1	1	1.94b	0.25b	11.9a	0.23b	1.71a	33.2b	3.6a	51.5b
	2	2	2.60a	0.33a	12.0a	0.31a	1.75a	45.5a	3.5a	61.3a

<sup>2</sup>Expressed as tartaric.

<sup>y</sup>No 2-seeded berries containing 2 mature seeds were present in this fruit maturity category.

<sup>x</sup>No berries containing immature seeds were present in this fruit maturity category.

<sup>w</sup>gfw = grams fresh weight.

<sup>v</sup>Mean separation within columns and fruit maturities by Duncan's multiple range test, 5% level.

The physiological mechanisms triggering ABA production in grapes are not known but seem to relate to seed maturation. ABA production or accumulation in grape berries does not depend upon the presence of seeds. Seedless grape cultivars as well as seeded cultivars with chemically induced parthenocarp show typical increases in ABA (1, 13). Naturally seedless berries and those with induced parthenocarp often mature earlier (1, 4, 13), implying that the presence of seeds may delay the onset of fruit maturation.

Since IAA contents were similar in ripening and nonripening 'Concord' berries, IAA does not appear to be directly involved in uneven ripening. However, IAA cannot be discounted based on these data nor can the possible involvement of other regulatory agents be ignored. Accumulation of IAA or any other regulatory compound in the berry flesh would not necessarily be a prerequisite for establishing senescence-inhibiting activity. Direct import or export of materials between seeds and the parent vine via placental tissue is possible and could influence berry physiology with no net accumulation in the berry tissue *per se*. However, reports indicate that the grape seed abscises from the placental tissue when it matures (27), reducing the possibility of mature seed influence and strengthening the argument for the regulatory involvement of immature seeds in grape berry maturation.

#### Literature Cited

- Bhullar, J. S. and B. S. Dhillon. 1977. ABA activity in the developing berries of 'Perlette' and 'Anag-E-Shahi'. J. Res. 14:170-174.
- Cawthon, D. L. and J. R. Morris. 1977. Yield and quality of 'Concord' grapes as affected by pruning severity, nodes per bearing unit, training system, shoot positioning, and sampling date in Arkansas. J. Amer. Soc. Hort. Sci. 102:760-767.
- Ciha, A. J., M. L. Brenner, and W. A. Brun. 1977. Rapid separation and quantification of abscisic acid from plant tissue using high performance liquid chromatography. Plant Physiol. 59:821-826.
- Clore, W. J. 1965. Responses of 'Delaware' grapes to gibberellin. Proc. Amer. Soc. Hort. Sci. 87:259-263.
- Coombe, B. G. 1969. Relationship of growth and development to changes in sugars, auxins and gibberellins in fruit of seeded and seedless varieties of *Vitis vinifera*. Plant Physiol. 35:241-250.
- Coombe, B. G. and C. R. Hale. 1973. The hormone content of ripening grape berries and the effects of growth substance treatments. Plant Physiol. 51:629-634.
- Cooper, J. R. and J. E. Vaile. 1939. Response of American grapes to various treatments and vineyard practices. Ark. Agr. Expt. Sta. Bul. 378.
- Cross, F. B. and J. E. Webster. 1935. Physiological studies of uneven ripening of 'Concord' grapes. Proc. Amer. Soc. Hort. Sci. 32:361-364.
- During, H. 1974. Abscisinsäure in reifenden Weinbeeren (abscisic acid in ripening grape berries). Vitis 13:112-119.
- During, H. 1977. Analysis of abscisic acid and indole-3-acetic acid from fruits of *Vitis vinifera* L. by high pressure liquid chromatography. Experientia 33:1666-1667.
- Hale, C. R. and B. G. Coombe. 1974. Abscisic acid—an effect on the ripening of grapes. In: Mechanisms of regulation of plant growth. R. L. Bielecki, A. R. Ferguson, M. M. Cresswell (eds.), Royal Soc. New Zealand, Bul. 12. p. 831-836.
- Inaba, A., M. Ishida, and Y. Sobajima. 1974. Regulation of ripening in grapes by hormone treatments. Sci. Rpt. Kyoto Pref. Univ. Agr. 26:25-31.
- Inaba, A., M. Ishida, and Y. Sobajima. 1976. Changes in endogenous hormone concentrations during berry development in relation to the ripening of 'Delaware' grapes. J. Japan Soc. Hort. Sci. 45:245-252.
- Kriedemann, P. E. 1968. Photosynthesis in vine leaves as a function of light intensity, temperature, and leaf age. Vitis 7:213-220.
- Kriedemann, P. E. and R. E. Smart. 1971. Effects of irradiance, temperature, and leaf water potential on photosynthesis of vine leaves. Photosynthetica 5:6-15.
- Liu, W. T., R. Pool, W. Wenkert, and P. E. Kriedemann. 1978. Changes in photosynthesis, stomatal resistance and abscisic acid of *Vitis labruscana* through drought and irrigation cycles. Amer. J. Enol. Vitic. 29:239-246.
- Loomis, N. H. and J. M. Lutz. 1938. The relationship of leaf area and leaf area fruit ratios to composition and flavor of 'Concord' grapes. Proc. Amer. Soc. Hort. Sci. 35:461-465.
- Morris, J. R. and D. L. Cawthon. 1980. Yield and quality response of 'Concord' grapes to training systems and pruning severity in Arkansas. J. Amer. Soc. Hort. Sci. 105:307-310.
- Morris, J. R. and D. L. Cawthon. 1980. Mechanical trimming and node adjustment of cordon-trained 'Concord' grapevines. J. Amer. Soc. Hort. Sci. 105:310-313.

20. Morris, J. R. and D. L. Cawthon. 1982. Effects of irrigation, fruit load and potassium fertilization on yield and juice quality of 'Concord' grapes. *Amer. Soc. Enol. Vitic.* 33:145-148.
21. Morris, J. R., D. L. Cawthon, and J. W. Fleming. 1979. Effects of temperature and SO<sub>2</sub> addition on quality and postharvest behavior of mechanically-harvested juice grapes in Arkansas. *J. Amer. Soc. Hort. Sci.* 104:166-169.
22. Nitsch, J. P., C. Pratt, C. Nitsch, and N. J. Shaulis. 1960. Natural growth substances in 'Concord' and 'Concord Seedless' grapes in relation to berry development. *Amer. J. Bot.* 47:566-576.
23. Olmo, H. P. 1946. Correlations between seed and berry development in some seeded varieties of *Vitis vinifera*. *Proc. Amer. Soc. Hort. Sci.* 48:291-297.
24. Sacher, J. A. 1973. Senescence and postharvest physiology. *Annu. Rev. Plant Physiol.* 24:197-224.
25. Shaulis, N. J. 1966. Light intensity and temperature requirements for 'Concord' grape growth and fruit maturity. *Proc. XVII Intern. Hort. Congr.* 1:589.
26. Singh, R. K. N. and R. W. Campbell. 1964. Some effects of 4-thianaphthene-acetic acid on ripening of 'Concord' grapes. *Proc. Amer. Soc. Hort. Sci.* 84:259-262.
27. Skirvin, R. M. 1971. The differential ripening effects of a pre-harvest application of gibberellic acid to uneven ripening 'Concord' grapes. MS Thesis, S. Ill. Univ., Carbondale.
28. Vaile, J. E. 1936. Factors influencing the uneven ripening of grapes. *Ark. Agr. Expt. Sta. Bul.* 337.
29. Webster, J. E. and F. B. Cross. 1942. The uneven ripening of 'Concord' grapes: chemical and physiological studies. *Okla. Agr. Expt. Sta. Tech. Bul.* T-13.
30. Winkler, A. J. and W. O. Williams. 1935. Effect of seed development on the growth of grapes. *Proc. Amer. Soc. Hort. Sci.* 33:430-434.

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## Slow-release Fertilizers Optimize Mycorrhizal Development in Container-grown Pine Seedlings Inoculated with *Pisolithus tinctorius*<sup>1</sup>

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**Abstract.** Seedlings of pitch pine (*Pinus rigida* mill.) and Virginia pine (*P. virginiana* mill.) were grown with and without inoculum of the ectomycorrhizal fungus *Pisolithus tinctorius* [(Pers.) Coker & Couch] in a sphagnum peatmoss-perlite medium supplemented with various rates of the slow-release fertilizer (18N-2.5P-10K Osmocote or single rates of 14N-6P-11.6K Osmocote and 19N-3P-8.3K Sierrablen plus ON-19.8P-OK superphosphate) or a soluble 20N-8.6P-16.4K fertilizer treatment. Mycorrhizal development was evaluated after 5 months of growth and then after a 3-month cold storage period. Seedlings heavily mycorrhizal with *P. tinctorius* and of acceptable planting size were produced with 2.3 to 4.5 kg 18N-2.5P-10K Osmocote/m<sup>3</sup> medium. Higher fertilizer rates reduced or eliminated mycorrhizal development and reduced plant growth. Seedlings grown with soluble fertilizer were comparable in size to those produced with slow-release fertilizers, but mycorrhizal development was eliminated. The 3 slow-release fertilizer formulations produced seedlings of comparable size and mycorrhizal development. Superphosphate with or without slow-release or soluble fertilizer did not influence seedling growth or mycorrhizal development. Mycorrhizae continued to develop while plants were in cold storage. The ITW One-Way tube produced seedlings equal in size to those produced in the Leach Pine Cell, but mycorrhizal development appeared to be more sensitive to high fertilizer rates with the ITW tube. Mycorrhizal development did not affect seedling size.

During the past decade, mycorrhizal fungi have been found to be important in the efficient production of a number of woody plants, and in most instances, some mycorrhizal fungal isolates have been found superior to others. Seedlings infected with mycorrhizal fungi which were selected for ecological adaptation

to adverse conditions have been found to survive and grow better on adverse sites than nonmycorrhizal plants or plants mycorrhizal with fungi naturally present in nursery soil. The exploitation of mycorrhizal fungi to improve plant growth has just begun (8).

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Common nursery production practices are not suitable for the production of seedlings infected with specific mycorrhizal fungi (8, 15). One cultural factor which requires modification for production of mycorrhizal seedlings is fertilization. Fertility influences both development of mycorrhizae and the effects fungi have on their hosts. The conventional method of fertilizing container- and field-grown nursery seedlings with large amounts of soluble fertilizer inhibits mycorrhizal development (3, 11, 13). Consequently, current production methods of producing mycorrhizal seedlings often involves a reduction in soil fertility which also may be at the sacrifice of target sizes for plantable nursery stock (12).

Slow-release fertilizers incorporated into the medium before seeding may permit both adequate plant growth and mycorrhizal