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The Effect of Paclobutrazol on Growth and Response to Water Stress of Apple Seedlings

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Additional index words. leaf water potential, *Malus domestica*, plant growth regulator, polyethylene glycol, PP333, root respiration, stomatal resistance

Abstract. **The addition of (2RS, 3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-1,2,4-triazol-1-yl-) pentan-3-ol) (paclobutrazol, PP333) at 0.05 or 0.20 ppm to a nutrient solution in which 4-month-old apple (*Malus domestica*, Borkh.) seedlings were growing, reduced terminal growth and increased root to leaf ratio. Plants pretreated with 0.20 ppm PP333 did not show a reduction in transpiration due to subsequent applied water stress induced by polyethylene glycol (PEG), whereas untreated plants decreased their transpiration in response to PEG stress at −0.5 and −0.75 MPa. The PP333 pretreatment at 0.20 ppm improved water balance of the seedlings since they had a higher water potential than untreated seedlings at equal or higher transpiration rates. Leaf osmotic adjustment to lower water potentials was shown to be leaf age-dependent irrespective of PP333 pretreatment.**

Various plant growth regulators, most notably daminozide, influence vegetative growth in apple. Recently, a new growth regulator, PP333 from ICI Americas, Inc. (Goldsboro, NC 27530) has been reported to have a very strong, inhibitory effect on shoot growth in apple and some other fruit trees (14, 15, 20, 25). D. Atkinson (personal communication) found that very high rates of PP333 inhibited root growth, while moderate and low rates may have stimulated root growth. This differential effect of PP333 on growth leads to increased root to shoot ratios (14). Changes in the root to shoot ratio may affect the plant-water status and tolerance to drought (23). The present study was undertaken to obtain information on the effect of PP333 on growth and water-stress adaptability of apple seedlings.

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Materials and Methods

'Golden Delicious' apple seedlings were grown in the greenhouse in Jiffy Mix potting medium. When about 20 cm tall (4 months old), seedlings were transferred to 1-liter brown plastic bottles (2 plants/bottle) filled with a nutrient solution (7) which was continuously aerated. After one week, PP333 was added to the nutrient solution at 3 different rates: 0, 0.05, or 0.20 ppm with 12 seedlings in each treatment. Water loss from the bottles was replaced daily and nutrient solutions were changed weekly, with PP333 being added to maintain the above concentrations.

The experiment was conducted in a laboratory room with 14 hr of light at 250 μmol $s^{-1}m^{-2}$ photosynthetic photon flux density provided by fluorescent lamps. Temperature and humidity were not controlled. Variation in daily air temperature were 20.5° to 24.4°C maxima and 18.9° to 21.1° minima. Daily air humidity was 50–60% minima and 62–72% maxima.

Root-tip respiration was measured on a Gilson single-valve differential respirometer 2 weeks after PP333 pretreatments were initiated. Actively growing root tips, 1-cm-long, were detached and samples weighing 0.200 ± 0.002 g were placed in the outer well of a 15-ml reaction vessel with 3 ml of nutrient solution (pH 4.7) containing 0, 0.05, or 0.20 ppm PP333. The inner well of the reaction vessel contained 0.2 ml 10% KOH and a 2-cm piece of corrugated filter paper. Root respiration was measured

hourly for 3 hr at 25°C. Eight root samples (replications) were taken from individual seedlings from each PP333 pretreatment.

PP333 pretreatments were discontinued after 4 weeks and half of the plants in each pretreatment (6 seedlings) then were exposed to water stress and half were left unstressed. Seedlings were water-stressed by lowering water potential of the nutrient solution with PEG (MW 3200–3700) (7). Nutrient solution water potentials gradually were lowered stepwise every 3 days to −0.1 MPa, −0.25 MPa, −0.5 MPa, and finally to −0.75 MPa. Water potential of the control nutrient solution remained at −0.03 MPa. Daily water consumption (transpiration) was measured gravimetrically as described previously (18) and expressed on a leaf area basis. In all treatments, leaves present on the seedlings 6 and 12 days after PEG treatments commenced were marked and their total area measured 13 days after PEG treatment was initiated with a LI-COR Model LI-3000 leaf area meter.

At the PEG-induced water stress of −0.75 MPa, stomatal resistance (r_s) and leaf water potential components were measured on mature and young leaves with a LI-COR Diffusive Resistance Meter Model LI-60 and pressure bomb, respectively. Seedlings preconditioned with 0.20 ppm PP333 produced new leaves which were too small for stomatal resistance and water potential measurements. Young leaves for r_s and water potential (ψ_w) measurements were selected between the 8th and 10th fully expanded leaf basipetally. A pressure chamber technique was used to measure leaf water potential components (4, 16). Leaves were enclosed in plastic bags before detachment to prevent rapid water loss (22). The pressure-volume curves for each leaf were based on 8 points. Extrapolation of the linear portion of those curves to the ordinate gave an estimation of osmotic potential (ψ_s) at the initial ψ_w. Turgor potential (ψ_p) was calculated as the difference between the ψ_w and ψ_s. Three young and mature leaves from 3 different plants were used in each treatment, except young leaves from the 0.20 ppm PP333. One of 2 plants growing in each bottle was selected for water potential measurements.

Increases in the length of the terminal shoot after the 4-week PP333 treatment period and after 13 days of water stress were measured separately. Seedlings were harvested 13 days after water stress was initiated. Leaves, stems, and roots were separated and oven-dried at 80°C for 48 hr to determine dry weight.

Terminal growth and root respiration data collected during PP333 pretreatment period were elaborated statistically using regression analysis. Data collected during water-stress period and at the end of the experiment were analyzed as 2-factor, split-plot experiment.

Results and Discussion

The mean increase in terminal shoot length per plant during the first 4 weeks of PP333 treatment was 31.7, 14.5, and 4.0 cm for seedlings treated with 0, 0.05, or 0.20 ppm PP333, respectively. Despite the fact that PP333 was withdrawn from the nutrient solution during the subsequent 13-day water-stress period, the retardation of terminal growth on seedlings previously treated with PP333 still was pronounced (Table 1).

At the conclusion of the experiment and independent of PEG treatment, total leaf area, dry weight of leaves + stems, and leaves showed a decreasing trend with increasing rate of PP333 (Table 1). New leaves produced on plants at 0.20 ppm PP333 were very small. Regardless of PEG treatments, plants preconditioned with 0.20 ppm PP333 had the highest root to leaf ratio at the end of the experiment, a result of decreased leaf dry weight and increased root dry weight in PP333-treated seedlings (Table 1). This effect of PP333 at 0.20 ppm on root dry weight was not, however, significant statistically. Seedlings in all treatments produced new, white roots. Roots of plants pretreated with PP333 (especially the highest rate) were much thicker than in the control treatment. However, the length of individual white roots from PP333-treated seedlings did not appear to differ from control seedlings at the conclusion of the experiment. The effects of PP333 on apple terminal growth, dry matter partitioning among different tissues, and root morphology are in agreement with those reported by Atkinson (1).

Table 1. Effect of gradually increasing, PEG-induced water stress from −0.1 to −0.75 Pa and PP333 pretreatments on the increase in terminal shoot length, total leaf area, and tissue dry weight in apple seedlings.[z]

Treatment	PP333 0 ppm	PP333 0.05 ppm	PP333 0.20 ppm	Mean	Significance Linear	Significance Quadratic
Increase in terminal shoot length (cm/2 seedlings—13 days)						
Unstressed	64.0	42.2	2.8			
Stressed	59.7	42.7	2.5	NS		
Mean	61.8	42.4	2.7		**	NS
Leaf area (cm^2/2 seedlings)						
Unstressed	3556	2641	1628	2608		
Stressed	2720	2453	1585	2253 *		
Mean	3138	2547	1606		**	NS
Top = leaves + stems (g/2 seedlings)						
Unstressed	25.1	20.0	15.4			
Stressed	22.2	20.5	15.0	NS		
Mean	23.6	20.2	15.2		**	NS
Leaves (g/2 seedlings)						
Unstressed	16.4	14.0	11.2			
Stressed	14.6	14.4	11.4	NS		
Mean	15.5	14.2	11.3		**	NS
Roots (g/2 seedlings)						
Unstressed	6.1	6.4	7.1	6.5		
Stressed	8.3	9.8	11.8	9.9 **		
Root–leaf dry wt ratio						
Unstressed	0.37	0.46	0.63	0.49		
Stressed	0.63	0.67	1.04	0.78 *		
Mean	0.50	0.57	0.83		**	NS

[z]Stress × PP333 interaction was not significant for any variable. Mean separation according to F test for stress effect and regression analysis for PP333 effect.

NS, *, **Nonsignificant (NS) or significant at 5% (*) or 1% (**) levels.

Increasing the concentration of PP333 had a negative effect on root respiration rate 2 weeks after initiation of PP333 pretreatments (Table 2). This indicated reduced physiological activity of the roots which was reported to reduce plant water uptake (6, 10). It is doubtful that reduced root respiration was caused by a shortage of substrate since Atkinson (personal communication) observed starch accumulation in apple roots treated with PP333.

Plants stressed at −0.10 MPa consumed significantly more water than unstressed seedlings regardless of PP333 pretreatment (Table 3). This supports previous observations that mild water stress can increase apple seedling water consumption (18). A PEG-induced stress of −0.25 MPa did not affect plant water consumption (Table 3). Untreated seedlings or those pretreated with 0.05 ppm PP333 consumed significantly less water when

Table 2. Effect of PP333 level on apple root-tip respiration.

PP333 (ppm)	Respiration (μl O_2/g fresh wt · hr^{-1}) Incubation in nutrient solution (hr) 1	2	3
0	396.8	372.5	345.2
0.05	346.9	343.6	317.6
0.20	326.5	310.9	297.6
Significance			
Linear	**	**	*
Quadratic	NS	NS	NS

NS, *, **Nonsignificant (NS) or significant at 5% (*) or 1% (**) levels.

stressed at −0.50 or −0.75 MPa compared to unstressed seedlings, while plants pretreated with 0.20 ppm PP333 showed no difference in water consumption due to stress (Table 3). Thus, in terms of water consumption, seedlings preconditioned with 0.20 ppm PP333 had a greater adaptability to water-stress conditions than those pretreated with none or 0.05 ppm PP333 (7).

Stomata of mature leaves did not respond to the applied water stress (data not shown), regardless of PP333 pretreatment. The r_s of young leaves increased in response to −0.75 MPa PEG-induced stress as compared to unstressed seedlings when pretreated with none or 0.05 ppm PP333 (Table 4). The r_s of young leaves from seedlings preconditioned with 0.20 ppm PP333 was not measured due to the small size of the young leaves on these plants. It is assumed that reduced water consumption in stressed plants (Table 3) was caused by reduced transpiration of young leaves. Since seedlings pretreated with 0.20 ppm PP333 had a limited area of young leaves, water consumption for these plants was not affected by stress (Table 3).

Table 3. Daily water consumption of apple seedlings as affected by various levels of PEG-induced water stress and PP333 pretreatments.

Treatment	Daily water consumption (ml H_2O/dm^2 leaf area · day) PP333 level 0 ppm	0.05 ppm	0.20 ppm	Mean
Unstressed	7.1	7.6	6.8	7.2
Stressed (PEG at −0.1 MPa)	8.5	7.8	8.0	8.1
Unstressed	7.8	7.9	6.5	
Stressed (PEG at −0.25 MPa)	7.6	7.3	7.6	
Unstressed	8.4	8.4	8.1	
Stressed (PEG at −0.50 MPa)	6.4	7.1	8.0	
Unstressed	7.8	7.5	7.4	
Stressed (PEG at −0.75 MPa)	5.0	5.5	7.1	

ANOVA Table

Source of variation	df	Sum of squares −0.1 MPa	−0.25 MPa	−0.50 MPa	−0.75 MPa
PP333	2	0.554 NS	1.421 NS	1.213 NS	2.468 NS
Error	4	2.879	1.249	4.953	3.476
Stress	1	3.645**	1.722 NS	5.120**	13.005**
Stress × PP333	2	1.343 NS	2.341 NS	3.293**	4.563*
Error	6	1.647	2.097	1.637	2.777

NS,*,**Nonsignificant (NS) or significant at 5% (*) or 1% (**) levels.

Table 4. Stomatal resistance of young apple leaves as affected by a PEG-induced water stress of −0.75 MPa and PP333.[z]

Treatment	Stomatal resistance (sec/cm) PP333 0 ppm	0.05 ppm	Mean	Significance
Unstressed	1.4	1.6	1.5	
Stressed	6.1	4.5	5.3**	
Mean	3.7	3.0		*

[z]Stress × PP333 interaction was not significant. Mean separation, according to F-test.
*,**Significant at 5% (*) or 1% (**) levels.

PEG-induced water stress of −0.75 MPa decreased ψ_w in young and mature leaves irrespective of PP333 pretreatment (Tables 5 and 6). Mature leaves of stressed plants had reduced osmotic potential ψ_s compared to unstressed plants; however, there were no differences in ψ_p (Table 5). In contrast, the ψ_s of young leaves did not change with water stress and consequently ψ_p decreased significantly (Table 6). Thus, stomata of mature leaves from stressed plants remained open as a result of an osmotic adjustment to lower ψ_w that enabled turgor maintenance (5, 11, 12). Independent of PEG treatment, PP333 levels did not influence ψ_w in young leaves and ψ_s and ψ_p in young and mature leaves (Tables 5 and 6). These results agree with those published by Wample and Culver (24) for PP333-treated sunflower; however, in contrast to their study we found that the ψ_w of mature leaves increased in response to the highest rate of PP333 (Table 5).

Leaf expansion was diminished significantly by water stress (Table 1). This was assumed to be due to a loss in turgidity of young leaves, which reduced cell expansion (8, 9). The effect of water stress on leaf area in plants pretreated with 0.20 ppm PP333 was rather negligible, due to less total leaf area.

Water stress did not affect significantly the amount of terminal growth or dry weight of tops and leaves (Table 1). However,

Table 5. Effect of a −0.75 MPa PEG-induced water stress and PP333 pretreatments on water potential components in mature apple leaves.[z]

Treatments	PP333 0 ppm	0.05 ppm	0.20 ppm	Mean	Significance Linear	Quadratic
		Water potential (MPa)				
Unstressed	−0.77	−0.73	−0.59	−0.70		
Stressed	−1.21	−1.28	−1.05	−1.18**		
Mean	−0.99	−1.01	−0.82		**	NS
		Osmotic potential (MPa)				
Unstressed	−1.74	−1.81	−1.84	−1.80		
Stressed	−2.16	−2.20	−2.17	−2.18**		
		Turgor potential (MPa)				
Unstressed	0.97	1.08	1.25			
Stressed	0.95	0.92	1.12	NS		

[z]Stress × PP333 interaction was not significant for any of the variables. Mean separation according to F-test for stress effect and regression analysis for PP333 effect.
NS,**Nonsignificant (NS) or significant at 1% (**) level.

Table 6. Effect of a −0.75 MPa PEG-induced water stress and PP333 on water-potential components in young apple leaves.[z]

Treatment	PP333 0 ppm	PP333 0.05 ppm	Mean
	Water potential (MPa)		
Unstressed	−0.78	−0.68	−0.73
Stressed	−1.22	−1.17	−1.20**
	Osmotic potential (MPa)		
Unstressed	−1.77	−1.81	
Stressed	−1.81	−1.80	NS
	Turgor potential (MPa)		
Unstressed	0.99	1.13	1.06
Stressed	0.59	0.63	0.61**

[z]Stress × PP333 interaction was not significant for any of the variables. Mean separation according to F-test.
[NS,**]Nonsignificant (NS) or significant at 1% (**) level.

there was a tendency for water stress to inhibit the amount of terminal shoot growth and dry weight of aerial parts of seedlings not treated with PP333 (Table 1). Since the duration of water stress that affected plant water consumption lasted only for 6 days (i.e., PEG stress at −0.50 and 0.75 MPa), it is possible that insufficient time occurred to induce statistically significant changes in growth and dry-matter accumulation. However, water stress increased dry weight of roots and root to leaf dry-weight ratios, a response similar to that induced by the 0.20 ppm PP333 pretreatment (Table 1). Similar responses to water stress were reported for some field crops (13, 17) and are regarded as an adaptive mechanism to water stress (21, 23). However, such interpretation can be criticized in the view of recent review by Taylor (19) and the fact that dry weight of a root system does not always correlate with surface area (2). Nevertheless, seedlings preconditioned with 0.20 ppm PP333 showed improved water balance as they had a higher water potential than seedlings pretreated with none or 0.05 ppm PP333 (Table 5), at equal or higher transpiration rates (Table 3). It is possible that this effect was caused by increased root to leaf ratio and/or decreased root resistance for water flow in plants pretreated with 0.20 ppm PP333.

The present study shows that apple seedlings can adapt to water stress by osmotic adjustment and possibly through increased root dry weight and increased root to leaf ratio. Leaf osmotic adjustment to lower water potentials was found to be a leaf-age-dependent phenomenon. Mature leaves are able to adjust osmotically to decreased water potentials, whereas young, fully developed leaves do not appear to respond in this manner. Thus, PP333 applications at the rates that inhibit the expansion of new foliage and increase root to leaf ratio may make apple seedlings more adaptive to water stress. T.E.O. Asamoah and D. Atkinson (unpublished manuscript) have found soil-potted cherry rootstocks to be more adaptive to drought when treated with PP333 as a soil drench. PP333 reduced transpiration of cherry plants and increased r_s in their study. The effect on transpiration was not noted in our experiment, possibly due to PP333 withdrawal from the nutrient solution before the transpiration (water consumption) measurements were initiated. Wample and Culver (24) found no significant effect of PP333 on r_s in sunflower although the highest rate tended to increase r_s.

Severe inhibition of development of new foliage due to PP333 may adversely affect productivity and fruit size under field conditions (3). Studies on mature plants are needed to establish whether PP333 application may combine a dwarfing effect with enhanced productivity and increased adaptation to water stress.

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Breeding for Resistance to *Aphanomyces euteiches* Root Rot and *Rhizoctonia solani* Stem Rot in Peas

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Abstract. **A modified Environmental Shift Technique based on use of a disease index (scoring) gave consistent separation between susceptible and moderately resistant pea (*Pisum sativum* L.) genotypes to *Aphanomyces euteiches* Drech. root rot in 3 tests. A moderately high association ($r = -0.63$ to -0.83) between disease index and percentage of plant survival was found in segregating populations. Minnesota 108, moderately resistant to *A. euteiches*, produced adventitious roots readily at an early stage. Root rot resistance and number of adventitious roots were inherited independently. Broad sense heritability (BSH) ranging between 0.45 and 0.57 for resistance to *A. euteiches* root rot, and between 0.39 and 0.44 for resistance to *Rhizoctonia solani* Kuehn stem rot, varied by parental combination, experiment, and method of estimation. However, heritability based on gain by selection in the F_3 ranged from 0.28 to 0.46 and from 0.21 to 0.44 for resistance to *A. euteiches* and *R. solani*, respectively. Frequency distribution of resistant and susceptible plants suggested quantitative inheritance of resistance to both diseases. Recurrent selection, in which each cycle includes one intermating, selfing, and testing generation, is suggested to improve and transfer resistance.**

Root rot caused by *Aphanomyces euteiches* was reported to cause serious damage in green peas as early as 1925 (4, 10). Large-scale pea screening programs have been conducted during the last 30 years. Only a few PI lines and selections from these lines were found to have resistance and all were described as tall plant types having pigmented flowers and seeds (12, 15, 18). Several improved methods of screening for resistance to this disease were developed (7, 13, 16, 18), and 2 moderately resistant breeding lines—Minnesota 108 and Minnesota 494-A11—were released recently (2, 12). One of these, Minnesota 108, has short internodes, short overall stature, and white flower color (2, 18), making it closer to commercial type than Minnesota 494-A11. Inheritance of the "tolerance" to *A. euteiches* found in PI 175227 has been found to be linked genetically with 3 "wild type" genes (tall plants, colored flowers, and colored seed) (15). However, inheritance of the Minnesota source of resistance has not been investigated.

Stem rot caused by *Rhizoctonia solani* AG4, has been investigated recently and a few pea genotypes with moderate resistance were found (19). Factors affecting the expression of resistance to this disease were investigated also (21). However, inheritance of resistance to this disease is not known.

Although progress was reported on finding resistance to the above diseases, difficulties persist in breeding commercial pea cultivars with an acceptable level of resistance. This may be due to the lack of knowledge of the strategy of transferring resistance, because: 1) little is known about the mode of resistance and its inheritance; and 2) resistance may be closely associated via linkage or pleiotropy with undesirable horticultural traits.

The Environmental Shift Technique (EST), which relies on the use of 2 consecutive environments (i.e., a first-phase or incubation environment followed by a 2nd phase or recovery environment) and which is used in screening for resistance to *A. euteiches*, has given consistent separation between resistant and susceptible plants (2, 18). However, because the EST requires individually potted plants incubated in plastic bags, its utilization is laborious and limited to small populations. Modification of this technique to permit screening of larger segregating populations was considered essential for our breeding program.

During screening for resistance to *A. euteiches* (18), we noted that Minnesota 108 produced more adventitious roots at an early growth stage than did other pea genotypes. The relationship between adventitious root formation and root rot resistance has not been studied in peas. However, adventitious root formation in pea cuttings has been found to be influenced highly by environment, e.g., nutrients and light (3, 5). Ability of the host to regenerate new roots was suggested as one of the components responsible for *A. euteiches* root rot resistance in peas (18).

Inheritance of resistance to some of the major soil-borne pathogens has not been investigated extensively in peas although much work has been done on other crops. Monogenic resistance to *Fusarium oxysporum* f. sp. *pisi* was reported in garden peas as early as 1929 (8) and 1949 (23). A quantitiative inheritance pattern for reaction to *Fusarium solani* f. sp. *phaseoli* was found in beans (1), the pattern being influenced by testing procedure,

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