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Salt sensitivity of cowpea at various growth stages

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Summary. The relative salt tolerance of cowpea (*Vigna unguiculata* (L.) Walp. cv. California Buckeye No. 5) at different stages of growth was determined in a greenhouse. Plants were grown in sand cultures that were irrigated four times daily with modified half-strength Hoagland's solution. Salination with NaCl and $CaCl_2$ (2:1 molar ratio) provided seven treatment solutions with osmotic potentials (Ψ_s) ranging from −0.05 to −1.05 MPa (electrical conductivities of 1.4 to 28 dS/m). Salt stress was imposed for 20 days beginning at either 7, 27, or 52 days after planting. The three 20-day stages are referred to here as vegetative, flowering, and pod-filling stages. Pod and seed yields from plants stressed during either the vegetative, flowering, or pod-filling stages indicated that cowpea was the most sensitive to salinity during the vegetative stage and became less sensitive the later plants were stressed. Seed yield was reduced 50% at $\Psi_s = -0.45$, −0.76, and −0.88 MPa for plants salinized during the vegetative, flowering, and pod-filling stages, respectively. Salinity reduced seed yield by reducing seed number; it had little, if any, effect on the weight of individual seeds. Vegetative growth was significantly reduced by salt stress during all three stages but the effect was much less when stress was imposed during the last two stages than during the first stage.

It is well known that the salt tolerance of plants not only differs among species, but that it also changes during their growth and development (Maas and Hoffman 1977). A useful database of crop tolerances to salinity has been compiled but these data apply only where soil salinity is relatively constant from the late seedling stage to maturity (Maas 1986). In order to efficiently utilize salt-affected soils and waters, it is now essential to determine the tolerances of crops at specific growth stages. Such data would be useful to growers in managing their soil and water resources and to researchers developing crop growth simulation models to predict crop response when soil salinity varies throughout the growing season. For example, if it is known that a crop becomes much more tolerant after seed set, irrigation water now considered unacceptable based on current salt tolerance data could be used without harm during the later part of the growing season.

Several studies have shown that the earlier salinity is applied in the growth season, the greater are its detrimental effects on yield (Kaddah and Ghowail 1964; Lunin et al. 1963; Maas et al. 1983; Pasternak et al. 1986; and other studies cited therein). However one cannot be sure from these studies whether the plants yielded less because they were more sensitive during the early growth stages or because salt stress was imposed for a longer period of time when salinized early. In studies where salt stress treatments were of equal duration during different growth stages, sorghum and wheat were found to be more sensitive to soil salinity during the vegetative and early reproductive stage of development than during later stages of development (Maas et al. 1986; Maas and Poss 1989). The present study was conducted to determine the sensitivity of cowpea, a leguminous crop, to soil salinity at three different growth stages. When stressed continuously, cowpeas appear to be moderately tolerant of salinity. West and Francois (1982) found that seed yield of California Blackeye No. 5 was decreased 12% per dS/m when the EC_e (electrical conductivity of saturated-soil extracts from the rootzone) exceeded 4.9 dS/m. No information was available on whether tolerance changes as plants mature.

Experimental procedure

Experiments were conducted in 60 sand tanks in the greenhouse at Riverside, CA as described previously (Maas and Poss 1989). Cowpea (cv. California Buckeye No. 5) seeds treated with Thiram, a fungicide, were planted in the sand on June 29. Four seeds were placed in each of 12 "hills" spaced on a grid, 18×30 cm apart. The seedlings were later thinned to one plant per hill. The plants were irrigated four times daily with a modified Hoagland solution consisting of 2.5 mM $Ca(NO_3)_2$, 3.0 mM KNO_3, 0.17 mM KH_2PO_4, 1.5 mM $MgSO_4$, 50 μM Fe as sodium ferric diethylenetriamine pentaacetate, 23 μM H_3BO_3, 5 μM $MnSO_4$, 0.4 μM $ZnSO_4$, 0.2 μM $CuSO_4$, and 0.1 μM H_3MoO_4 added to Riverside tap water. The nutrient solutions were allowed to drain from the saturated sand into 565-liter reservoirs after each irrigation and were reused in subsequent irrigations. Water lost by evapotranspiration was replenished each day to maintain constant osmotic potentials (Ψ_s) in the solutions. The solution pH was maintained between 6.0 and 6.5 by adding H_2SO_4.

The nutrient solutions were salinized by adding NaCl and $CaCl_2$ at a 2:1 molar ratio. The Ψ_s of the irrigation solutions was decreased 0.2 MPa per day split equally between morning and afternoon. At the end of the treatment period, the saline solutions were diluted to obtain a desalination rate of approximately 0.2 MPa per irrigation. All nutrient solutions were replaced with fresh solution at the beginning of the second and third stages.

The experimental design was a randomized block factorial consisting of six salinity treatments ($\Psi_s = -0.25, -0.35, -0.45, -0.65, -0.85$, and -1.05 MPa) imposed during three different growth stages: the vegetative stage, the flowering stage, and the pod-filling stage. Each treatment was replicated three times. A control treatment in which Ψ_s was maintained at -0.05 MPa throughout all three stages was replicated six times. On the seventh day after planting, a full and uniform plant stand was established and salination of the vegetative stage was begun and continued until Day 27. Salination of the flowering stage was begun on Day 27 when floral buds first appeared and continued until Day 47. The third stage, designated the pod-filling stage although some flowering continued to occur, was salinized from Day 52 to Day 72. Plants on Day 52 had 16 nodes on the main stem and seeds were just beginning to develop (Growth stage V16, R5 according to Fehr et al. 1971). All plants were irrigated with nonsaline nutrient solution before and after the saline treatments.

Air temperatures in the greenhouse ranged from 26.2 to 43.1 °C (mean = 37.2 °C) during the day and from 16.6 to 27.1 (mean = 23.3 °C) during the night. The growing degree days or heat units (defined as the Σ of mean daily minimum and maximum air temperature minus 10 °C by Grantz and Hall 1982) from planting until the beginning of the flowering and pod-filling treatment periods were 644 and 1,144 °C days, respectively. Relative humidity ranged from 42 to 99% with a mean of 60% during the day and 96% during the night.

Seed pods were harvested as they matured beginning on Day 80. The final harvest on Day 95 included the remaining pods as well as shoots. The plant material was oven-dried at 60 °C to obtain dry weight yields of the shoots, mature and immature pods, and seed. Seed mass was determined by weighing random samples of 100 oven-dry seeds.

Treatment effects were tested for statistical significance by analysis of variance and Duncan's Multiple Range test (SAS 1982). A nonlinear, least-squares inversion method (van Genuchten and Hoffman 1984) was used to determine the relationships between relative yield and Ψ_s. With option 12 of their model, relative yield (Y_r) can be related to osmotic potential of the soil solution (Ψ_s) by the following equation:

$$Y_r = 1/[1 + (\Psi_s/\Psi_{50})^p]$$

where $\Psi_{50} = \Psi_s$ corresponding to a 50% yield reduction, and p = an empirical constant that specifies the steepness of the curve.

Results and discussion

Vegetative growth

Vegetative growth was significantly reduced by salt stress imposed during all three stages of growth (Table 1). Because of the indeterminate growth behavior of cowpea, vegetative growth continued during the flowering and pod-filling stages. However, since a substantial proportion of vegetative growth occurred prior to salination of the latter two stages, the effect of salinity decreased when plants were stressed later in the growing season. The analysis of variance confirmed that the effects of salinity, the period of salt stress, and their interaction were all highly significant ($P = 0.0001$).

Pod production

Increased salinity markedly decreased the number and dry weight of mature pods produced per plant (Table 2). The effects of both the level of salinity and the growth stage it was imposed were significant ($P = 0.0001$) but the interaction was not. A Duncan's multiple range test indicated that the pod dry weights were significantly lower when plants were stressed during the first stage than during the latter two stages. Not only were the number of pods per plant reduced by salt stress, but at

Table 1. Shoot and immature pod yield of cowpea as influenced by salinity at the vegetative (*V*), flowering (*F*), and pod filling (*P*) stages of growth

Salinity treatment	Shoot dry weight[a]			Immature pod dry weight		
	V	*F*	*P*	*V*	*F*	*P*
Mpa	g/plant			g/plant		
−0.05	80.3	80.3	80.3	4.45	4.45	4.45
−0.25	58.4	53.9	54.9	2.52	8.30	1.25
−0.35	38.3	42.2	62.6	1.96	10.57	2.89
−0.45	37.2	39.3	66.1	4.20	8.49	2.12
−0.65	17.1	26.0	59.0	0.97	6.57	2.13
−0.85	11.1	23.2	52.5	0.80	5.65	0.82
−1.05	12.3	24.5	49.8	1.10	4.62	0.35
Means[b]	36.4[c]	41.4[b]	60.8[a]	2.29[b]	6.95[a]	2.00[b]

Source	df	Analysis of variance			
		Shoot		Immature pods	
		F value	$P > F$[c]	*F* value	$P > F$[c]
Rep	2	3.85	0.0294	2.00	0.1492
Growth stage	2	87.94	0.0001	44.25	0.0001
Salinity	6	76.05	0.0001	3.65	0.0056
$GS \times S$	12	7.35	0.0001	2.01	0.0498

[a] Excluding all pods
[b] Means followed by the same letter are not significantly different according to the Duncan multiple range test ($P < 0.05$)
[c] Probability that a significant *F* value would occur by chance

$\Psi_s \leq -0.65$ MPa, the number of seed per pod was also reduced which resulted in a large reduction in number of seed per plant (Table 3).

A number of green and immature pods unsuitable for market remained on the plant and were harvested separately (Table 1). Immature pods on control plants comprised less than 8% of the total pod weight. Only when plants were stressed during the flowering stage did salinity increase the number of immature pods at harvest. Generally, salt stress decreased the weight of immature pods on plants stressed during the vegetative and pod-filling stages, but increased the weight in the flowering-stage treatment.

Seed yield

The effects of salinity at the three stages on seed yield closely matched its effects on pod yields (Table 4). An analysis of variance indicated that the effects of both salinity and growth stage treatments on dry bean yields were significant ($P = 0.0001$); however, the interactive effects were not. Mean separation by Duncan's multiple range test indicated that the reduction in seed yield from salt stress during the vegetative growth stage was significantly greater than stress during the latter two stages. The reductions in yield caused by stress during the flowering and pod-filling stages were not statistically different from each other.

Table 2. Pod yield of cowpea as influenced by salinity at the vegetative (*V*), flowering (*F*), and pod filling (*P*) stages of growth

Salinity treatment	No. of pods per plant			Dry weight of mature pods		
	V	*F*	*P*	*V*	*F*	*P*
Mpa	g/plant			g/plant		
−0.05	20.8	20.8	20.8	53.5	53.5	53.5
−0.25	16.5	19.9	15.1	41.7	51.1	36.6
−0.35	12.1	16.9	15.2	30.4	41.5	42.4
−0.45	11.1	14.9	16.0	31.0	34.4	41.9
−0.65	7.9	13.1	14.2	16.5	27.5	34.8
−0.85	5.0	13.9	11.2	9.0	27.1	23.6
−1.05	5.3	12.5	9.3	8.7	25.2	17.4
Means[a]	11.2[b]	16.0[a]	14.5[b]	27.3[b]	37.2[a]	35.8[a]

Source	df	Analysis of variance			
		No. of pods		Pod dry weight	
		F value	$P>F$[b]	*F* value	$P>F$[b]
Rep	2	3.70	0.0334	3.72	0.0329
Growth stage	2	15.78	0.0001	13.33	0.0001
Salinity	6	19.51	0.0001	33.87	0.0001
$GS \times S$	12	1.41	0.2006	1.92	0.0619

[a] Means followed by the same letter are not significantly different according to the Duncan multiple range test ($P<0.05$)

[b] Probability that a significant *F* value would occur by chance

Table 3. Number of seed per plant and per pod as influenced by salinity at the vegetative (*V*), flowering (*F*), and pod filling (*P*) stages of growth

Salinity treatment	No. seed per plant			No. seed per pod		
	V	*F*	*P*	*V*	*F*	*P*
Mpa						
−0.05	204	204	204	9.81	9.81	9.81
−0.25	155	194	139	9.38	9.76	9.23
−0.35	115	160	150	9.51	9.46	9.84
−0.45	112	133	158	10.11	8.94	9.85
−0.65	64	100	123	8.11	7.63	8.65
−0.85	33	93	93	6.64	6.66	8.33
−1.05	34	89	68	6.37	7.14	7.29

Yield response curves (Fig. 1) were obtained from a nonlinear least squares analysis (van Genuchten and Hoffman 1984, option 12). Mean values of C_{50}, with standard errors, for seed yield were −0.45 (SE = 0.04), −0.76 (SE = 0.17), and −0.88 (SE = 0.09) MPa for the vegetative, flowering, and pod-filling stages, respectively. Mean values of *p* were 2.1 (SE = 0.31), 1.3 (SE = 0.52), and 2.4 (SE = 0.80) for the three stages, respectively.

Table 4. Seed yield of cowpea as influenced by salinity at the vegetative (*V*), flowering (*F*), and pod filling (*P*) stages of growth

Salinity treatment	Seed dry weight			100-seed dry weight		
	V	*F*	*P*	*V*	*F*	*P*
Mpa	g/plant			g/100 seed		
−0.05	49.6	49.6	49.6	24.3	24.3	24.3
−0.25	38.4	47.0	34.0	24.8	24.2	24.4
−0.35	28.2	38.7	39.8	24.5	24.2	26.6
−0.45	28.5	32.1	39.4	25.4	24.1	25.0
−0.65	15.5	25.5	32.9	24.2	25.5	26.8
−0.85	8.2	24.8	22.2	24.7	26.8	23.8
−1.05	8.1	23.2	16.2	24.0	26.0	23.9
Means[a]	25.2[b]	34.4[a]	33.4[a]	24.5[a]	25.0[a]	25.0[a]

Source	df	Analysis of variance			
		Seed dry weight		100-seed weight	
		F value	$P > F$[b]	*F* value	$P > F$[b]
Rep	2	3.68	0.0342	4.67	0.0150
Growth stage	2	14.22	0.0001	2.16	0.1289
Salinity	6	34.83	0.0001	2.34	0.0497
$GS \times S$	12	1.99	0.0516	5.40	0.0001

[a] Means followed by the same letter are not significantly different according to the Duncan multiple range test ($P < 0.05$)

[b] Probability that a significant *F* value would occur by chance

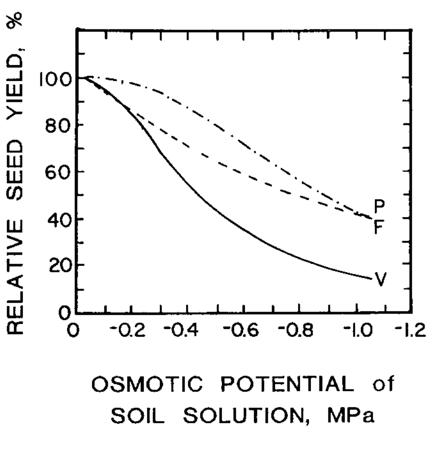

Fig. 1. Relative seed yields of cowpea as a function of the osmotic potential of the soil solution imposed for 20 days during three different growth stages – vegetative (*V*), flowering (*F*) or pod-filling (*P*)

Seed mass

Although the effect of salt stress on individual seed weights was statistically significant ($P = 0.05$), the differences among salt treatments were very small (Table 4). Increased salt stress (Ψ_s decreased from −0.05 to −1.05 MPa) during the vegetative stage had no effect, but during the flowering stage it increased seed mass slightly. Increased stress up to −0.56 MPa during the pod-filling stage tended to increase seed mass but at higher salinity levels, seed mass was decreased. The different responses among growth stages resulted in a highly significant interaction between salinity and growth stage but differences in seed mass between growth stages were not significant. Clearly, the decrease in seed yield caused by salt stress was the result of fewer seed per plant and not smaller seed.

General discussion

These data, like those for sorghum (Maas et al. 1986) and wheat (Maas and Poss 1989), indicate that salt tolerance increases as the plants mature. However, since cowpea is an indeterminate crop, the effects cannot be correlated as well with specific physiological stages of growth as in determinate crops. Flowering occurs over a longer period of time than in the cereals. Nevertheless, seed yield was affected most by salinity when plants were stressed prior to flowering.

The growth behavior of the cowpeas in the greenhouse was more "viney" than that normally observed in the field. However, pod and seed yield of the control plants in the greenhouse were representative of yields in the field. Turk et al. (1980) reported seed yields of 3,885 kg/ha, or approximately 47 g/plant, for 'CB5' grown at a plant population of 83,000 plants/ha in Riverside in 1976. Our yield of 49.6 g/plant compares favorably with this yield. A direct comparison of the effect of salinity in the greenhouse with that in the field is not possible because similar treatments have not been conducted. However, the yield reduction caused by salt stress during the vegetative stage in the greenhouse was greater than that reported by West and Francois (1982) in the field. This, in part, may be because salt stress in their study was initiated when plants were older and applied more slowly. They salinized the irrigation waters over a 3-week-period beginning 21 days after planting and the salinities reported were not established in the soil profile until a few weeks later.

The finding that cowpea is more sensitive to salt stress prior to the floral bud formation than during equivalent length later stages contrasts with its response to drought stress. Turk et al. (1980) found that drought during the vegetative stage did not reduce yield if irrigations were resumed and conditions were conducive to rapid recovery of growth and pod set. They further observed that drought during flowering and pod filling substantially reduced yields. Shouse et al. (1981) also reported that the flowering and pod-filling stages were the most sensitive to drought. It should be noted, however, that Summerfield et al. (1976) found the vegetative stage to be the most sensitive to drought. It is not known if the effects of salinity and drought differ or if, as Turk et al. (1980) suggest, plant responses to drought (stress) in controlled environments differ from responses in the field.

The plants did not exhibit any symptoms of excess salt accumulation, although no mineral analyses were performed to verify the amount of salt uptake. However, the data of West and Francois (1982) indicate that Na is essentially excluded from cowpea leaves. Cl was accumulated, but they found that leaf concentrations remained below 300 mmol/kg DW even at salinity levels that caused a 50% reduction in yield.

Conclusion

Salt stress imposed for 20 days during three different periods of plant development (from 7 to 27, 27 to 47, and 52 to 72 days of age) indicated that cowpeas were most sensitive to salinity when stressed during the first, i.e. vegetative, stage. This was true for both vegetative shoot growth and seed yield. The osmotic potentials of the soil solution during the 20-day treatments that decreased seed yield by 50% were −0.45, −0.76, and −0.88 MPa for the three periods, resp. The decrease in seed yield resulted from fewer pods per plant and fewer seed per pod. Individual seed weights were not appreciably affected by salt stress at any stage.

Cowpeas become increasingly more salt tolerant as plants progressively develop during the growing season. This finding has important practical implications for managing irrigation waters that reduce crop yields. If cowpeas are irrigated with water containing salt levels at or below the salt tolerance threshold (see West and Francois 1982) prior to the flowering stage, saltier water could be used without deleterious effects on seed yield at the later stages of development.

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