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Pepper Seedling Growth Response to Drought Stress and Exogenous Abscisic Acid

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Abstract. **ABA and drought stress were evaluated on growth morphology and dry weight of pepper *(Capsicum annuum* L.) seedlings subjected to continuous watering (CV) or alternate watering (AW) subflotation irrigation. When ABA (10^{-4} M) was sprayed on to leaves 28, 32, or 37 days after seeding (DAS), leaf growth was limited relative to the controls. Root dry weight, basal root count, and diameter decreased in AW compared with CW-treated seedlings. ABA did not influence root growth of the transplants or subsequent total fruit yield. When ABA was applied to leaves at 20,23, or 29 DAS, there was a transient inhibition of leaf weight increase, but root growth was unaffected. Exogenous ABA may have a practical application as a substitute for drought stress to control transplant growth in the nursery. Chemical name used: abscisic acid (ABA).**

The use ‘of containerized transplants in pepper is important to improve plant growth and productivity (Leskovar et al., 1990). A subflotation recirculating system has recently been developed for growing transplants (Beirenger and Bostdorff, 1989). Frequent irrigations promote root growth that eventually might exteed the volume of the bottom of the cell. This response requires either mechanical or heated-air root pruning, thus disrupting the root-tip zone which is critical for axial root growth (Pilet and Saugy, 1987).

ABA, synthesized in the root cap (Rivier et al., 1977), is generally involved in plant regulatory processes (Addicott, 1983), particularly in drought-stressed plants (Davis et al., 1981; Watts et al., 1981). The influence of drought stress on root and shoot growth was suggested to be mediated through endogenous changes of ABA concentration acting as a signal for control of growth processes (Davis et al., 1986). ABA synthesis induced by water stress has been correlated with a reduction of shoot : root ratio either by shoot growth reduction (Creelman et al., 1990) or by a -larger root growth relative to shoot growth (Karmoker and Van Steveninck, 1979). In vegetables, ABA effects on transplant growth reduction for plant acclimation was studied in eggplant (Latimer and Mitchell, 1988) and on leaf resistance and leaf water potential changes in pepper seedlings (Berkowitz and Rabin, 1988).

Our study was conducted to determine the effects of exogenous ABA on pepper seed germination and seedling growth, and investigate how ABA and drought stress alter pepper seedling root and shoot dry-matter partitioning.

Materials and Methods

Germination and seedling experiments. Preliminary experiments were conducted to determine the inhibitory effects of a range of exogenous ABA concentrations on ‘Jupiter’ bell pepper seed germination and seedling growth. One of two procedures were followed. First, seeds were placed on Whatman no. 1 (top) and no. 3 filter papers in 9-cm petri dishes and germinated in an incubator in the dark at 25 ± 1C. ABA(+ / – cis, trans) (Sigma Chemical Co., St. Louis) concentrations of 10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, 10^{-7}, or 10^{-8} M were prepared and 5 ml of solution was added to the filter paper initially, followed by daily additions of 1 ml ABA solutions. Second, a rolled-towel germination test was performed similar to that described by the Association of Official Seed Analysts (AOSA) (1983). Three nontoxic germination papers (Anchor Paper Co., St. Paul, Minn.) were soaked for 30 min in the above described ABA solutions. Fifty seeds were divided between two rows and the paper towels were rolled, placed in plastic containers (21.5 × 32.5 × 5.5 cm), and incubated for 7 days in a dark germinator at 25 ± lC. Seedlings were classified into normal (with complete morphological parts); abnormal (with broken cotyledons, less than one cotyledon, missing primary root, poorly developed, or absence of hypocotyl); and dead.

To test effects of ABA on seedling growth, seeds were sown on 10 Nov. on a commercial mix (Terra-Lite Metro Mix 200; W.R. Grace & Co., Cambridge, Mass.) and covered with 1.25 ml of vermiculite in Speedling polystyrene trays with 200 inverted pyramid cells 2.5 × 7.2 cm (side length x depth; 18 cm^3). Trays were transferred to germination chambers at 25C and 98% RH for 4 days and then to a glasshouse held at 10C minimum and 29C maximum. Each cell was thinned to one seedling 17 DAS. Irrigation was applied three times/week with a soluble fertilizer (20N–10P–20K) at 50 mg of N/liter. This original concentration was doubled 30 DAS. ABA at 10^{-3}, 10^{-4}, 10^{-5}, 10^{-6}, 10^{-7}, or 10^{-8} M plus 0.l% (v/v) Tween 20 was sprayed 33 and 37 DAS on the upper leaves until runoff. Since the upper soil-mix surface was unprotected, ABA solution was carefully sprayed to minimize drifting. At 60 DAS, two plants per replication were removed from the trays with forceps and shoots were cut off at the soil surface. Stem diameter was measured with a digital caliper below the cotyledonary node. Stem length was measured from the shoot apex down to the cut end, and leaf area was measured with a LI-COR (Model LI-31OO; LI-COR, Lincoln, Neb.) leaf area meter. Roots were washed, blotted, and root fresh weight was determined. Plant material was oven-dried at 65C for 3 days, and dry weights of leaves, stems, and roots were recorded.

In each experiment a randomized complete-block design (RCBD) was used and each ABA concentration was replicated

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Abbreviations: AW, alternate watering; CW, continuous watering; DAS, days after seeding, MDG, mean days of germination; NAR, net assimilation rate; RCBD, randomized complete-block design; RGR, relative growth rate.

four times. Fifty seeds were used in each replication. Germination was counted daily and total and mean days to germination calculated. Percentage of germination, normal, abnormal, and dead seedlings were transformed to square root arcsin before performing an analysis of variance (ANOVA). Root length of the primary root from 10 normal seedlings was measured and seedling vigor estimated by the mean dry weight of normal seedlings (AOSA, 1983). The main effect of ABA concentration was partitioned into linear, quadratic, or cubic orthogonal contrasts.

Growth chamber experiment. This study was conducted to evaluate if exogenous 10^{-4} M ABA could mimic the effects of mild drought stress on root and shoot growth of pepper transplants. Speedling trays with cells of 2.5 × 7.2 cm (each side length × depth; 18 cm^3) were cut into mini-trays of 40 cells each and filled with 180 g Terra-Lite Metro Mix 200 with a water-holding capacity 4.8 times greater than its own weight. Before germination, seeds were disinfected by soaking them in 1% NaOCl for 10 rein, rinsed with distilled water for 10 rein, than sown in each cell and covered with 1.25 ml of vermiculite. To promote uniform and fast germination, trays were irrigated with distilled water to 50% of water-holding capacity of the mix and placed in a germination chamber in darkness at 25C, 98% RH for 4 days. Trays were then placed in a four-section plastic container so that independent bottom watering and drainage systerns could be used. The plastic containers (each considered a replication) were transferred to a 1.7-m^3 growth chamber (CONVIRON CMP 3023; Conviron Products Co., Whinnipeg, Man., Canada) maintained at 60% RH and day/night temperature of 27/20C. Photoperiod was 14 h with a combination of cool-white fluorescent and incandescent lamps (Sylvania F72217/CW/VHO 160 W/Sylvania 52 W, 4:1 input wattage ratio). The initial photosynthetic flux (LI-COR LI-185 A) measured in 12 locations at 30 cm from the growth chamber floor averaged 326 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Seedlings were watered daily with distilled water to 50% water-holding capacity at 1400 HR until 22 DAS by means of a subflotation irrigation system. Plants were thinned to one seedling per cell 13 DAS. Fertilization (20N-10P–20K) was initiated 10 DAS at 50 mg of N/liter, and at 30 DAS, the concentration was doubled. The solution pH was adjusted to 6.2 with 0.1 M NaOH. At 23 DAS, plants in each block were randomly divided in four groups (experimental plots): two received CW and two received AW, In the AW-treated seedlings, water was withheld until plants had symptoms of drought stress (passive leaf flagging), which occurred below ≈ 20% of water-holding capacity, and then seedlings were rewatered (24, 26, 28, 30, 32, 34, 37, 39,43,45, and 48 DAS). Based on the results of the preliminary experiments, a 10’4 M ABA solution plus 0.1% (v/v) Tween 20 as a surfactant was prepared. At 28, 32, and 37 DAS, one each of the two groups of CW- and AW-treated plants were sprayed with the ABA solution on the upper leaf surfaces until runoff. Other experimental plots were sprayed with water plus Tween 20.

Stem diameter, stem length, leaf area, and dry weights of leaves, stems, and roots were determined on two plants per replication as previously described and measured at 22, 26, 30, 35, 41, and 48 DAS. Shoot : root ratio, relative growth rate, and net assimilation rate were calculated from the original data set (Hunt, 1982). At 48 DAS, basal and lateral roots were counted. Root diameter of basal roots (originated from the hypocotyl), first-order basal roots (originated from basals), lateral roots, and first-order laterals (originated from laterals) were measured with a DRC stereomicroscope (Zeiss, Oberkochen, Germany).

The remaining seedlings were set in a field located in Naples, Fla. (sandy, siliceous, hyperthermic, Alfic Arenic) on 29 Dec. 1988. Raised beds, 0.15 m in height, were spaced 1.8 m apart with each bed 0.8 m wide. Plants on single rows were spaced 0.3 m within the bed, and each plot consisted of 20 plants. Fertilizer [36N–202P–72K (kg-ha-l)] was broadcast and incorporated in the center of the bed. Topdress fertilizer [235N-432K ($kg \cdot ha^{-1}$)] was applied in two bands in shallow grooves on the bed surface 20 cm to each side of the bed center. Beds were fumigated with 67 methyl bromide : 33 chloropicrin at 192 $kg \cdot ha^{-1}$ and covered with black polyethylene mulch. The water table was maintained at a depth of 30 cm with subseepage irrigation. Subseepage irrigation ditches were located between every six beds. Standard pesticides and cultural practices were used (Hochmuth, 1988). Fruits were harvested from 18 plants per replication on 22 Mar. and 11 and 25 Apr. 1989, counted, and graded by size into fancy (7.5 cm minimum diameter) and U.S. No. 1 (6.25 cm).

A RCBD with treatments replicated four times was used at each harvest time. Main effects were partitioned into orthogonal contrasts. Since variance heterogeneity was measured for leaf and root dry weight over time, data were subjected to a log(x + 1) transformation for ANOVA. Transformed means were separated by LSD ($P = 0.05$).

Greenhouse exqeriment. To evaluate the growth inhibitor effects of 10^{-4} M ABA applied on the leaves or rooting media, seedlings were grown in mini-trays (40 cells) with the subflotation irrigation system in a greenhouse using the same initial procedures as in the growth chamber experiment. At 20 DAS, treatments were randomly assigned to the four mini-trays in each block. Treatments were a) control, b) drought stress, c) ABA-leaf, and d) ABA-root. In the control plants, the growing medium was maintained between 50% and 25% of water-holding capacity. Drought-stress plants were not irrigated until 85% of the available water had been removed from the medium. ABA-leaf consisted of 10-^{4} M ABA foliar spray application, and ABA-root consisted of ABA application to the roots by subirrigation. ABA was applied at 20, 23, and 29 DAS. At these times, 0.l% (v/v) Tween 20 and water was applied in the other experimental plots. Plant samples (two per each of four replications) were taken at 23, 29, 35, 41, 47, and 53 DAS. Growth measurements and data analysis were done as

Results and Discussion

ABA delayed germination and seedling development, and the number of abnormal seedlings increased linearly with increasing ABA concentrations (Table 1). The mean days of germination (MDG) had a quadratic increase that was attributed to 10^{-5} and 10^{-4} **M** ABA. ABA at 10^{-3} M totally suppressed germination (data not presented). The inhibitory effect on root elongation was most evident at 10^{-4} M ABA. ABA applied to leaf surfaces 33 and 37 DAS reduced root fresh and dry weights and increased stem weight and shoot : root ratio as compared with the control (Table 2). Stem diameter and leaf area were not affected by ABA application. Stem length reached a maximum at 10^{-6} M ABA. In the greenhouse experiment, seedlings were grown from mid-November to mid-January. Although the greenhouse was maintained between 10 and 29C, the average temperature was probably lower than the optimal (21 to 24C) for seedling growth. Based on these germination and emergence experiments, 10^{-4}

Table 1. Effects of ABA on germination and seedling growth of pepper. Germination test was performed in petri dishes at 25C in darkness. Data on seedlings were based in a rolled-towel test after 7 days at 25C in a dark incubator.

ABA concn (M)	Germination (%)	MDG[z] (days)	Seedlings Normal (%)	Abnormal (%)	Dead (%)	Dry wt (mg)	Root length (mm)
Control	97	4.4	76	16	7	3.4	47
10^{-8}	94	4.3	64	27	10	3.5	46
10^{-7}	96	4.4	63	22	15	3.2	47
10^{-6}	93	4.5	54	32	14	3.2	38
10^{-5}	89	5.1	58	28	14	3.4	33
10^{-4}	26	5.9	27	52	20	3.2	22
Orthogonal contrasts							
Control vs. others	**	**	**	**	*	NS	**
ABA	Q**	Q**	L*	L*	NS	NS	O**

[z]MDG = Mean days of germination.
[NS],*,**Nonsignificant or significant F test at $P = 0.05$ or 0.01, respectively. ABA concentration effect was linear (L) or quadratic (Q).

Table 2. Shoot and root characteristics of pepper seedlings as affected by ABA. Seedlings were grown in polystyrene trays in a greenhouse at 10/29C minimum/maximum. Measurements were done 60 DAS. ABA was applied on the upper leaf surface at 33 and 37 DAS.

ABA concn (M)	Root fresh wt (mg)	Dry wt Leaf (mg)	Stem (mg)	Root (mg)	Shoot : root ratio	Stem length (cm)
Control	147	58	17	10	8.4	5.9
10^{-8}	146	58	19	10	8.5	6.1
10^{-7}	157	61	20	10	8.8	6.0
10^{-6}	139	59	21	9	9.5	6.3
10^{-5}	148	59	21	9	9.1	5.9
10^{-4}	132	60	20	9	10.1	5.5
10^{-3}	101	54	17	7	11.1	5.8
Orthogonal contrasts						
Control vs. others	**	NS	*	**	**	NS
ABA	NS	NS	NS	NS	NS	Q*

NS,*, **Nonsignificant or significant F test at $P = 0.05$ or 0.01, respectively. ABA concentration effect was quadratic (Q).

M ABA was selected as the critical concentration to limit growth without visible phytotoxic effects when applied to pepper seedlings in early development.

In other research, germination of tomato *(Lycopersicon esculentum* Mill.) seeds was inhibited at ABA concentrations between 1.5×10^{-4} and 5×10^{-4} M (Liptay and Schopfer, 1983). ABA at 10^{-4} M caused an osmotic stress, lowering the ability of rape *(Brassica napus* L.) embryos to absorb water, and at 10^{-3} M ABA completely inhibited germination and seedling growth (Schopfer and Plachy, 1984). Maize *(Zea mays* L.) seedlings' root elongation was limited at 10^{-4} M ABA and was completely suppressed at 10^{-3} M ABA (Wightman et al., 1980).

In the growth chamber experiment, seedlings grown under CW had significantly more root growth and a lower shoot : root ratio than those grown with AW (Table 3). However, both leaf and root weights had a treatment × time of application interaction. The effect of ABA applied at 28 DAS on leaf dry weight became apparent in samples collected 2 days later (Fig. 1A). During this period, net assimilation rate (NAR) was 0.90 and 1.58 $g \cdot m^{-2} \cdot day^{-1}$ for CW + ABA- and AW + ABA-treated plants and 4.16 and 5.41 $g \cdot m^{-2} \cdot day^{-1}$ for CW- and AW-treated plants without ABA. As NAR is considered a physiological index (Evans, 1972), ABA seemed to reduce the photosynthetic capacity of the seedlings. ABA increases stomatal closing

Table 3. Shoot and root characteristics of pepper seedlings as affected by watering and ABA treatments (growth chamber experiment).

Source of variation	Stem diam (mm)	Leaf area (cm²)	Dry wt Leaf (mg)	Stem (mg)	Root (mg)	Shoot : root ratio
Treatment (Trt)						
CW − ABA	1.8	16.5	56	27	24	3.8
CW + ABA	1.8	15.4	49	26	23	3.6
AW − ABA	1.7	16.1	50	24	19	4.1
AW + ABA	1.8	16.9	50	28	21	4.0
Orthogonal contrasts						
CW vs. AW	NS	NS	NS	NS	**	*
−ABA vs. +ABA	NS	NS	*	NS	NS	NS
Time						
22	1.3	8.9	33	6	8	4.9
26	1.5	11.5	43	11	12	4.7
30	1.7	17.9	49	17	18	3.7
35	1.8	17.0	51	29	25	3.6
41	2.0	17.9	61	36	32	2.8
48	2.2	24.1	70	57	36	3.6
Significance	Q*	C**	L**	Q*	L**	C**
Interaction						
Trt. × Time	NS	NS	**	NS	**	NS

[z]− ABA = without ABA, + ABA = with ABA. Treatment means were averaged across all times (22, 26, 30, 35, 41, and 48 days). Time in DAS. ABA 10^{-4}M was applied 28, 32, and 37 DAS.
[NS], *, * *Nonsignificant or significant F test at $P = 0.05$ or 0.01, respectively. Watering × ABA interaction was not significant. Time effect was linear (L), quadratic (Q), or cubic (C).

(Raschke, 1975), reducing photosynthesis rates (Mittelheuser and Van Steveninck, 1971). Between 22 and 36 DAS, only CW + ABA-treated seedlings had a significantly lower (0.022 $g \cdot g^{-1} \cdot day^{-1}$) mean leaf relative growth rate (RGR) as compared with CW – ABA (0.059), AW – ABA (0.046), and AW + ABA-treated seedlings (0.058). Overall, ABA did not reduce the leaf RGR, which averaged 0.033 $g \cdot g^{-1} \cdot day^{-1}$. A mean relative growth rate reduction was reported for eggplant *(Solanum melongena* L.) seedlings when 10^{-3}M ABA was applied to the roots (Latimer and Mitchell, 1988).

Between 28 to 37 DAS, the greater inhibition of leaf dry weight gain by applied ABA in seedlings irrigated with CW as compared to seedlings irrigated with AW (Fig. 1A) suggests that seedlings under continuous water regime may be more sensitive to applied ABA than AW-treated seedlings. The latter

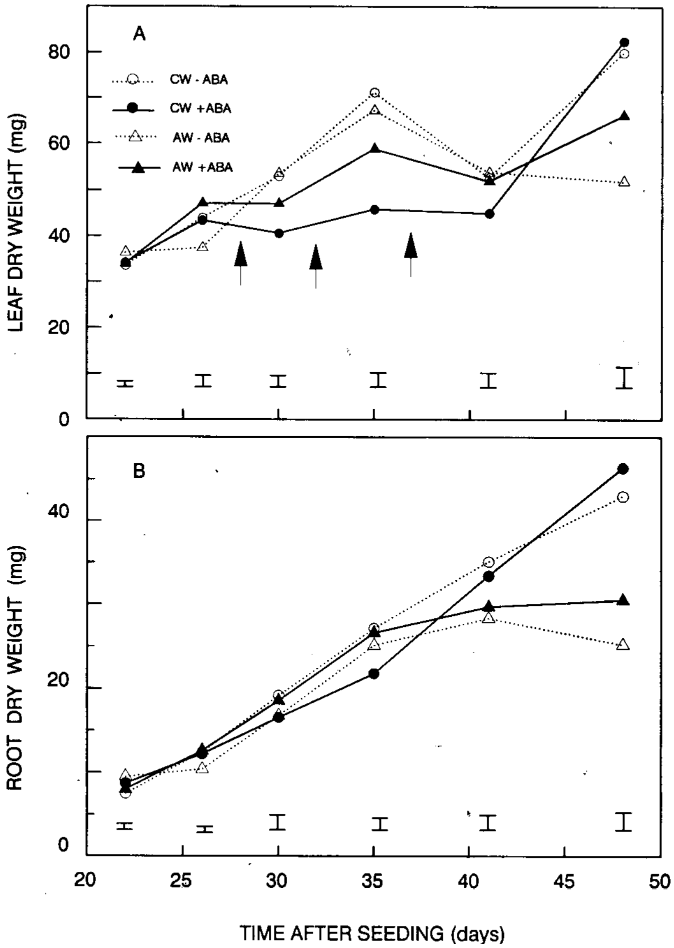

Fig. 1. Leaf **(A)** and root **(B)** dry weights of pepper seedlings in response to watering regime and 10^{-4} M ABA sprayed on the leaves at 28, 32, and 37 DAS (arrows) in the growth chamber experiment. Vertical bars represent LSD at *P* = 0.05. – ABA = without ABA, + ABA = with ABA.

may have acquired an endogenous increase of ABA levels due to mild stress (Dorffling et al., 1977). At 30 and 35 DAS, significantly lower leaf dry weight was measured in ABA-treated seedlings in both watering regimes (Fig. 1A). At 33 DAS, seedlings treated with ABA had premature cotyledon abscission that was 50% and 67% of the total for CW + ABA- and AW + ABA-treated seedlings, respectively. The accelerated abscission response is one of the first detected physiological effects of ABA (Addicott, 1983). At 35 DAS, light and/or nutrient limitation and subsequent cotyledon abscission may have caused a net loss in leaf weight, reducing the shoot : root ratio (Table 3). The decline in leaf growth for seedlings under AW has been previously reported by Watts et al. (1981). Root dry weight increase was unaffected by water regime or ABA until 35 DAS (Fig. 1B). Thereafter, seedlings grown under CW with or without ABA had. uniform root growth, which was greater than that under alternate watering.

Continuously watered seedlings had a significantly higher number of basal roots with larger basal and first-order basal root diameter than AW-treated seedlings (Table 4). Basal roots constitute an important root component of the pepper root system (Leskovar et al., 1989). Root counts and basal root diameter were unaffected by ABA. Similarly, lateral root counts and diameters were not affected by watering or ABA (Table 4).

Table 4. Root count and root diameter of pepper seedlings as affected by watering and ABA treatment at 48 DAS (growth chamber experiment).

Source of variation	Root count		Root diam (mm)	
	Basals	Laterals	Basal	Basal first order
Treatment[z]				
CW − ABA	31	19	0.44	0.29
CW + ABA	37	17	0.49	0.32
AW − ABA	13	17	0.36	0.22
AW + ABA	19	17	0.39	0.25
Orthogonal contrasts				
CW vs. AW	**	NS	*	**
−ABA vs. +ABA	NS	NS	NS	NS

[z]– ABA = without ABA, + ABA = with ABA. ABA 10^{-4}M was applied at 28, 32, and 37 days.
[NS], *, ** Nonsignificant or significant F test at *P = 0.05* or 0.01, respectively. Watering × ABA interaction was not significant.

Wightman et al. (1980) reported that 10^{-4} M ABA caused a decrease in the number of lateral root primordia in maize seedlings.

In the greenhouse experiment, at 35 DAS, 6 days after the last ABA application, ABA-leaf- and ABA-root-treated seedlings had a significantly lower leaf dry weight than the control (Fig. 2A). At 41 DAS, significantly lower leaf dry weight was measured for ABA-leaf as compared with ABA-root seedlings, suggesting that when ABA was applied to the leaves a faster response was obtained than when applied directly onto the rooting medium. However, at 53 DAS, ABA-root-treated seedlings had significantly lower root dry weight than ABA-leaf-treated seedlings (Fig. 2B). The root dry weight decline of ABA-root-treated seedlings is difficult to relate to ABA effects, since it occurred 3 weeks after the last ABA application. Whether ABA might have been bound and/or accumulated in the rooting medium is not known. When 10^{-3}M ABA was applied as a soil drench to eggplant seedlings 3 days before they were transferred to outdoors, ABA continued to be available to the plant for an additional 3 days and reduced RGR (Latimer and Mitchell, 1988). Similarly, 7.6×10^{-5} M ABA applied to geranium *(Pelargonium × hortorum)* roots for 9 h reduced RGR, transpiration, and photosynthesis (Arteca et al., 1985). In a study with maize, where plants were grown in 1000-cm^3 containers, 10^{-4} M ABA -sprayed on leaves or applied in the nutrient solution did not affect root growth, but induced leaf necrosis (Watts et al., 1981).

In our experiments, exogenous ABA applied to the leaves caused a transient inhibition of leaf weight gain, more evident in seedlings grown under CW rather than AW (Fig. 1A). In wheat *(Triticum aestivum* L.), leaf growth reduction by ABA was previously indicated by Quarrie and Jones (1977). ABA applied to seedlings that were continuously watered did not affect root growth (Fig. 1B). Fruit size and total yields were unaffected by ABA and watering treatments (data not presented). However, higher yields of fancy fruit ($t \cdot ha^{-1}$, were found for AW + ABA-treated seedlings, which yielded 11.3 ± 0.9 as compared to 9.1 ± 0.8 for AW – ABA, 8.6 ± 0.4 for CW + ABA and 7.5 ± 1.6 for CW – ABA-treated seedlings. More pepper seedlings treated with 10^{-3} M ABA and grown under dry soil conditions survived and had higher yields than untreated seedlings (Berkowitz and Rabin, 1988).

The results of this study underlie the importance of watering and ABA on dry-matter partitioning. ABA can be considered as an antitranspirant to control stomata behavior and reduce

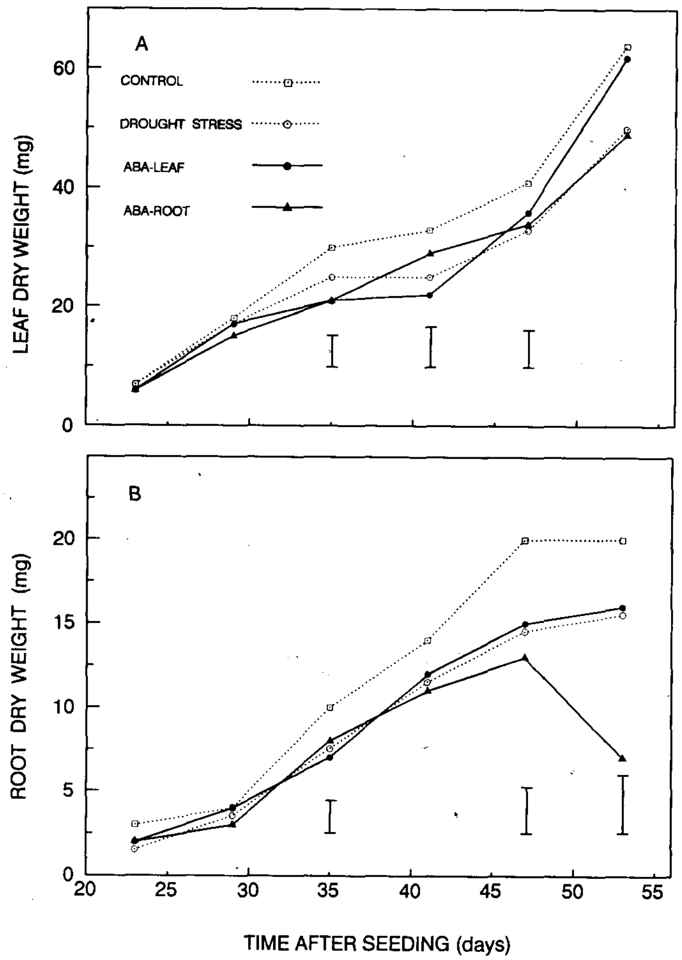

Fig. 2. Leaf **(A)** and root **(B)** dry weights of pepper seedlings in response to watering regime and 10^{-4}M ABA spray on the leaves (ABA-leaf) or applied to the rooting medium (ABA-root) in the greenhouse experiment. Vertical bars represent LSD at $P = 0.05$; data at sample dates without LSD bars were nonsignificant at $P = 0.05$. ABA was applied at 20, 23, and 29 DAS.

water loss (Mansfield et al., 1978). The possibility of using exogenous ABA as a substitute for drought stress may be advantageous to control transplant growth in the nursery and improve transplant field establishment.

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