

Paclobutrazol Reduces Some Negative Effects of Salt Stress in Peach

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ABSTRACT. One-year-old rooted cuttings of 'Nemaguard' peach [*Prunus persica* (L.) Batsch.] were irrigated with 0, 1000, or 2000 mg·L⁻¹ salts under greenhouse conditions to study the effect of foliar paclobutrazol (PBZ) application on salt stress response. Salinity reduced growth of nontreated plants by ≈60%, but only by ≈30% for PBZ-treated plants. PBZ-treated plants also had less defoliation and fewer leaves per plant showing salt stress symptoms, and had higher rates of leaf gas exchange than nontreated plants. PBZ application generally reduced Na⁺ and Cl⁻ contents in leaves, roots, and stems, regardless of salt treatment. Furthermore, total Na⁺ per plant in PBZ-treated plants was about half that found in nontreated plants, although total Cl⁻ per plant was reduced by PBZ in only one of two salt treatments. The data suggested that PBZ promoted salt stress avoidance in peach by reducing the uptake and accumulation of harmful Na⁺ and Cl⁻ ions in plant tissues.

It is estimated that one-third of the world's irrigated soils are affected by excess salinity (Richard and Gary, 1984). The problem is particularly acute in arid regions such as Egypt, where ≈60% of the arable soils are classified as salt affected (Balba 1969). Today, the most commonly used practice for alleviating salt stress is leaching, where large quantities of water are used to flush salts from the root zone. With diminishing supplies of irrigation water and competition between agricultural and domestic uses intensifying, leaching may become an expensive or impractical option. Clearly, new approaches to agricultural production in arid, salt-affected regions are needed.

Genetic improvement of crop salt tolerance may be the best long-term solution to the problem of soil salinity. Recent advances in molecular biology appear promising for improvement of plant salt tolerance (Tarczynski et al., 1993). However, breeding and/or genetic engineering of many horticultural crops, such as woody perennials, lags well behind that of herbaceous crop plants, and it is likely to require a much longer time to become implemented.

Short-term solutions to salt stress are needed to bridge the gap between today's approach and a future agriculture that uses genetically improved plants. A few studies have focused on alleviation of environmental stresses by means of growth regulators. Stress-tolerant plants often grow more slowly than intolerant plants; therefore, growth retardants may induce adaptive mechanisms or at least cause intolerant plants to mimic the behavior of tolerant plants during environmental stress. For example, Behairy et al. (1985) found that Cycocel, a gibberellin (GA) biosynthesis inhibitor, decreased stem length of guava and olive seedlings and simultaneously increased salt tolerance. Similarly, Sharaf et al. (1985) found that Cycocel decreased stem length of American and European grapes and increased salt tolerance. In citrus, paclobutrazol (another GA biosynthesis inhibitor) may enhance freezing resistance (Yelenosky et al., 1987). Paclobutrazol (PBZ) has also improved plant performance during drought in apple (Asamoah and Atkinson 1985) and *Prunus* species (Ranney et al., 1989).

Earlier research by the authors indicated that PBZ reduced the effect of salt stress on guava and grapes (Abou El-Khashab 1991;

Elaidy et al., 1992; Salama et al., 1992). It was hypothesized that PBZ-treated plants had better quality of growth under salt stress than nontreated plants due to the slower growth rate of the former. Based on these preliminary observations, this investigation was conducted to confirm the effect of PBZ on salt tolerance in peach and determine the physiological mechanism by which PBZ reduces the effects of salt stress in plants.

Materials and Methods

Plant material and growing conditions

Terminal cuttings of peach were rooted (Couvillon and Erez 1980) in August 1994. After removal from the mist bench, rooted cuttings were stored at 4.5 °C until March 1995. At the beginning of March, cuttings were transplanted to 20-L pots filled with field soil (Cecil sandy clay loam, obtained from the Horticultural farm of the Univ. of Georgia), sand, and pine bark with a ratio of 3:3:4, respectively. Plants were irrigated and fertilized to promote strong growth until 23 May 1995, when salinity and PBZ treatments were imposed (plants were 50 to 75 cm in height).

The experiment was conducted in Athens, Ga. (35 °N lat. and 85 °W long.). Plants were grown in a greenhouse yielding ≈70% integrated daily light transmission and temperatures ranging from 22 °C minimum to 35 °C maximum.

Treatments and design

On 23 May, 36 plants were arranged in a randomized complete-block design of six treatments with six single-tree replications along a greenhouse bench. Three salt concentrations, 0, 1000, and 2000 mg·L⁻¹ total salts, were derived from mixing stock solutions of CaCl₂ (2 M), NaCl (4 M), KCl (1 M), MgSO₄ (1 M), K₂SO₄ (1 M), and Na₂SO₄ (1 M) as follows. One liter of 1000 mg·L⁻¹ solution was derived by adding 0.34 mL of CaCl₂, 1.72 mL of NaCl, 0.42 mL of MgSO₄, 0.29 mL of K₂SO₄, and 2.97 mL of Na₂SO₄ per liter to a 100 mg·L⁻¹ nitrogen fertilizer solution. For the 2000 mg·L⁻¹ treatment, 0.90 mL of CaCl₂, 2.80 mL of NaCl, 1.24 mL of MgSO₄, 1.03 mL of K₂SO₄, 1.49 mL of KCl, and 5.00 mL of Na₂SO₄ were mixed per liter of 100 mg·L⁻¹ nitrogen fertilizer solution. This yielded a milliequivalent ratio of about 1 Cl⁻ : 1 SO₄²⁻ and a sodium adsorption ratio of 12 [SAR = Na⁺ / (Ca²⁺ + Mg²⁺)] in both cases. An SAR of 12 is typical for salt-affected Egyptian soils. Total concentrations of Na⁺ and Cl⁻ ions for the 1000 mg·L⁻¹ treatment were 13 and 8 mM, respectively, and for the 2000 mg·L⁻¹ treatment, 21 mM Na⁺

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Table 1. Dry mass and leaf area of 1-year-old 'Nemaguard' peach trees 3 months after salinity and paclobutrazol (PBZ) treatments were applied.

Salt treatment (mg·L ⁻¹)	PBZ ²	Leaves (g)	Stem (g)	Root (g)	Total (g)	Root to shoot ratio	Abscised leaves (cm ²)	Leaves w/ salt symptoms (%)	Total leaf area (cm ²)
0	—	32.0* ^y	43.0*	44.5*	119*	0.60*	0.0	0.0	3893*
	+	21.5	18.8	31.4	71.7	0.79	0.0	0.0	2553
1000	—	18.1	21.3*	20.4	59.8	0.52	299*	34.2*	2348
	+	20.4	14.3	20.2	54.9	0.58	154	14.0	2662
2000	—	16.2	15.7	15.4	47.3	0.49	968*	49.4*	2278
	+	16.9	15.8	17.8	50.4	0.55	251	27.1	2115
Salt effect ^x		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0027

²PBZ = paclobutrazol foliar spray at 200 mg·L⁻¹.

^yMeans for -PBZ treatments followed by an asterisk (*) are different from means for +PBZ treatments immediately below for a given variable.

^xP > F value for the main effect of salt concentration for a given variable.

and 16 mM Cl⁻. These treatments yielded significant decreases in growth and physiological parameters in a pilot study conducted on peach the previous year. Plants were irrigated with 1 L of salt solution as needed and leached with tap water after every fourth irrigation to prevent salt accumulation. Salt treatments were continued for 3 months, and plants were destructively harvested on 23 Aug. 1995.

Paclobutrazol treatments were applied on 23 May 1996 using 200 mg·L⁻¹ active ingredient from Bonsi (ICI Inc., Haslemere, England). A hand sprayer was used to apply PBZ to runoff.

Measurements

LEAF EXPANSION. Leaf expansion was estimated by measuring the length and width of a newly emerging leaf every other day until the leaf stopped enlarging. The relationship between leaf area and length × width was obtained by regression of these variables using 100 leaves from similar plants:

Leaf area = 0.696 × (length × width) + 0.287 (folded leaves)

Leaf area = 0.666 × (length × width) + 0.809 (unfolded leaves)

where r^2 was >0.95 in both cases.

Leaf expansion measurements were made four times, at intervals of 2 to 3 weeks. The rate of leaf expansion was calculated as the difference between two successive measurements divided by 2, yielding units of cm²·d⁻¹. The mean area of an individual leaf was obtained from the final leaf expansion readings.

LEAF GAS EXCHANGE. Net CO₂ assimilation (A), stomatal conductance (g), and intercellular CO₂ (C_i) were measured three times (monthly) beginning 1 month after treatment application using a portable photosynthesis meter (LI-6200, LI-COR, Lincoln, Neb.). Measurements were made between 1100 and 1300 hr when photosynthetic photon flux density was >1000 μmol·m⁻²·s⁻¹. The most recent fully expanded leaf on an upright shoot (generally six nodes below the terminal) was selected for measurement on each occasion.

RELATIVE WATER CONTENT. RWC was measured three times, beginning 1 month after treatment application. In each treatment, six discs of leaf tissue (1 cm in diameter) were weighed fresh and then floated on distilled water for 4 h to become fully turgid. Initial tests had shown 4 h to be sufficient time for full water imbibition. Discs were weighed again, dried at 70 °C, and then weighed a final time. The relative water content (RWC) was calculated as RWC = [(fresh mass - dry mass)/(turgid mass - dry mass)] × 100.

LEAF AREA AND DRY MASS. Soil was gently washed from roots, and plants were divided into leaves, stems and roots. Total leaf area was measured using a LI-3000 leaf area meter (LI-COR) after dividing leaves into symptomless and symptom-showing classes. Symptoms of salt stress in peach appear first as tip necrosis and

marginal chlorosis, followed by marginal and interveinal chlorosis as leaves age. Abscised leaves were collected and their area measured as they fell during the growth period, and the cumulative area of abscised leaves per plant was recorded. Leaves, stems, and roots were oven dried at 70 °C until they reached a constant mass.

SODIUM AND CHLORIDE CONTENT OF TISSUES. Dried leaves, stems and roots were finely ground and used for analyses of Na⁺ and Cl⁻ content. Sodium was determined by a private laboratory using ICP emission spectroscopy after ashing 0.5 g of dried tissue at 500 °C for 4 h. Chloride was determined using a Cl⁻ ion-selective electrode (Fischer Scientific, Pittsburgh) after the method of Islam et al. (1983). Briefly, 0.5 g of dried, ground tissue was dissolved in 50 mL of 0.5 N HNO₃ and allowed to stand for at least 5 min. Stable values were obtained 1 to 2 min after inserting the electrode into the sample mixture, which was gently stirred. The electrode was calibrated using NaCl standards yielding 10, 100, and 1000 mg·L⁻¹ Cl⁻.

The total amount of Na⁺ and Cl⁻ in the plants at harvest was estimated by multiplying the organ dry mass (g) by the corresponding Na⁺ and Cl⁻ content (mg·g⁻¹) to give milligrams of ion per organ, then summing the parts to get the total ion per plant.

STATISTICAL ANALYSIS. Data were analyzed using SAS's (Cary, N.C.) PROC GLM using a factorial analysis of variance model. Differences between PBZ-treated and nontreated plants at each salt level were separated by *t* test.

Results and Discussion

DRY MASS. Salinity reduced total dry mass and mass of all organs, and decreased root to shoot ratio (Table 1). Dry mass was reduced by

Table 2. Area per leaf after cessation of expansion of 1-year-old 'Nemaguard' peach trees on four dates after salt and paclobutrazol (PBZ) treatments were applied.

Salt treatment (mg·L ⁻¹)	PBZ ²	Area per leaf (cm ²)			
		Week 6	Week 8	Week 10	Week 12
0	—	27.4* ^y	22.2*	22.1*	16.4
	+	14.0	15.1	11.5	13.0
1000	—	26.0*	23.2*	19.3*	23.3
	+	14.9	13.7	11.4	16.8
2000	—	25.5*	16.4	20.4	30.6*
	+	15.4	17.2	14.9	18.8
Salt effect ^x		0.9877	0.6634	0.5757	0.0073

²PBZ = paclobutrazol foliar spray at 200 mg·L⁻¹.

^yMeans for -PBZ treatments followed by an asterisk (*) are different from means for +PBZ treatments immediately below for a given variable.

^xP > F value for the main effect of salt concentration for a given variable.

>50% for nontreated plants, but salt-induced dry mass reductions were only 23% to 30% for PBZ-treated plants. This difference was due to reductions in dry mass caused by PBZ in nonstressed (0 mg·L⁻¹ salts) plants, as mass was generally similar for nontreated and PBZ-treated plants in the treatments receiving salts.

LEAF AREA AND LEAF EXPANSION. Overall, salinity reduced leaf area per plant, increased abscission, and increased the percentage of the canopy showing marginal and tip necrosis (Table 1). PBZ-treated plants in the 1000 and 2000 mg·L⁻¹ salt treatments had similar leaf area to nontreated counterparts, but a lower proportion of leaves showed marginal and tip necrosis and there was less defoliation. Furthermore, analyzing the response of PBZ-treated plants separately via regression showed that total leaf area did not decrease with salinity ($P = 0.3548$). Thus, PBZ treatment prevented a reduction in leaf area with salinity, yet leaf area was reduced nearly 2-fold in plants not sprayed with PBZ. Similar to the dry mass response, the lack of sensitivity of leaf area to salinity for PBZ-treated plants was largely caused by a reduction in leaf area for nonstressed plants.

Expansion rates of individual leaves were affected by PBZ and less uniformly by salinity, but results were variable. For simplicity, only the area per leaf after cessation of expansion is presented, which reasonably reflected leaf expansion rate. Area per leaf was unaffected by salinity on the first three of four dates, but reduced by PBZ application in most cases (Table 2). Salinity increased area per leaf by ≈ 10 cm² between the 0 and 2000 mg·L⁻¹ salts treatment on the fourth measurement date. In a related study with peach in 1994 (Abou El-Khashab, 1996), there were also occasions where leaf expansion rate and area per leaf were increased by salinity. Reasons for this response are unclear, but suggest that water deficit was not induced by salt treatment because leaf expansion is generally reduced by water deficit (Bradford and Hsiao, 1982). It is possible that ion accumulation in expanding leaves may have caused osmotic adjustment, thereby raising turgor, which could have led to enhanced expansion compared to nonstressed plants (Cosgrove, 1984).

GAS EXCHANGE AND RELATIVE WATER CONTENT. Salinity reduced A and g , but increased C_i (Table 3). Higher C_i with lower photosynthesis could indicate a nonstomatal inhibition of photosynthesis by salinity, although the relative effects of stomatal and nonstomatal factors cannot be separated using instantaneous measurements such as these (Farquhar and Sharkey, 1982). Both stomatal and nonstomatal factors were responsible for decreased photosynthesis in a related species *Prunus salicina* during salt stress (Ziska et al., 1991).

PBZ increased A in both treatments receiving salts, but this was accompanied by an increase in g for only the 1000 mg·L⁻¹ salt treatment (Table 3). Lower C_i for PBZ-treated plants in the 2000 mg·L⁻¹ salt treatment was accompanied by higher A for these plants, which could be due to lower mesophyll resistance to CO₂ fixation in plants treated with PBZ (Farquhar and Sharkey, 1982).

Gas exchange results were similar on the three other measurement dates, and

therefore have been omitted from Table 3. The lack of differences in dry mass for PBZ-treated and nontreated plants suggests that higher midday photosynthesis of recently expanded leaves did not translate into greater growth. In a related study (Abou El-Khashab, 1996), PBZ also increased photosynthesis of salt-treated 'Manzanillo' olive plants, but also failed to produce an increase in total dry mass. These observations suggest that respiration may also be increased by PBZ, or alternatively, the most recent fully expanded leaf is not representative of the gas exchange characteristics of the canopy as a whole.

Salinity did not affect leaf RWC, although PBZ application increased RWC in the 2000 mg·L⁻¹ salt treatment (Table 3). Lack of an effect of salinity on RWC suggests that stress resulted from specific ion effects, not from osmotic stress, as commonly acknowledged for tree fruits (Bernstein, 1965). The RWC data support the conclusion based on leaf expansion data that water deficit was not a factor in the salinity response of peach.

SODIUM AND CHLORIDE CONTENT. The Na⁺ and Cl⁻ contents in peach tissues were strongly affected by both salinity and PBZ (Table 4). As expected, salinity increased the Na⁺ and Cl⁻ content in leaves, roots, and stems. PBZ application consistently reduced the Na⁺ and Cl⁻ content when a significant effect occurred (Table 4). In leaves, the Na⁺ content was reduced by PBZ application over 6-fold, whereas the Cl⁻ content was reduced by only 24% to 38% in the treatments receiving salts. Thus, PBZ seems to be more effective at controlling Na⁺ than Cl⁻ accumulation. The results suggest that PBZ may be effective in reducing salt stress in peach by reducing Na⁺ and Cl⁻ uptake and subsequent accumulation in leaves.

The total Na⁺ content (mg/plant) of PBZ-treated plants receiving

Table 3. Net CO₂ assimilation (A), stomatal conductance (g), intercellular CO₂ (C_i) and relative water content (RWC) of 1-year-old 'Nemaguard' peach trees 2 months after salt and paclobutrazol (PBZ) treatments were applied.

Salt treatment (mg·L ⁻¹)	PBZ ^z	A (μmol·m ⁻² ·s ⁻¹)	g (mmol·m ⁻² ·s ⁻¹)	C_i (μL·L ⁻¹)	RWC (%)
0	–	10.4	297*	241	74.9
	+	11.4	469	249	78.2
1000	–	5.4* ^y	203*	258	72.8
	+	8.8	300	283	73.4
2000	–	4.3*	249	302*	69.7*
	+	8.2	199	267	76.8
Salt effect ^x		0.0001	0.0001	0.0016	0.1156

^zPBZ = paclobutrazol foliar spray at 200 mg·L⁻¹.

^yMeans for –PBZ treatments followed by an asterisk (*) are different from means for +PBZ treatments immediately below for a given variable.

^x $P > F$ value for the main effect of salt concentration for a given variable.

Table 4. Sodium and chloride contents (mg·g⁻¹ dry mass) of 1-year-old 'Nemaguard' peach 3 months after salt and paclobutrazol (PBZ) treatments were applied.

Salt treatment (mg·L ⁻¹)	PBZ ^z	Root		Stem		Leaf	
		Na	Cl	Na	Cl	Na	Cl
0	–	0.26 ^y	2.80	0.42	2.31*	0.14	2.97
	+	0.24	2.50	0.34	1.00	0.18	5.30
1000	–	0.98	4.80*	3.40	6.67*	2.53*	24.37*
	+	0.84	3.00	2.15	4.65	0.38	15.22
2000	–	1.01*	4.75*	3.92*	7.88*	3.63*	29.02
	+	0.73	3.51	2.08	5.00	0.56	25.72
Salt effect ^x		0.0001	0.0001	0.0001	0.0001	0.0003	0.0001

^zPBZ = paclobutrazol foliar spray at 200 mg·L⁻¹.

^yMeans for –PBZ treatments followed by an asterisk (*) are different from means for +PBZ treatments immediately below for a given variable.

^x $P > F$ value for the main effect of salt concentration for a given variable.

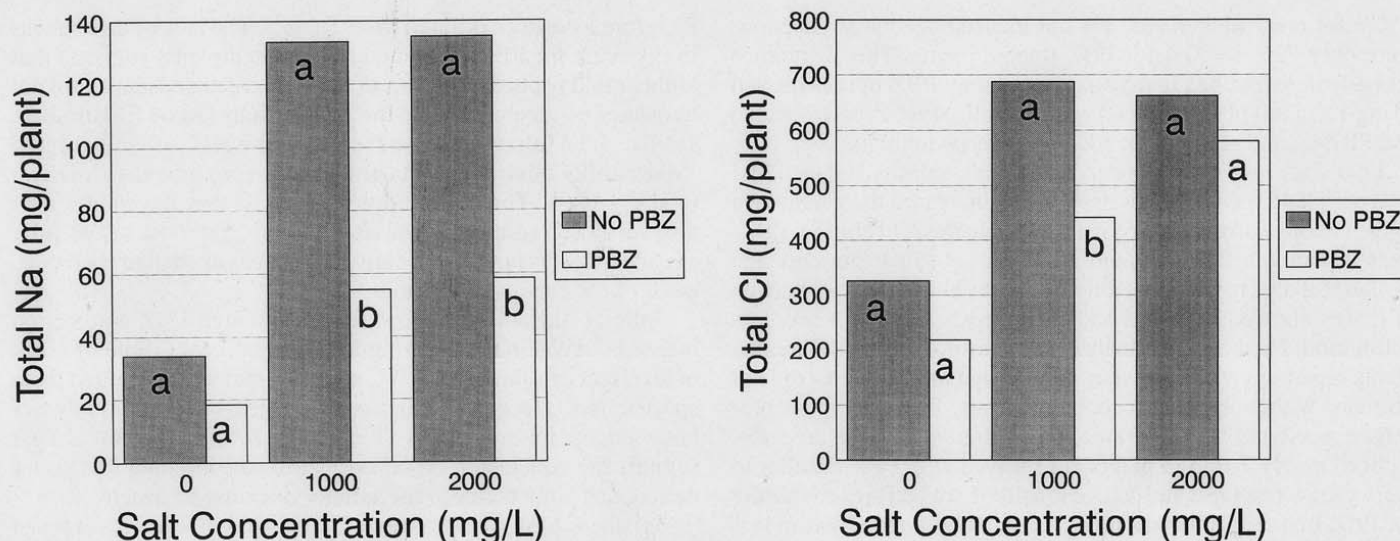


Fig. 1. Calculated total quantities of (a) Na^+ and (b) Cl^- in peach plants 3 months after salt and paclobutrazol (PBZ) treatments were applied. Bars with the same lower case letter within a salt concentration are not significantly different, t test, $P < 0.05$.

salts was less than half that of nontreated plants (Fig. 1a), further suggesting a role for PBZ in inhibition of Na^+ uptake. This was largely an effect of differing concentrations of Na^+ , because plant dry mass did not differ between PBZ-treated and nontreated plants receiving salts. Total Cl^- content of PBZ-treated plants was lower in the 1000 $\text{mg}\cdot\text{L}^{-1}$ salt treatment only (Fig. 1b), suggesting a similar, but less pronounced role for PBZ in inhibition of Cl^- uptake.

The interpretation of these data is confounded somewhat by the ability of PBZ to improve plant response to salt stress, but simultaneously reduce growth of plants by inhibiting GA biosynthesis. One interpretation might be that PBZ did not improve salt stress resistance, because dry mass was similar for all plants receiving salts. However, in a relative sense, it can be argued that salt resistance was improved by PBZ because in the highest salt treatment, PBZ-treated plants maintained 70.3% of the dry mass of controls, whereas nontreated plants maintained only 39.7%. Clearly, PBZ improved the quality of growth, as salt-stressed plants showed less foliar necrosis, milder symptom expression, and less defoliation when treated with PBZ. Studies with mature peach trees (Martin et al., 1987) show that fruit yield and quality can be improved by PBZ, further providing incentive for peach growers in saline areas to test this approach.

In terms of salt resistance mechanisms, the data favor Na^+ and Cl^- exclusion (avoidance) at the whole-plant level, particularly Na^+ . A related study (Abou El-Khashab et al., 1996) provides evidence for reductions in Na^+ and Cl^- uptake by PBZ application, as well as changes in ion partitioning among organs, which substantiate the present results. Munns (1993) argues that reducing accumulation of harmful ions in the leaves maintains greater leaf area and hence yield, and is the most viable means of improving growth on saline soils. PBZ may act in this way and provide a means of improving the quality of growth and perhaps yield of peach on saline soils.

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