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# The relationship of dwarfing and IAA oxidase activity in sweet cherry (*Prunus avium* L.) rootstocks

(Kaitan pengerdilan dengan aktiviti IAA oxidase terhadap pokok penanti ceri manis, *Prunus avium* L.)

S.T. Chong* and P.K. Andrew**

Key words: dwarfing, vigour, rootstock, IAA oxidase, sweet cherry (*Prunus avium* L.)

**Abstract**

Greenhouse experiments were conducted on mazzard (*Prunus avium* L.), Giessen (Gi) 148/1*(Gisela 6) (Prunus cerasus* x *Prunus canescens)* and Gi148/8 *(Gisela 7) (Prunus cerasus* x *Prunus canescens)* rootstocks to determine the relationship of their dwarfing potentials with IAA oxidase activity. Trunk bark was sampled and analysed for indole-3-acetic acid (IAA) oxidase activity at 1 day and 7 days after initial treatment. At the end of the experiment, both root and trunk bark were analysed for IAA oxidase activity. The effects of the inhibitors, scopoletin (7-Hydroxy-6-methoxy-2H-1-benzopyran-2-one) and 2,3,5-triiodobenzoic acid (TIBA) on IAA oxidase activity were examined. The IAA oxidase activities in these clonal sweet cherry rootstocks varied significantly in all the samples. The most vigorous mazzard rootstock had the lowest enzyme activity. Both Gi148/1 and Gi148/8 rootstocks had significantly higher enzyme activity than mazzard. Scopoletin (100 ppm) and TIBA (100 μM) treatments increased IAA oxidase activity significantly at 1 day and 7 days but not 30 days after initial treatment.

## Introduction

Indole-3-acetic acid (IAA) oxidase is ubiquitous in the plant kingdom (Arteca 1996). It is a relatively small protein with a molecular weight of about 30 kD (Laurema 1974). The distribution of IAA oxidase is ordinarily related to growth rate. Galston and Dalberg (1954) showed that stem and root tips have generally less of the enzyme than older tissues; and roots are often markedly richer in the enzyme than stems. Greatest IAA oxidase activity was found in the integument tissue, an intermediate level in the embryo, and only a trace in the endosperm of sour cherry seeds (Valpuesta and Bukovac 1983). Waldrum and Davies (1981) found that this enzyme's activity was closely associated with the golgi apparatus and to a lesser extent with lysosomes and endosplasmic recticulum in pea epicotyl segments. In barley, enzyme activity was reported in protoplast, chloroplast and cytoplasm (Sandberg et al. 1983).

IAA oxidase is an adaptive enzyme which maintains optimum amounts of auxins. The amount of this enzyme has an inverse relationship to growth, suggesting that it may contribute to the termination of growth as tissues mature. IAA oxidase system was proposed to consist of a flavoprotein and peroxidase (Galston et al.

*****Horticulture Research Centre, MARDI Headquarters, Serdang, P.O. Box 12301, 50774 Kuala Lumpur, Malaysia
**Department of Hort. & LA, Washington State University, Pullman, WA 99163, USA
Authors' full names: Chong Swee Teck and Preston K. Andrews
E-mail: stchong@mardi.my

1953). Therefore, peroxidase was used occasionally instead of IAA oxidase.

Studies have also shown that dwarf plants have higher peroxidase protein content than normal and giant types (Kamerbeek 1956). van Overbeek (1935) found greater destruction of IAA, a lower IAA level, and a higher peroxidase content in dwarf strains of corn than in normal-sized strains. Galston (1957) found less inhibitor of IAA oxidase in various parts of dwarf pea 'Laurel' than corresponding parts of non-dwarf 'Alaska' plants. In other words, there was more IAA oxidase activity in the dwarf plants.

The optimum pH of IAA oxidase varied with plant species, ranging from 3.5–6.7 (Tang and Bonner 1947; Wagenknecht and Burris 1950; Gortner and Kent 1953; Stutz 1957; Mudd et al. 1959). Generally, the optimum pH is of 5.0–5.5. For enzyme activity, the protein requires $Mn^{2+}$ and a phenolic, either p-coumaric or ferulic acid, as cofactors. IAA oxidase is very specific for IAA (Tang and Bonner 1947). The affinity or $K_m$ of this enzyme for IAA is 0.1 mM IAA (Sequiera and Mineo 1966).

Inhibitors of IAA oxidase include potassium and sodium cyanide (Tang and Bonner 1947; Gortner and Kent 1953; Steeves et al. 1953), chlorogenic acid (Gortner and Kent 1953), scopoletin (Andreae 1952a, b; Imbert and Wilson 1970), kaempferol or its derivatives (Mumford et al. 1961) and gibberellin (Pilet 1957; Galston 1959; McCune and Galston 1959; Housley and Deverall 1961; Kuraishi and Muir 1962). Derivatives of kaempferol can be promoters (Furuya et al. 1961), and scopoletin can also be a promoter at low concentrations (Imbert and Wilson 1970).

Dwarfing is usually associated with either higher IAA oxidase activity and/or IAA oxidase content or lower IAA levels (van Overbeek 1935; Kamerbeek 1956; Galston 1957; Martin and Stachly 1967; Jindal et al. 1974). IAA is transported basipetally in shoots and acropetally in roots primarily through parenchyma cells that are in contact with vascular bundles. IAA affects growth by stimulating cambial activity and cell enlargement. With either high IAA oxidase activity or limited availability of IAA, plant growth and development would be reduced. Low IAA concentrations in the rootstock would result in numerous, smaller xylem vessels, which would reduce water and nutrient conductivity.

The objectives of this research were to determine the relationships between the dwarfing potential of three sweet cherry clonal rootstocks and IAA oxidase enzyme activities.

**Materials and methods**

Two-year-old rootstocks of mazzard, Gi148/1 and Gi148/8 were planted in containers. The rootstocks were placed on benches in a greenhouse in randomized complete block design consisting of four blocks with one plant of each genotype either treated with scopoletin, TIBA or untreated. These rootstocks were spaced 36 cm apart and grown at air temperatures between 20–31 °C, with 14 h daylengths. TIBA (100 µM), an auxin transport inhibitor, was applied in a lanolin paste around the trunk 5 cm above soil level. Scopoletin, an IAA oxidase inhibitor was applied at 100 ppm foliarly to run-off. Both treatments were repeated at 2, 4 and 6 days after initial treatment.

After 30 days, the potting medium was washed thoroughly from the roots. Trunk bark was sampled for IAA oxidase activity at 1, 7 and 30 days after initial treatment. In addition, root bark was sampled at the end of the experiment, 30 days after initial treatment. Three pieces of bark measuring about 1.5 cm x 1.5 cm were removed from the trunk or roots of each tree per replicate. A total of 12 pieces of trunk and/or root bark tissues were taken from four replicates of each treatment. These samples were immediately frozen in liquid nitrogen and kept on dry ice before transferring

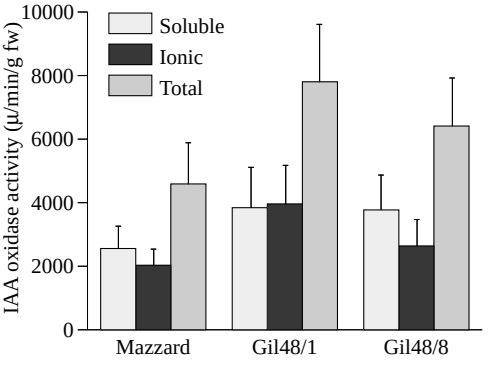
to a –60 °C freezer until analysis. An ANOVA general linear models procedure of SAS (SAS Inst. Inc., Cary, N.C.) was performed on the data. A least significant difference test was used to separate the means at $\alpha = 5\%$, when ANOVA showed significant differences.

The extraction procedure of Quesada et al. (1992) was followed with some modifications. Enzyme activity was determined by measuring the increase in absorbance at 247 nm after incubation of the extracts with 0.6 mM IAA, 0.5 mM $MnCl_2$, and 0.1 mM p-coumaric acid in 60 mM phosphate buffer, pH 5.25, at 30 °C. An activity unit represents a $1 \times 10^{-3}$ increase in absorbance at 247 nm per minute under these assay conditions using a HP8453 UV-visible spectrophotometer.

**Results and discussion**

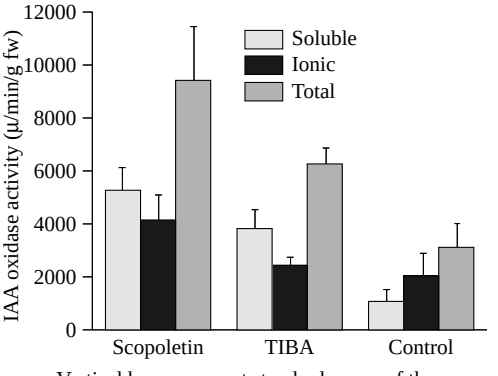
Sweet cherry rootstocks exhibited differences in their IAA oxidase activities one day after initial treatment *(Figure 1)*. Mazzard, the most vigorous rootstock, had the lowest enzyme activity (4,590 m/min/g fw), Gi148/1 had significantly higher enzyme activity (7,804 μ/min/g fw) than mazzard for total activity and in both the soluble and ionic-bound fractions. The dwarfing Gi148/8 rootstock, however, exhibited IAA oxidase activity (6,412 μ/min/g fw) similar to Gi148/1 rootstock.

Scopoletin and TIBA treatments significantly increased IAA oxidase activity (ionic and soluble fractions) for all three clonal sweet cherry rootstocks *(Figure 2)*. Instead of inhibiting, scopoletin at 100 ppm, significantly stimulated IAA oxidase activity. Scopoletin is a competitive inhibitor of IAA oxidase. It competes with IAA oxidase for IAA, which was referred to as an auxin-sparing action (Andreae 1952a; Hare 1964). In vitro studies by Imbert and Wilson (1970) in sweetpotato demonstrated that scopoletin inhibited IAA oxidase activity at high concentrations (12.5–250 nmol/ml; 2.4–48 ppm) but stimulated




Vertical bars represent standard errors of the means
$\mu = 1 \times 10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions

*Figure 1. The rootstock main effects of soluble, ionic-bound and total IAA oxidase activity in trunk bark of three sweet cherry rootstocks grown in containers at 1 day after initial treatment with inhibitors*




Vertical bars represent standard errors of the means
$\mu = 1 \times 10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions

*Figure 2. The inhibitor main effects of soluble, ionic-bound and total IAA oxidase activity in trunk bark of all three sweet cherry rootstocks grown in containers at 1 day after initial treatment with inhibitors*

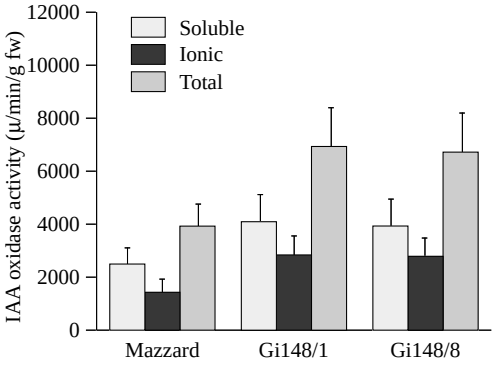
activity at low concentrations (0.25–10 nmol/ml; 0.05–2 ppm). For these sweet cherry rootstocks, 100 ppm scopoletin appeared to be sufficiently low to stimulate IAA oxidase activity.

TIBA, an auxin transport inhibitor, probably indirectly stimulated IAA oxidase activity. Reports have shown that IAA oxidase is an adaptive enzyme (Galston and Dalberg 1954; Rossi 1959; Bhide 1961).

Therefore, it was not surprising to observe high IAA oxidase activity in trunk bark above TIBA treatment where IAA accumulation was expected.

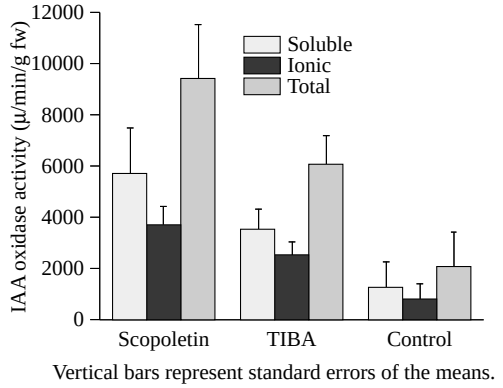
Similar trends of IAA oxidase activity in these rootstocks and by scopoletin and TIBA were observed at 7 days after initial treatment *(Figures 3–4)*. These trends did not persist at 30 days after initial treatment *(Table 1)*. The only significant increase in enzyme activity by scopoletin after 30 days was in the soluble fraction only. These results appeared to show that the effects of scopoletin and TIBA were short term and diminished quite rapidly over time.

Variable results of IAA oxidase activity were observed in root and trunk barks of mazzard, Gi148/1 and Gi148/8 rootstocks at 30 days after initial treatment *(Table 1)*. IAA oxidase activities increased as cells aged (Galston and Dalberg 1954; Henderson 1956; Pilet and Galston 1957). In pineapple, highest activity was found in stem tips, and the lowest activity was in leaves and roots (Gortner and Kent 1953). In *Lupin* plants, however, Stutz (1957) found that hypocotyls were the richest source of IAA oxidase activity and leaves were the poorest sources.




Vertical bars represent standard errors of the means
$\mu = 1x10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions

*Figure 3. The rootstock main effects of soluble, ionic-bound and total IAA oxidase activity in trunk bark of all three sweet cherry rootstocks grown in containers at 7 days after initial treatment with inhibitors*




Vertical bars represent standard errors of the means.
$\mu = 1x10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions

*Figure 4. The inhibitor main effects of soluble, ionic-bound and total IAA oxidase activity in trunk bark of all three sweet cherry rootstocks grown in containers at 7 days after initial treatment with inhibitors*

Table 1. Soluble, ionic-bound and total IAA oxidase activities in root and trunk barks of sweet cherry rootstocks grown in containers, 30 days after initial treatment

| | Enzyme activity (units*/min/g fw) | | |
|---|---|---|---|
| | Soluble | Ionic | Total |
| **Rootstock main effect** | | | |
| Mazzard | 3898 | 2372 | 6290 |
| Gi148/1 | 4481 | 2695 | 7176 |
| Gi148/8 | 3890 | 2768 | 6658 |
| $LSD_{0.05}$ | 1438 | 1013 | 2334 |
| **Treatment main effect** | | | |
| Control | 3435b | 2236a | 5671a |
| Scopoletin | 4943a | 2787a | 7730a |
| TIBA | 3891ab | 2812a | 6704a |
| $LSD_{0.05}$ | 1438 | 1013 | 2334 |
| Bark main effect | | | |
| Root | 4222 | 2870 | 7092 |
| Trunk | 3957 | 2353 | 6311 |
| $LSD_{0.05}$ | 1174 | 827 | 1905 |

*One activity unit represents 1 $x10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions
fw = Fresh weight
Means with the same letter are not significantly different at $\alpha = 0.05$
TIBA = 2,3,5-Triiodobenzoic acid

Table 2. Trunk bark IAA oxidase activities of sweet cherry rootstocks grown in containers, one day after initial treatment with 2,3,5-Triiodobenzoic acid

| | Enzyme activity (units*/min/g fw) | | |
|---|---|---|---|
| | Soluble | Ionic | Total |
| **Rootstock main effect** | | | |
| Mazzard | 3445 | 1728 | 5173 |
| Gi148/1 | 3879 | 2617 | 6496 |
| Gi148/8 | 4110 | 3014 | 7124 |
| $LSD_{0.05}$ | 1463 | 1495 | 2298 |
| **Location main effect** | | | |
| Above treatment | 3825 | 2442 | 6268 |
| Below treatment | 3797 | 2464 | 6261 |
| $LSD_{0.05}$ | 1194 | 1221 | 1876 |

*One activity unit represents 1 $x10^{-3}$ increment increase in absorbance at 247 nm/min at assay conditions
fw = Fresh weight

Due to the polarity of auxin transport and the adaptive formation of the IAA oxidase protein, roots are expected to have higher activity (Galston and Dalberg 1954). But, no significant differences were observed for IAA oxidase activity of trunk barks above and below TIBA treatment one day after initial treatment *(Table 2).* These results were unexpected because the auxin levels were expected to be higher above TIBA treatment than below it. Besides auxin, IAA oxidase activity also depends on the balance of inhibitors and cofactors (Mumford et al. 1962). This protein may not be able to express its activity in the presence of inhibitors or in the absence of cofactors. This may explain why IAA oxidase activities were not significantly different above and below TIBA treatment.

**Conclusion and future research**

Dwarfing in these sweet cherry clonal rootstocks may be due to the higher IAA oxidase activities measured. IAA oxidase activity, however, does not indicate the actual IAA levels in vivo, which is a balance among biosynthesis, transport, conjugation or binding and oxidation. Enzymatic oxidation by IAA oxidase in vivo depends on the presence of inhibitors, co-factors and the intracellular localization of IAA oxidase.

Further research is needed to determine auxin levels (free and bound forms) and IAA oxidase activity simultaneously in the same samples. A gas chromatographic-selected ions monitoring-mass spectrometric technique should be employed for IAA assay (Dunlap and Guinn 1989). The first difficulty in measuring IAA is that the recovery is usually low, about 30–50% (Mann and Jaworski 1970; Sweetser and Swartzfager 1978). Secondly, the IAA levels in most plant tissues are in extremely low concentrations, i.e. nanogramme to picogramme per gramme of fresh weight. Thirdly, variation in IAA levels within individual plants due to such factors as tissue age, time of day, light conditions, and water stress can easily cause 10–50% variations (Sweetser and Swartzfager 1978; Valpuesta et al. 1989).

Inhibitor treatments using scopoletin and 2,3,5-triiodobenzoic acid (TIBA) or others can still be incorporated into these studies. However, their optimum concentrations for transport inhibition or promotion or inhibition of IAA oxidase activity in sweet cherry needs to be established and should not be based merely on research on other species and tissues. IAA oxidase activity has been shown to be localized in different tissues of sour cherry seed (Valpuesta and Bukovac 1983), and in different cell compartments of pea epicotyl segments (Waldrum and Davies 1981).

To fully understand how IAA oxidase regulates the quantity of IAA in sweet cherry rootstocks, further research on localization of IAA and IAA oxidase at the cellular level is essential. In view of the importance of the phenolic inhibitors and cofactors in affecting IAA oxidase activities (Hare 1964), the identification, quantification and interactions of inhibitors and co-factors should be thoroughly studied.

In general, the results of this research support the hypothesis that tree size control

by sweet cherry clonal rootstocks is associated with higher IAA oxidase activity. Although some of the inhibitor trials were inconclusive, they did provide useful background for future work. While this research provides a better understanding of the mechanisms involved in size control of temperate fruit trees, the complexity of this phenomenon suggests that other factors are probably involved. These findings probably could be used for the process of screening and selecting dwarfing individuals as rootstocks for tropical fruit trees which are usually large and vigorous at maturity and are difficult to manage efficiently.

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**Abstrak**

Eksperimen di dalam bekas dijalankan di dalam rumah kaca untuk menentukan kaitan potensi pengerdilan antara pokok-pokok penanti mazzard (*Prunus avium* L.), Giessen (Gi) 148/1*(Gisela 6) (Prunus cerasus* x *Prunus canescens)* dan Gi148/8*(Gisela 7) (Prunus cerasus* x *Prunus canescens)* dengan aktiviti IAA oxidase. Tisu kulit batang pokok ceri disampel dan analisis aktiviti IAA oxidase dilakukan pada 1 hari dan 7 hari selepas rawatan. Pada penghujung eksperimen, kedua-dua tisu kulit batang dan akar dianalisis untuk aktiviti IAA oxidase. Kesan perencat, scopoletin dan TIBA terhadap aktiviti IAA oxidase juga dikaji. Aktiviti IAA oxidase antara pokok-pokok penanti ceri manis adalah berbeza dengan nyata pada semua sampel. Mazzard yang paling subur mencatatkan aktiviti enzim yang terendah. Sebaliknya, kedua-dua Gi148/1 dan Gi148/8 yang kurang subur memberikan aktiviti enzim yang lebih tinggi dibandingkan dengan mazzard. Rawatan scopoletin (100 ppm) dan TIBA (100 μM) meningkatkan aktiviti IAA oxidase secara nyata pada hari pertama dan ketujuh. Sebaliknya pada hari ke-30 pula tidak menunjukkan apa-apa perbezaan dalam aktiviti enzim. Tiada perbezaan yang nyata direkodkan dalam aktiviti IAA oxidase bagi kulit batang di bahagian atas dan bawah kawasan rawatan TIBA selepas sehari dari rawatan awal.

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