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Paclobutrazol, Root Growth, Hydraulic Conductivity, and Nutrient Uptake of 'Nemaguard' Peach

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Abstract. Paclobutrazol (PBZ) was supplied in nutrient solution culture to 'Nemaguard' peach rootstock [*Prunus persica* × *P. davidiana*] at concentrations of 0, 0.001, 0.01, 0.1, and 1.0 mg·liter⁻¹. PBZ increased root : shoot ratio and decreased root length by ≈ 5-fold over the range of PBZ concentrations tested. Root tip diameter, stele diameter, and width of the root cortex were not significantly affected by PBZ. Root hydraulic conductivity decreased log-linearly with increasing PBZ concentration; however, this decrease did not affect midday leaf conductance or net photosynthetic rate. Foliar levels of N, P, K, Fe, and Mo were reduced, whereas levels of Ca, Mg, B, and Mn were increased by PBZ. The magnitude of changes in foliar nutrition were proportional to the degree of growth suppression. Chemical name used: (2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1H-1,2,4-triazol-1-yl)pentan-3-ol (paclobutrazol).

Paclobutrazol (PBZ) is a potent gibberellin synthesis inhibitor that effectively con-

trols vegetative growth of fruit trees (Curry, 1988; Sanchez et al., 1988). PBZ can reduce the need for and costs associated with dormant-pruning (Sanchez et al., 1988; Stan et al., 1985) or summer-pruning (Martin et al., 1987), and is currently used on a limited basis in Australia and regions of Europe for this purpose (B. G. Lever, ICI Plant Protection Div., personal communication). However, several effects other than shoot growth suppression have been reported, including decreased leaf area and increased specific leaf weight (Early and Martin, 1988; Wood, 1984), alteration of fruit size and quality (Looney and McKellar, 1987; Martin et al., 1987; Shaltout et al., 1988), increased root :

shoot ratio (Atkinson and Crisp, 1983; Early and Martin, 1988; Swietlik and Miller, 1983; Wang et al., 1985), and altered root growth and physiology (Atkinson and Crisp, 1983; Bausher and Yelenosky, 1986; Early and Martin, 1988; Steffens and Wang, 1984; Wang et al., 1985; Williamson et al., 1986).

Increased diameter and decreased length of young roots due to PBZ treatment has been reported for citrus (Bausher and Yelenosky, 1986) and peach (Williamson et al., 1986). Such morphological changes may influence water and nutrient uptake because these processes occur most actively in young, unsubsized roots (Atkinson, 1980). Furthermore, PBZ treatment may reduce drought avoidance of nonirrigated trees by decreasing the soil volume occupied by roots. The effects of PBZ on root hydraulic conductivity and nutrient uptake have not been studied in peach. The objective of this study was to determine the effect of paclobutrazol on root growth and morphology, root hydraulic conductivity, and nutrient uptake for 'Nemaguard' peach rootstock.

Terminal semihardwood cuttings of 'Nemaguard' peach rootstock were taken in Aug. 1987 and rooted as described by Couvillon and Erez (1980). Rooted cuttings were stored at 4.5C until June 1988 to satisfy chilling and prevent budbreak. Forty plants ≈20 cm tall and exhibiting uniform budbreak were selected and prepared for nutrient solution culture by washing vermiculite from roots and removing vegetation from the lower 6 cm of the stems. Four plants were placed into each of ten 14-liter containers filled with half-strength nutrient solution (Jones, 1985). Aeration and agitation of the solution was provided by a pressurized air line inserted at the bottom of each container. Plants were grown in a greenhouse with 90% transmission of solar radiant flux and a temperature regime of 25 to 35C day, 15 to 25C night. After a 3-day acclimation period, the half-strength nutrient solution was replaced with full-strength solution to which PBZ was added

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Table 1. Growth characteristics of rooted cuttings of 'Nemaguard' peach rootstock as affected by PBZ in nutrient solution during 47 days of growth.¹

PBZ concn (mg·liter ⁻¹)	Root dry wt (g)	Shoot dry wt (g)	Root : shoot ratio	Leaf area/plant (m ²)	Specific leaf wt (g·m ⁻²)
0.0	7.2	29.0	0.26	0.40	201
0.001	6.0	20.0	0.29	0.26	201
0.01	9.5	20.1	0.48	0.24	203
0.1	6.0	9.8	0.61	0.11	228
1.0	4.6	7.4	0.62	0.05	288
Significance ²					
L	*	**	**	**	**
Q	**	NS	NS	NS	**
C	**	NS	*	NS	NS

¹n = 8 for each characteristic.

²Significance level of regression model. Regression analysis performed on log-transformed values of PBZ concentration.

NS, *, ** Nonsignificant at P > 0.05 or significant at P < 0.05 or 0.01, respectively.

Table 2. Anatomical characteristics and hydraulic conductivity of 'Nemaguard' peach root systems as affected by PBZ in nutrient solution during 47 days of growth.¹

PBZ concn (mg·liter ⁻¹)	Mean root length (mm)	Root tip diam (mm)	Stele diam (mm)	Width of cortex (mm)	Root hydraulic conductivity (ml·MPa ⁻¹ ·min ⁻¹ per g)
0.0	268	0.97	0.13	0.40	0.161
0.001	149	0.82	0.16	0.33	0.070
0.01	143	1.20	0.16	0.52	0.077
0.1	92	1.32	0.16	0.58	0.052
1.0	53	1.14	0.22	0.46	0.028
Significance ²					
L	**	NS	NS	NS	**
Q	NS	NS	NS	NS	NS
C	NS	NS	NS	NS	NS

¹n = 40 for mean root length; n = 20 for root tip diameter, stele diameter, and width of cortex; n = 8 for root hydraulic conductivity.

²Significance of regression model. Regression analysis performed on log-transformed values of PBZ concentration.

NS, *, ** Nonsignificant at P > 0.05 or significant at P < 0.05 or 0.01, respectively.

to give concentrations of 0.0, 0.001, 0.01, 0.1, and 1.0 mg·liter⁻¹. There were eight plants per treatment divided among two containers. Water was added daily and solutions were changed completely each week. Solution pH was 5.8 when fresh, but increased to 7.0 by the end of each week. Plants were grown under these conditions for 47 days in July and Aug. 1988.

Leaf conductance and net photosynthesis were monitored on days 7, 21, and 28 of the experiment on uppermost fully expanded leaves between 0900 and 1200 HR using a LI-6200 portable gas exchange unit (LI-COR). Two leaves on each of two plants per treatment were sampled on each date.

At the end of 47 days of growth, plants were brought into the laboratory and separated into leaves, stems, and root systems for subsequent analyses. Leaf area of each plant was measured with a LI-COR LI-3000 leaf area meter. Root hydraulic conductivity was measured on all plants in the experiment immediately upon severing the root system from the plant using the pressure-induced flow technique (Rieger, 1989). Root systems typically exhibited steady-state flux after 30 to 45 min at an applied pressure of 0.35 MPa, although measurements were continued for at least 1 hr after the steady state was obtained.

The length of 20 roots per root system was

measured on at least two plants per treatment after determination of root hydraulic conductivity. Root systems were laid flat and the distance between the point of attachment to the stem and root tip was measured to the nearest millimeter. Ten representative root segments were excised 5 to 10 mm from the tip of fibrous roots on two plants in each treatment for microscopic examination of root tissues. Root segments were stored in FAA before dehydration in an alcohol series. Segments were embedded in paraffin and sectioned at 10 μm, mounted, and stained with 0.05% Toluidine blue. Root tip diameter and stele diameter were measured using a stage micrometer on 20 root cross-sections per treatment.

Dry weights of roots, leaves, and stems were measured by placing tissues in an oven at 70C for 1 week. Dried leaf tissue was ground to 20-mesh size and ashed in a muffle furnace at 500C overnight to then determine elemental composition of leaves by inductively coupled plasma spectroscopy (Jones, 1977). Sulfur, chlorine, and nitrogen concentrations cannot be obtained using this method; therefore, the concentrations of the former two elements were not determined. Leaf nitrogen content was determined on a separate 0.2 g of dried leaf tissue sample by Kjeldahl digestion.

Regression analyses were carried out using

the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS) (SAS Institute, Raleigh, N.C.), with the logarithm (base 10) of PBZ concentration as the independent variable. A value of 10⁻⁵ was added to all PBZ concentrations to avoid an illegal mathematical argument for the log of zero (0.0 mg·liter⁻¹ treatment), which produced only a 1% error in PBZ concentration for the 0.001 mg·liter⁻¹ treatment, and smaller errors for other treatments. Similar results were obtained from regression analyses by substituting small numbers such as 10⁻⁸ or 10⁻⁷³ for the 0.0 mg·liter⁻¹ treatment and leaving other values unchanged.

PBZ significantly reduced vegetative growth and plant dry weight. The effects of PBZ on shoot and root growth were clearly visible after 1 week. By the end of the experiment, leaf area per plant was reduced ≈ 8-fold and specific leaf weight increased by 43% in response to PBZ at 1.0 mg·liter⁻¹ (Table 1). Daily water use by the plants was markedly reduced as PBZ concentration increased, and directly related to leaf area per container (data not shown).

Root systems of plants exposed to 0.01 mg PBZ/liter had the greatest dry weight of all treatments, whereas untreated plants were intermediate and the 1.0 mg·liter⁻¹ treatment resulted in lowest root dry weight (Table 1). The significant cubic regression model suggests a biphasic dose response of root dry matter accumulation to PBZ; i.e., relatively low concentrations may enhance dry matter accumulation, while higher concentrations cause inhibition. A similar biphasic dose response of root growth to PBZ was found for M.25 apple rootstock (Atkinson and Crisp, 1983) and 'Nemaguard' seedlings (Early and Martin, 1988).

There was a strong positive relationship between root : shoot ratio and PBZ concentration (Table 1), which has been reported previously (Atkinson and Crisp, 1983; Early and Martin, 1988; Swietlik and Miller, 1983; Wang et al., 1985). The highly significant cubic response of root : shoot ratio to PBZ concentration may be explained by the sigmoidal nature of the increase in this characteristic in response to PBZ. This result suggests that no further increase in root : shoot ratio can be expected above 0.1 mg PBZ/liter, and that, at 0.001 mg·liter⁻¹ or below, root : shoot ratio is unaffected by PBZ.

The length of individual roots decreased log-linearly with increasing PBZ concentration (Table 2). Roots of plants exposed to 0.01, 0.1, and 1.0 mg PBZ/liter had a greater degree of suberization and appeared to be larger in diameter compared to root systems exposed to 0.0 or 0.001 mg·liter⁻¹. However, root tip diameter was not significantly related to PBZ concentration, nor were stele diameter and the width of the root cortex. An increase in radial elongation of inner cortical cells of root tips was apparent in photomicrographs of root tips, which has also been reported for rooted cuttings of 'Redhaven' peach (Williamson et al., 1986) and 'Nemaguard' seedlings (Early and Martin,

Table 3. Leaf nutrient composition of rooted cuttings of 'Nemaguard' peach as affected by various concentrations of PBZ in nutrient solution during 47 days of growth.'

PBZ concn (mg·liter ⁻¹)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	B (μg·g ⁻¹)	Cu (μg·g ⁻¹)	Fe (μg·g ⁻¹)	Mn (μg·g ⁻¹)	Mo (μg·g ⁻¹)	Zn (μg·g ⁻¹)
0.0	4.5	0.56	3.2	1.1	0.32	40	5.8	133	84	0.28	24
0.001	4.1	0.46	2.9	1.1	0.31	41	2.2	112	95	0.26	21
0.01	4.2	0.53	3.0	1.2	0.36	43	4.7	117	97	0.26	20
0.1	3.7	0.37	2.6	1.5	0.42	58	2.8	120	101	0.25	22
1.0	3.4	0.28	2.7	1.5	0.43	66	4.2	123	92	0.24	22
Significance ^y											
L	**	**	**	**	**	**	NS	NS	*	**	NS
Q	NS	**	NS	**	**	**	NS	*	NS	NS	NS
C	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

^yn = 8 for each nutrient.

^ySignificance of regression model. Regression analysis performed on log-transformed values of PBZ concentration.

NS, *, **Nonsignificant at P > 0.05 or Significant at P < 0.05 or 0.01, respectively.

1988). Although PBZ affected cortical cell growth of plants in this study in a manner similar to previous studies, this did not translate into an increase in root tip diameter, as found previously. Perhaps the longer period of growth in this study (47 days) compared to previous studies (21 to 27 days) allowed for greater natural thickening of roots of untreated plants, thereby resulting in a lack of difference in root tip diameter among treatments.

Root hydraulic conductivity showed an inverse relationship to PBZ concentration (Table 2). Since hydraulic conductivity was expressed on a root dry-weight basis, this result indicates that efficiency of water uptake per gram of carbon allocated to roots was decreased in PBZ-treated plants. Daily water flux per gram of root for M.25 apple and 'Colt' cherry rootstock decreased in response to PBZ, which may have been due, in part, to decreased root hydraulic conductivity (Atkinson and Chauhun, 1987; Atkinson and Crisp, 1983).

Root hydraulic conductivity was linearly related to root length ($r = 0.85$, $P < 0.01$), suggesting that the decrease in root hydraulic conductivity of PBZ-treated root systems was largely attributable to decreased root length. However, the intrinsic ability of a given length of root to conduct water may not have been altered by PBZ. In fact, had hydraulic conductivity been expressed on a unit root-length basis (i.e., ml·MPa⁻¹·min⁻¹ per cm root length), then the relationship between conductivity and PBZ concentration may have been less negative or nonsignificant. However, total root length was not determined, and, even if data were expressed alternatively as proposed, a cause-effect relationship between root length and hydraulic conductivity could not be established by these data alone. Other factors may have contributed to reduced hydraulic conductivity, such as air increased degree of suberization of young roots receiving PBZ treatment (Atkinson, 1980).

PBZ may reduce drought resistance of peach rootstock by decreasing root system hydraulic conductivity and volume of soil occupied by roots. However, increased root : shoot ratio and decreased leaf area may compensate for reduced capacity for soil water

extraction. In a similar study, PBZ improved water status and polyethylene glycol-induced stress resistance of apple seedlings, largely due to increased root : leaf ratio (Swietlik and Miller, 1983). Also, PBZ treatment delayed the onset of drought stress in 'Colt' cherry rootstock, since the rate of soil water extraction and total water use were reduced compared to untreated plants (Asamoah and Atkinson, 1985).

Periodic measurements of leaf conductance and net photosynthesis on uppermost fully expanded leaves indicated that PBZ did not affect either criterion on days 7, 21, or 28 of the experiment (data not shown). Therefore, if leaf water deficits arose in response to decreased root hydraulic conductivity in PBZ-treated plants, leaf function apparently was not impaired as a result. PBZ did not affect leaf conductance or photosynthesis in mature nectarine (DeJong and Doyle, 1984) or young pecan trees (Andersen and Aldrich, 1987).

Leaf nutrient content, reflective of root nutrient uptake, was significantly altered by PBZ, resulting in decreased levels of N, P, K, Fe, and Mo and increased levels of Ca, Mg, B, and Mn (Table 3). Relationships between nutrient content and PBZ concentration were either linear or quadratic, suggesting a progressive dose response, or a curvilinear or threshold-type response, respectively, over the range of concentrations tested. An inverse relationship between leaf nutrient content and PBZ concentration might be expected since ion uptake and water flux are strongly correlated (Bowling, 1976) and daily water flux was inversely related to PBZ concentration. Other mechanisms must be involved in the case of Ca, Mg, B, and Mn, since the concentration of these elements was highest in plants exhibiting the lowest root hydraulic conductivity and daily water uptake. Because the plants were grown in well-agitated solution, lack of root interception or reduced root length density cannot account for the observed effects; rather, PBZ may have affected the uptake mechanisms within the roots. Since the location of nutrient uptake mechanisms within roots is poorly understood, it is inappropriate to speculate on whether abnormal development of inner cortical cell layers of PBZ-treated roots affected nutrient

uptake mechanisms. Atkinson (1986) discussed possible mechanisms and potential consequences of altered levels of N, P, K, and Ca in apple leaves following PBZ treatment. Due to conflicting results, it is unclear whether the proposed mechanisms are applicable to this study. Martin et al. (1987) reported that PBZ decreased leaf K and increased Ca in mature 'Flavorcrest' peach trees as found in this study, although, in contrast, concentrations of N and Mg were unaffected, and P was increased in one of three years. PBZ increased leaf N and P in M.25 apple rootstock (Atkinson and Crisp, 1983), also in contrast to results of this study. Although the present study and earlier studies contain some contrasting information, it is clear that PBZ can affect the uptake and/or accumulation of nutrient elements in leaves. Potentially, this change could benefit or harm fruit tree growth and cropping. Among the many published reports of PBZ on fruit trees, however, we found none that present either positive or negative effects of altered foliar nutrition on fruit yield or quality.

Reduced root hydraulic conductivity and altered nutrient uptake appear to be side-effects of PBZ treatment on roots of 'Nemaguard' peach rootstock, the magnitude of both being proportional to the degree of vegetative growth suppression and changes in root growth and morphology. Further studies are necessary to determine whether or not these side effects manifest themselves in a desirable or undesirable fashion under orchard conditions.

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Survival of Young Cold-hardened 'Hamlin' Orange Trees at – 6.7C

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Abstract. Potted greenhouse-grown, 1-year-old 'Hamlin' orange [*Citrus sinensis* (L.) Osbeck] trees on 1.5-year-old rough lemon (*C. jambhiri* Lush.) rootstock were temperature-conditioned for 6 consecutive weeks in a controlled-environment room to test cold-hardening ability. Holding at $15.6 \pm 0.6C$ during 12-hr days [$425 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ photosynthetic photon flux (PPF) at top of trees] and $4.4C$ during nights resulted in 100% tree survival and no leaf loss "after 4 hr of – 6.7C in a dark freeze test room. Unhardened greenhouse trees were killed to rootstock. Solute efflux ($\text{dS}\cdot\text{m}^{-1}$) from unhardened frozen leaves was > 20-fold that from frozen leaves on hardened trees and nonfrozen leaves on unhardened trees. Oxygen uptake was not significantly impaired in frozen hardened leaves. No O_2 uptake was evident for frozen unhardened leaves.

'Hamlin' orange is one of the world's major early maturing (October-January) sweet orange cultivars and is second to the late-maturing (March-June) major juice orange, 'Valencia,' in hectareage and number of trees in Florida. The 1988, commercial citrus tree inventory (Fla. Agr. Stat. Ser., 1988) showed about a 31% increase in 'Hamlin' plantings to $\approx 61,400\text{ha}$ from a low of 46,900 in 1986 and to 16 million from 12 million trees. Much of this increase is in replanting of areas devastated after freezes in the 1980s. The choice of 'Hamlin' for replanting frozen-out areas apparently was partly based on its high yield potential (Fla. Agr. Stat. Ser., 1989; C.J. Hearn, personal communication); early maturing of fruit, which decreases the risk of total loss to freezes; and wide acceptability in fresh fruit and processed juice where blending with 'Valencia' orange increases color acceptability (Wutscher and Bistline, 1988). However, there are few published reports on cold hardiness of 'Hamlin' (Hearn et al., 1963) because it is a relatively new cultivar in extensive plantings of freeze-risk areas.

The objective of this study was to test the cold-hardening ability of 'Hamlin' on a cold-sensitive rootstock in a severe freeze situation to obtain basic information on the freeze survival of this cultivar and its potential in low-temperature stress tolerance (Ashworth, 1986; Barrett, 1981).

Forty-five trees, matched for uniform growth and appearance, were selected from a greenhouse population of 100 one-year-old

'Hamlin' orange trees on 1.5-year-old rough lemon rootstock. Single trees were grown in 2.5-liter plastic pots containing Pro-Mix (shredded sphagnum peat with equal parts of vermiculite and perlite and major and minor elements added; Premier Brands, Inc., New Rochelle, N.Y.). Rootstock were from open-pollinated seed from a single source tree near Leesburg, Fla. 'Hamlin' scions were from state-registered budwood from a single source tree near Dundee, Fla. Buds were grafted, 10 cm above soil level, into 5-month-old rootstock. Single-stem trees were maintained in a 50% shaded greenhouse under natural day conditions. Air temperatures in the greenhouse ranged from $32C$ during the day to $15C$ at night. Relative humidity ranged from 35% during the day to 98% at night. Trees were watered every 2 days and each tree was fertilized monthly with 12N-5P-4.3K liquid fertilizer containing microelements at 100 ml per pot. Trees averaged 88 ± 4 cm in total height, 0.7 ± 0.2 cm stem diameter 10 cm above budunion, 1.4 ± 0.1 cm mid-diameter of rootstock, and 29 ± 2 leaves.

Fifteen trees were exposed to a cold-hardening regime of 6 consecutive weeks of 12-hr days ($425 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ PPF at the top of the trees) with $15.6C$ days and $4.4C$ nights, and 30 trees were left in the greenhouse. Hardened trees were frozen along with 15 unhardened trees in a controlled-freeze chamber (Yelenosky, 1975). In controlled freezes, temperatures were lowered $1.1C/hr$ from $4.4C$ to $-6.7C$ for 4 hr, and then returned to $4.4C$ at $1.1C/hr$. Temperatures were measured to $\pm 0.6C$; relative humidity was $60\% \pm 5\%$. Stem temperatures were measured with 24-gauge T-type thermocouples taped to the main stem of five trees and connected to a 15-channel digital recorder, and were within $1C$ of ambient air before trees froze. Leaf freezing was noted every hour by observing water soaking in the leaves. Soil temperatures did not drop below $1C$. Trees were kept at $\approx 25C$ for 3 hr after re-

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