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Differences in temperature or relative humidity may partially explain some of the visual appearances of calcium (Ca) deficiency disorders found in sorghum Sorghum bicolor (L.) Moench plants grown in controlled conditions. Independent temperature and relative humidity (R.H.) experiments were conducted using 'Redlan' and 'Martin' sorghum genotypes grown in three identical growth chambers with temperature treatments of 21/16, 23/23, and 35/30°C or R.H. regimes of 30, 60, and 90% at nutrient solution Ca levels of 25, 50, and 300 mg Ca L^{-1}. Calcium deficiency symptoms appeared on plants grown with the lowest Ca level at each temperature or R.H. Symptoms became progressively more severe as the temperature increased and were most severe at 60% R.H. The severity of deficiency was higher in Redlan than Martin in the R.H. experiment, but no differences between genotypes appeared with changing temperatures. Plant dry matter and Ca concentrations in plants increased with increasing Ca levels.

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EFFECTS OF TEMPERATURE AND RELATIVE HUMIDITY ON GROWTH AND CALCIUM UPTAKE, TRANSLOCATION, AND ACCUMULATION IN SORGHUM[1]

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ABSTRACT

Differences in temperature or relative humidity may partially explain some of the visual appearances of calcium (Ca) deficiency disorders found in sorghum [*Sorghum bicolor* (L.) Moench] plants grown in controlled conditions. Independent temperature and relative humidity (R.H.) experiments were conducted using 'Redlan' and 'Martin' sorghum genotypes grown in three identical growth chambers with temperature treatments of 21/16, 28/23, and 35/30°C or R.H. regimes of 30, 60, and 90% at nutrient solution Ca levels of 25, 50, and 300 mg Ca L^{-1}. Calcium deficiency symptoms appeared on plants grown when the lowest Ca level at each temperature or R.H. Symptoms became progressively more severe as the temperature increased and were most severe at 60% R.H. The severity

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of deficiency was higher in Redlan than Martin in the R.H. experiment, but no differences between genotypes appeared with changing temperatures. Plant dry matter and Ca concentrations in plants increased with increasing Ca levels. Lower leaves had higher Ca concentrations than upper leaves reflecting Ca immobility. Mean Ca concentrations in plants was highest at the lowest temperature and more dry matter was accumulated in roots at this temperature. Reduction in root growth at the 35/30°C temperature and a subsequent reduction in Ca absorption could explain the lower plant Ca concentrations for this temperature treatment. Dry matter yield of plants grown with 300 mg L^{-1} Ca was greatest at the medium temperature although dry matter yield generally increased as temperature declined. Lowest mean Ca concentration in leaves of plants occurred in plants at 90% R.H. Maximum dry matter yields occurred at 30% and minimum yields at 60% R.H. These results suggested that Ca absorption may be slowed in sorghum at high temperatures and relative humidities. A high rate of transpiration appears to enhance Ca mobility. Conditions detrimental to root growth inhibit adequate Ca absorption.

INTRODUCTION

The effects of temperature and relative humidity (R.H.) on growth and Ca nutrition in sorghum has received limited attention. Conflicting results on the effect of temperature on Ca absorption have been reported. The effect of temperature on Ca uptake in barley (*Hordeum vulgare* L.) was relatively small (10). Similarly, no difference in Ca uptake was observed for roots of soybean [*Glycine max* (L.) Merrill] grown at 5, 15, or 25°C (4). However, Johnson and Jackson (7) found a 25-fold increase in Ca absorption by wheat (*Triticum aesticum* L.) seedlings due to increasing temperature from 3 to 25°C. Highest Ca concentration in the aboveground portion of maize (*Zea mays* L.) occurred when plants were grown at 20°C (13). At the lowest (5°C) and highest (30°C) temperature, the concentrations of Ca were similar. Calcium concentrations in tomato (*Lycopersicon esculentum* Mill.) plants grown at 13°C were lower than at 24 and 29°C. Maximum growth occurred at the higher temperatures and light intensities (2).

Relative humidity of the air has a marked influence on transpiration by affecting the gradient of water vapor concentrations between

leaf cells and the air. Flow of water through plants by transpiration normally provides a transport system for most mineral elements from the roots to shoots. Calcium moves with the transpiration stream within plants by mass movement (6). However, Bell and Biddulph (1) reported that Ca moves in the stem by exchange reaction in the conducting tissues. They believed that metabolic removal of Ca from exchange columns was a major factor for upward translocation of Ca. Higher rates of water flow decrease the retention of Ca in the xylem, so the faster water moves, the greater the distance Ca moves before readsorption on other exchange sites (5).

Mobility of Ca in the phloem is still not fully understood. Some authors believe Ca is mobile in phloem tissues (9) and others believe Ca to be an immobile element (15). Movement of Ca is generally considered to be through the apoplast, and blockage of this pathway by deposition of suberin lamellae (casparian band) has been reported (12). The casparian band appeared to block Ca movement into the stele via the apoplast by forming a continuous suberin layer between the plasmalemma and cell wall. However, in newly initiated endodermal cells in the root tip, the casparian band is absent and the apoplast pathway is open for Ca movement.

Over the years, personal observation has shown that temperature and R.H. can affect the appearance and severity of Ca deficiency disorders in sorghum grown under controlled conditions. This study was conducted to better define these factors in the high incidence of Ca deficiency that sorghum plants commonly display when grown in the greenhouse and in growth chambers (11). Therefore, studies were conducted to measure the effects of different temperatures and R.H. regimes on growth and Ca uptake, translocation, and accumulation in sorghum plants grown with different levels of Ca in nutrient solutions.

MATERIALS AND METHODS

Seed of 'Redlan' and 'Martin' sorghum genotypes were germinated separately on paper towels moistened with distilled water. After 5 days, seedlings were selected for uniformity, transferred to plexiglass plates, and grown in 0.3-strength nutrient solution (3). After 5 days of additional growth, ten uniform sized seedlings were transferred to 7 L containers filled with treatment solutions. The levels of Ca in the

solutions were 25, 50, 300 mg L^{-1} (6.24, 12.48, and 74.88 mM). Concentrations (uM) of other elements in solutions were: 7240 K, 1550 Mg, 22 900 NO_3^--N, 2780 NH_4^+-N, 1940 Cl, 1820 S, 65 P, 18 Mn, 50 B, 1.2 Zn, 1.2 Cu, 1.6 Mo, and 47 Fe as FeHEDTA (ferric hydroxyethylene-diaminetriacetate) as described elsewhere (3). Distilled water was added every other day to maintain solution volumes and solutions were continuously aerated.

Two experiments were performed in three identical growth chambers. Both experiments were designed as randomized complete block with a split plot treatment arrangement. Main plots (growth chamber) were not replicated. Levels of Ca were replicated three times. In the first experiment, growth chambers were set at temperature regimes of 21/16, 28/23, and 35/30 ± 1°C (light/dark) with a light duration of 16 hr at 50 ± 5% R.H. The light intensity at plant level was 450 ± 25 uE m^{-2} s^{-1} in each chamber. The ten plants in each pot (experimental unit) were allowed to grow for 22 days in the treatment solutions. At harvest, plants were separated into roots, lower leaves (leaf nos. 1 to 5), and upper leaves (leaf no. 6 and above). Roots were thoroughly rinsed with distilled water, and all plant parts dried in a forced-air oven at 70°C for 4 days. Each plant part was weighed and ground to pass a 0.05 mm screen using a stainless steel mill. A 100 mg sample of ground material from each plant part was pelleted for analysis, and Ca was determined by energy dispersive x-ray fluorescence (8).

For the second experiment, the growth chambers were set at 30, 60, and 90 ± 5% R.H. at light/dark temperatures of 28/23 ± 1°C and light duration of 16 h. Five uniform sized plants were grown in 3.5 L treatment solutions which comprised an experimental unit. Plants were grown in treatment solutions for 27 days. Germination, Ca levels in solutions, experimental design, separation of plant parts, processing samples for Ca analysis, and statistical analysis were similar to those described for the temperature experiment.

Results and Discussion

Plant Appearance

Calcium deficiency symptoms appeared on plants grown in the lowest Ca solutions (25 mg L^{-1}) at each temperature regime. However, the deficiency symptoms became progressively more severe as temperatures

TABLE 1. Mean squares Ca concentrations in roots, lower leaves (LL), upper leaves (UL), whole plant (WP), and dry matter yields and shoot/root dry matter ratio of Redlan and Martin sorghum genotypes grown in nutrient solution at three temperature and three Ca levels.

Source of Variation	DF	Ca in Plant Parts				Dry Matter	Shoot/Root Dry matter Yield
		Roots	LL	UL	WP		
Total	53						
Temperature (T)†	2	0.06	32.69	1.03	2.75	62.87	3.34
Calcium level (Ca)	2	6.35**	285.87**	6.62**	42.43**	89.08*	0.25**
Genotype (G)	1	0.03	0.09	1.74*	0.06	1.25	0.78**
Ca x G	2	0.03	0.36	0.28*	0.05	0.79	0.02
T x Ca	4	0.16**	12.85**	0.10	0.51*	22.97**	0.13
T x G	2	0.12*	2.32*	0.09	0.16	6.66**	0.41*
T x Ca x G	4	0.12	5.20	0.08	0.17	2.05	0.02
Error	36	0.03	0.37	0.06	0.07	1.74	0.04

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

† Not tested for significance due to nonreplication.

increased. The appearance of Ca deficiency symptoms began at the tips and margins of young leaves and on growing points, with leaves becoming serrated and curled with marginal necrosis on upper leaves as previously noted (11). Root growth was severely restricted with increasing temperature, and the restriction was more pronounced at the two lower Ca levels. Roots were dark brown and shortened whereas healthy plants had extensive root growth and root tips were white. Visual Ca deficiency symptoms were consistent with the whole plant Ca concentrations. The expression of deficiency was similar for each genotype.

Plants grown with 50 or 300 mg Ca L^{-1} solutions did not show Ca deficiency symptoms at any R.H. regime. However, when the Ca level was

TABLE 2. Mean Ca concentrations in roots, lower leaves (LL), upper leaves (UL), whole plant (WP), and dry matter yields and shoot/root dry matter ratio of Redlan and Martin sorghum genotypes grown in nutrient solution at three temperature regimes and three Ca levels.

Genotype	Temp.	Ca level	Ca in Plant Part: Root	LL	UL	WP	Dry Matter Yield	Shoot/Root Dry Matter
	(°C)	mg L^{-1}	mg g^{-1}				g $plant^{-1}$	
Redlan	21/16	300	1.28	9.28	1.70	4.58	1.56	1.40
		50	0.58	3.09	0.69	0.91	1.52	1.25
		25	0.37	1.72	0.69	0.91	1.52	1.25
		Mean	0.74	4.70	1.02	2.36	1.52	1.28
	28/23	300	1.47	5.28	1.14	2.96	1.83	1.17
		50	0.48	2.05	0.39	0.97	1.33	0.92
		25	0.40	1.57	0.39	0.79	0.95	1.03
		Mean	0.78	2.96	0.64	1.57	1.37	1.04
	35/30	300	1.36	4.84	1.30	2.93	1.43	2.37
		50	0.33	1.51	0.84	0.98	1.25	2.06
		25	0.19	0.70	0.36	0.49	1.11	1.95
		Mean	0.63	2.38	0.83	1.46	1.26	2.13
Martin	21/16	300	1.65	7.83	2.58	4.18	1.61	1.10
		50	0.60	3.17	1.14	1.62	1.60	1.06
		25	0.30	1.59	0.89	0.83	1.59	0.92
		Mean	0.85	4.20	1.54	2.21	1.67	1.03
	28/23	300	0.89	6.66	1.79	3.42	1.79	1.15
		50	0.53	1.76	0.78	1.02	1.41	1.15
		25	0.28	1.36	0.44	0.66	1.01	1.02
		Mean	0.56	3.26	1.00	1.70	1.40	1.11
	35/30	300	1.51	5.77	1.74	3.44	1.48	1.78
		50	0.36	1.42	0.70	0.83	1.13	1.44
		25	0.30	1.29	0.70	0.77	0.91	1.55
		Mean	0.72	2.82	1.05	1.68	1.17	1.59
	LSD 0.05		0.27	1.01	0.40	0.43	0.21	0.33

LSD 0.05 for differences among overall means among temperatures for a particular variable.

25 mg L^{-1}, Ca deficiency symptoms were more severe on plants grown at 60% R.H. than at the other R.H.

Calcium Uptake and Distribution

Analysis of variance showed temperature x Ca level interactions for Ca concentrations in roots, lower leaves, and the whole plant to be significant (Table 1). This indicated a variation of Ca concentrations

in plants grown at various Ca levels over the three temperature regimes and the important effects of temperature on Ca absorption.

Within each temperature regime, Ca concentration in the plant parts or the whole plants was highest at the highest Ca level and decreased as Ca level decreased (Table 2). Calcium concentrations in the lower and upper leaves different. More Ca accumulated in the older than younger leaves reflecting low mobility of Ca from older to younger tissues. Mean plant Ca concentration tended to decrease over all Ca levels with higher temperature for both genotypes.

Results of this study indicated that root growth was restricted as temperature of the growth media was progressively increased. This reduced root growth resulted in high shoot/root dry matter ratios and was likely responsible, in part, for the subsequent reduction in Ca absorption at the two highest temperature regimes. Research has also shown that increasing temperature can increase K+ uptake which apparently hinders Ca absorbtion (14). The current experiment, however, did not address the issue of K^+ concentration in tissues. More dry matter accumulated in roots at the lower temperature and consequently shoot/root ratios were low and Ca absorption generally higher.

Significant Ca supply effect and Ca level x R.H. interactions were detected for Ca concentrations in lower and upper leaves (Table 3). Similar to the temperature experiment, calcium concentrations in plant parts increased with increasing Ca level at each R.H. (Table 4).

For Redlan grown with 300 mg Ca L^{-1}, concentrations of Ca in lower and upper leaves increased as the R.H. decreased. However, at low Ca levels, the effects of R.H. on Ca concentrations in leaves were small. This indicated that low R.H. might enhance Ca uptake in plants grown with high Ca levels. Calcium concentrations in lower and upper leaves averaged over all Ca levels for each R.H. were highest with the lowest R.H. treatment. Higher Ca concentrations in leaves of plants grown under conditions of low R.H. might have resulted from a higher plant transpiration (6) which accelerated the transpiration stream of xylem sap and subsequent movement of Ca into plant parts.

Martin reacted differently than Redlan. Calcium concentrations in roots increased with increasing Ca level at each R.H. regime (Table 4). This indicated a lower rate of Ca translocation from roots to shoots with increased R.H. for Martin. At a R.H. of 60%, Ca con-

TABLE 3. Mean squares for Ca concentrations in roots, lower leaves (LL), upper leaves (UL), whole plant (WP), and dry matter yields and shoot/root dry matter ratio of Redlan and Martin sorghum genotypes grown in nutrient solution at three relative humidity regimes and three Ca levels.

Source of Variation	DF	Ca in Plant Parts				Dry Matter	Shoot/root dry matter Yield
		Roots	LL	UL	WP		
Total	53						
Relative Humidity (RH) †	2	0.66	3.12	1.23	0.05	72.18	60.30
Calcium level (Ca)	2	25.43**	152.99**	7.63**	54.95**	173.75**	425.04**
Genotype (G)	1	0.37	1.40	0.27	0.61*	2.24	0.09
Ca x G	2	0.44	0.04	0.05	0.16	3.32	0.04
RH x Ca	4	0.45	1.98**	0.80**	0.07	21.63**	0.08
RH x G	2	1.02	0.03	0.62**	1.14**	1.43	0.04
RH x Ca X G	4	0.80	2.02**	0.27*	0.80**	3.26	0.16
Error	36	0.35	0.49	0.28	0.13	1.72	0.04

*, ** Significant at 0.05 and 0.01 probability level, respectively.

†Not tested for significance due to nonreplication.

centrations in lower leaves, upper leaves, or the whole plants grown with 50 and 300 mg Ca L^{-1} solutions were higher compared to the other R.H. treatments. At a Ca level of 25 mg L^{-1}, there was a nonsignificant trend for plant Ca concentration to be highest at 30% R.H. Calcium concentrations in the plant parts averaged over all Ca levels for each R.H. were highest at 60% and lowest at 90%. The mean Ca concentration in the whole plant was the lowest at 90% R.H. for Martin.

Dry Matter Yield

Dry matter yields increased with increasing Ca level in the nutrient solutions at each temperature. Significant temperature x Ca level interactions were detected for total dry matter production (Table

TABLE 4. Mean Ca concentrations in roots, lower leaves (LL), upper leaves (UL), whole plant (WP), and dry matter yield and shoot/root dry matter ratio of Redlan and Martin sorghum genotypes grown in nutrient solution at three relative humidity regimes and three Ca levels.

Genotype	Relative Humidity	Ca Level	Ca in Plant Parts: Root	LL	UL	WP	Dry Matter Yield	Shoot/Root Dry Matter
		mg L^{-1}	....mg g^{-1}....				g $plant^{-1}$	
Redlan	30%	300	2.86	7.60	2.19	4.48	3.63	1.07
		50	0.56	1.86	0.92	1.12	2.51	1.38
		25	0.47	1.01	0.63	0.69	1.90	1.28
		Mean	1.29	3.49	1.25	2.09	2.68	1.25
	60%	300	1.75	6.21	2.09	3.22	2.55	0.90
		50	0.46	1.40	0.72	0.89	2.00	1.52
		25	0.36	1.11	0.35	0.60	0.93	1.27
		Mean	0.85	2.90	1.05	1.57	1.83	1.23
	90%	300	2.20	5.07	1.08	3.32	2.70	1.63
		50	0.63	1.57	0.86	1.05	2.64	1.46
		25	0.35	1.02	0.52	0.65	2.06	1.41
		Mean	1.06	2.55	0.82	1.67	2.47	1.50
Martin	30%	300	1.97	5.91	1.60	3.44	3.50	1.10
		50	0.53	1.74	1.00	1.07	2.62	1.42
		25	0.34	1.43	0.72	0.78	1.79	1.17
		Mean	0.95	3.03	1.11	1.76	2.63	1.23
	60%	300	2.41	8.59	2.75	4.74	2.93	1.11
		50	0.66	2.57	1.66	1.41	1.76	0.84
		25	0.23	1.09	0.44	0.56	1.28	1.17
		Mean	1.10	4.08	1.61	2.23	1.99	1.04
	90%	500	3.93	5.56	1.24	3.10	2.69	1.45
		50	0.69	1.57	0.61	1.06	2.50	1.58
		25	0.33	1.30	0.64	0.77	2.58	1.34
		Mean	1.65	2.81	0.83	1.64	2.59	1.46
		LSD 0.05	1.20	1.16	0.46	0.60	0.43	0.33

LSD 0.05 for differences among overall means among relative humidities for particular variables.

1) indicating a variation in dry matter yield among Ca levels over the three temperature regimes. At 28/23°C, the dry matter yields of Redlan and Martin plants grown with 300 mg Ca L^{-1} was slightly higher at 21/16 and 35/30°C (Table 2). However, the highest dry matter yields at Ca levels of 25 or 50 mg L^{-1} were noted at the 21/16°C temperature regime. Plants of Redlan grown at 25 mg L^{-1} Ca and 21/16°C were not appreciably

smaller than those growing at 300 mg L^{-1} Ca and the lowest temperature. The mean dry matter yield over Ca levels increased as temperature declined. Less dry matter was accumulated in roots as growing temperatures progressively increased (Table 2). This was generally reflected in lower shoot/root values at the lowest temperature.

Significant effects of Ca level on dry matter yield and R.H. x Ca level interactions for dry matter yield were noted (Table 3). This reflected the variation of dry matter yield across Ca levels over the three R.H. environments. Dry matter yield increased, and an improvement in the physical appearance of the plants was noted at each R.H. with increasing Ca levels. The differences in dry matter yield across Ca levels decreased sharply at 90% R.H. (Table 4). For example, the difference in dry matter yields between Redlan plants grown with 25 and 300 mg Ca L^{-1} and R.H. of 30% was 1.73 g $plant^{-1}$. However, the dry matter yield difference was only 0.64 g $plant^{-1}$ for plants grown at 90% R.H. Although differences were less, trends for Martin were similar.

Dry matter yield averaged over all Ca levels in solutions showed maximum production for both genotypes at 30% R.H. while the minimum was at 60% R.H. Data for shoot/root ratios showed that the effect of R.H. was proportionately the same on both shoot and root growth.

Results of these studies suggested that Ca absorption may be slowed in sorghum at high temperatures and R.H., and that these conditions accentuated Ca deficiency disorders for plants grown in the greenhouse. A high rate of transpiration apparently enhances Ca mobility. Conditions detrimental to root growth would inhibit adequate Ca absorption.

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