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GROWTH AND WATER RELATIONS OF CEREAL CROPS AS INFLUENCED BY SALINITY AND RELATIVE HUMIDITY[1]

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ABSTRACT

The influence of atmospheric relative humidity (RH) on plant growth and how it interacts with salinity to influence the salt tolerance and water relations of cereal crops was determined for barley (*Hordeum vulgaris* L. 'CM67'), wheat (*Triticum aestivium* L. 'Siete Cerros'), and sweet corn (*Zea mays* L. 'Bonanza'). The studies were conducted in sunlit climate chambers with temperatures cycled daily between $\overset{50F}{10}$ and $\overset{81F}{27}$ C for barley and wheat and between $\overset{63F}{17}$ and $\overset{90F}{32}$ C for corn and with average daytime RH controlled near 45% for the low and near 90% for the high RH treatments. The root medium of each crop was maintained at four different root medium salinity levels osmotic potentials (${}^{S}\psi_{o}$), the range depending on the crop's salt tolerance.

With a nonsaline root medium, increasing the RH from 45 to 90%, increased the wheat yield by 24%, had no influence on corn yield, and reduced barley yield by 16%. High RH increased the salt tolerance of barley and corn but did not affect the tolerance of wheat.

For all three crops at all root medium salinity ${}^{S}\psi_{o}$ levels, water-use efficiency (yield per unit of water consumed) was higher at 90% than at 45% RH. Linear relationships were found between leaf total water leaf water potential (${}^{L}\psi_{t}$) and osmotic

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UC-II-6

leaf water salinity Root medium salinity
($^{L}\psi_o$) potentials and $^{S}\psi_o$ for barley and wheat. Leaf pressure potential
Leaf water pressure
($^{L}\psi_p$) was reduced by low RH and salinity. The relationship between
Leaf water potential
crop yield and $^{L}\psi_t$ was linear. The difference between full yield and
20 atmospheres of suction
almost no yield was 2.0 Megapascals (MPa) for both barley and wheat.

Previous studies have indicated that the interactive effect of atmospheric relative humidity (RH) and root medium salinity ($^{S}\psi_{o}$) on crop yield depends upon the crop's salt tolerance. The salt tolerance of those crops sensitive to salinity, like red kidney bean (*Phaseolus vulgaris* L.), onion (*Allvim cepa* L. 'F-1 Hybrid Yellow Granex), and radish (*Raphanus sativus* L. 'Champion'), was markedly increased by high RH (Hoffman and Rawlins, 1970, 1971), while crops tolerant of salinity, like cotton (*Gossypium hirsutum* L. 'Acala SJ-1') and garden beet (*Beta vulgaris* L. 'Burpee's Red Ball') showed no interaction with RH (Hoffman et al., 1971 and Hoffman and Rawlins, 1971). This apparent large difference in response to RH prompted study of other crops. Here we report the interactive effect of salinity and RH on three cereal crops.

EXPERIMENTAL PROCEDURE

During the winter and spring of 1970-71, barley (*Hordeum vulgaris* L. 'CM-67') and wheat (*Triticum aestivum* L. "Siete Cerros') were grown in gravel cultures in the sunlit climate chambers described by Hoffman and Rawlins (1970). The ambient temperature was programmed to vary diurnally in all four chambers from a minimum of 50F 10 C in the early morning to a maximum of 81F 27 C in the afternoon. The average daytime (0700 to 1900 hr, PST) temperature was 70F 21 C. Each crop was grown in both a high- and a low-RH chamber. The high-RH chambers were programmed to maintain a constant 90% RH; the low-RH chambers were programmed to lower the RH to about 35% during the afternoon from a nighttime RH of 65%. During the spring and summer of 1974, the experiment with barley and wheat was repeated, except different chambers were assigned to each crop-RH treatment. Sweet corn (*Zea mays* L. 'Bonanza') was grown following barley and wheat in the fall of 1974 with two chambers maintained at each of the two RH treatments. Thus, the RH treatments were duplicated for all three crops. For corn, the ambient temperature was increased to cycle diurnally between $\overset{63F}{17}$ and $\overset{90F}{32}$ C. The average daytime temperature was $\overset{81F}{27}$ C. The average values recorded for the two RH treatments throughout the experiments were 89 and 44% for barley, 87 and 44% for wheat, and 84 and 41% for corn. With few exceptions, the daily variation in both average ambient and average dew-point temperatures was within ± 1 C.

Four salinity levels, replicated four times, were established in a Latin square pattern in each chamber for all three crops. The salinity levels, however, were varied according to the crop's salt tolerance (U.S. Salinity Laboratory Staff, 1954). The osmotic potential of the treatment solutions (${}^{S}\psi_{o}$), including the -0.04 MPa[3] osmotic potential of the modified half-strength Hoagland nutrient solution (Maas et al., 1973), for barley were $\overset{EC_e=1.1}{-0.04}$, $\overset{EC_e=13.9}{-0.50}$, $\overset{EC_e=27.8}{-1.00}$, and $\overset{EC_e \approx 42}{-1.50}$ MPa; for wheat, $\overset{EC_e=1.1}{-0.04}$, $\overset{EC_e=8.3}{-0.30}$, $\overset{EC_e=16.7}{-0.60}$, and $\overset{EC_e=25}{-0.90}$ MPa; and for corn, $\overset{EC_e=1.1}{-0.04}$, $\overset{EC_e=5.5}{-0.20}$, $\overset{EC_e=9.7}{-0.35}$, and $\overset{EC_e=13.9}{-0.50}$ MPa. The saline treatments were initiated by adding chemically equivalent amounts of NaCl and $CaCl_2$ to the nutrient solution at the rate of $\underset{EC_w=2.8/day}{\overset{1\ atmo\ OP/day}{-0.1\ MPa/day}}$ for the most saline treatment; the other treatments were salinized proportionally less each day. Thus, salination required 15 days for barley, 9 days for wheat, and 5 days for corn. Salination was started 7, 6, and 20 days after planting for barley, wheat, and corn, respectively.

$$OP = .36\ EC\ ;\ EC = \frac{OP}{.36}$$

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[3] Pascal (Pa) × 10^{+5} = 0.1 MPa = 1.0 bar.

Seeds were planted directly into 18-liter containers filled with fine gravel, and seedlings were thinned to the same number in each container, i.e., 25 barley and wheat and 3 corn. The plants within each chamber were irrigated by pumping solution from a 220-liter drum into the four containers constituting a given salinity-humidity treatment for 30-min every hour. The solution filled each container within 6 to 8 min, after which the excess returned to the drum through an overflow drain. After each irrigation, the solution drained from the bottom of each container to the storage drum. The average transpiration rate of the plants in each treatment was determined every 2 to 5 days by measuring the quantity of demineralized water required to restore the solution level in each drum to a preset mark. The solutions ranged from pH 5, when fresh, to pH 8, when all the solutions were replaced after 3 weeks. For the corn, additional iron chelate was required to prevent chlorosis.

Leaf total water potential Leaf water potential ($^{L}\psi_{t}$) was measured on detached leaf disks from barley and wheat with thermocouple psychrometers. No fewer than 15 and as many as 30 mature, sunlit leaves were sampled between 1000 and 1100 hr when the chamber ambient temperature was near 77F 25 C. Between three and five samples were taken from each treatment each day for several days. Leaf sampling had no adverse effect on the remainder of the leaf, and it had no influence on growth or ultimate yield. Leaf osmotic potential Leaf water salinity ($^{L}\psi_{o}$) was measured on the same sample in the same psychrometer after dipping the leaf disk in liquid nitrogen to rupture the cell membranes. Leaf pressure potential ($^{L}\psi_{p}$) was calculated as the difference between $^{L}\psi_{t}$ and $^{L}\psi_{o}$.

The winter crop of barley and wheat was harvested 200 days after planting in 1970-71. In 1974, the spring crop of barley and wheat was harvested 125 and 140 days after planting, respectively. The corn plants were harvested 95 days after sowing; early maturing ears were harvested 24 days after initial silking.

At harvest the plants were divided into yield, stover, and roots, and dried at 158 F 70 C. For corn the entire husked ear was taken as the yield and the husk from the ear was included as stover. For barley and wheat, the stover included all shoot growth, except the threshed grain. The roots were removed from the gravel by washing and floating them onto a 1.5-mm mesh screen.

RESULTS AND DISCUSSION

Growth

The dry weights for yield, stover, roots, and total plant along with plant height as functions of salinity and RH are summarized in Table 1 for barley, wheat, and corn. The values are the average of the eight replications from the duplication of both RH treatments. Values in each column for each crop that are followed by the same letter are not significantly different at the 5% confidence level as determined by the Duncan's multiple range test.

Independent of RH, increased salinity consistently reduced the growth of all plant parts for all three crops. Plant height, the number of heads per plant, and grain weight were also reduced with increased salinity (Table 1). Data for barley and wheat agree with others [Jadav et al. (1976) and Torres and Bingham (1973)] that a major factor involved in yield reduction of wheat as salinity increases is the decrease in the number of tillers and thus a decrease in the number of heads per plant. The influence of salinity on yield is shown graphically in Fig. 1. For comparison, the linear salt tolerance line reported by Maas and Hoffman (1977) as the consensus of previous studies is shown in Fig. 1 as a dashed line. The salt tolerance results for barley at 45% RH agree with the consensus line; agreement is excellent for both RH treatments for wheat, while the tolerance results for both RH treatments indicate that Bonanza sweet corn is more tolerant than indicated by the concensus line.

The influence of RH without salinity can also be noted in Table 1. Increasing the RH from 45 to 90% increased wheat grain yield by 24%, had no significant influence on corn ear weight, and decreased barley grain yield by 16%. Of the five previously reported crops, only the yield of onion was not increased by high RH (Hoffman and Rawlins, 1971). Relative humidity had no significant effect on the height of barley or wheat plants, but significantly increased the height of corn for all salinity treatments. For barley and wheat, neither the number of heads per plant nor the weight of 100 seeds was influenced consistently by RH, except for significant differences in the number of wheat heads at low salinity levels.

The interaction of RH and salinity on cereal crop yields can be seen in Fig. 1 where the yields are placed on a relative basis, taking the nonsaline $\overset{EC_w = 1.1}{(-0.04 \text{ MPa})}$ yields as $\overset{100\%}{1.0}$ for each RH treatment. This transformation eliminates the direct effect of RH and emphasizes the interaction. The data for wheat indicate no interaction. In this respect, wheat resembles some other relatively salt-tolerant crops, like cotton (Hoffman et al., 1971) and garden beet (Hoffman and

Rawlins, 1971). However, barley, the most salt-tolerant plant of the three, interacted significantly with RH. The salinity level that caused a 50% yield decrease for barley decreased *increased from ECw = 16.7 to 23.3* from -0.60 to -0.84 MPa (40%) as RH was increased from 45 to 90%. Corn also exhibited a significant interaction with salinity. The salinity levels that caused a 50% yield decrease for corn, ~~decreased~~ *increased ECw = 7.2 to 9.7* from -0.26 to -0.35 MPa (35%) as RH was increased from 45 to 90%. The interaction observed with corn was not unexpected because other salt-sensitive plants, like bean, onion, and radish (Hoffman and Rawlins, 1970, 1971), indicated similar interactions. Thus, the data of these and previous experiments indicate that generally high RH increases the salt tolerance of salt-sensitive plants more than that of salt-tolerant ones, except for barley. This indicates that a water stress component, like RH, is a significant factor in the response of plants sensitive to salinity.

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Water Use

The influence of salinity and RH on water use for barley, wheat, and corn is summarized in Table 2, where the total amount of water transpired throughout the growing season, the daily peak rate of transpiration, and the transpiration ratio (ratio of water transpired to yield) are given. In agreement with the growth results, transpiration of all three crops consistently decreased as ${}^{S}\psi_{o}$ *— Osmotic Pressure* decreased. *(means increase in salinity)* The influence of RH on transpiration was greatest for the nonsaline treatments where total transpiration for barley, wheat, and corn, respectively, was 17, 37, and 31% less at 90% RH as compared with that at 45% RH. Increasing RH from 45 to 90% decreased transpiration in the salt treatments of each crop by about 15%. The influence of the salinity-RH treatments on the daily peak rates of transpiration, given in Table 2, was comparable with that for total transpiration, although RH effects on peak rates of transpiration were insignificant at high salinity levels.

The transpiration ratio is a measure of water-use efficiency: the lower the transpiration ratio the higher the water-use efficiency. For all three crops and at all $^{S}\psi_{o}$ levels, the tranpiration ratio was lower at 90% as compared with 45% RH. This was the expected consequence of a lower vapor pressure gradient at high RH. The ratio was lowest for the lowest saline treatment for all three crops ($^{S}\psi_{o}$ = $EC_w = 13.9$ -0.5 MPa for barley, $EC_w = 8.3$ -0.3 for wheat, and $EC_w = 5.6$ -0.2 for corn, which reflected the decrease in net growth per unit leaf area caused by salinity.

Water Potential

The influence of salinity and RH on $^{L}\psi_{t}$ and $^{L}\psi_{o}$ for barley and wheat is shown in Fig. 2. The potential measurements were made on 2-month-old barley in both 1971 and 1974 and on 2-month-old wheat in 1971. Data were not collected in 1974 for wheat and corn, because the psychrometers were not available. Standard deviations of both $^{L}\psi_{t}$ and $^{L}\psi_{o}$ measurements ranged from 0.15 to 0.30 MPa, with the largest deviations occurring at the lowest potentials. Generally, $^{L}\psi_{t}$ had larger deviations than the corresponding $^{L}\psi_{o}$.

Both $^{L}\psi_{t}$ and $^{L}\psi_{o}$ were highest in the least stressed plants. As $^{S}\psi_{o}$ decreased, both $^{L}\psi_{t}$ and $^{L}\psi_{o}$ decreased linearly, which agreed with the results of Aceves-N. et al. (1975) for wheat and those of Hoffman and Rawlins (1971) for root crops. Both $^{L}\psi_{t}$ and $^{L}\psi_{o}$ were lower at 45% than at 90% RH, except where low $^{S}\psi_{o}$ prevented wheat from responding to RH. The parameters for the linear regression lines for the $^{L}\psi_{t}$ and $^{L}\psi_{o}$

vs. ${}^{S}\psi_o$ data plotted in Fig. 2 are given in Table 3. The difference between ${}^{L}\psi_t$ and ${}^{S}\psi_o$ for nonsalinized plants is given by the intercept; for barley and wheat the intercept is about 0.5 MPa. The change in ${}^{L}\psi_t$ and ${}^{L}\psi_o$ with ${}^{S}\psi_o$ is given by the slope. The slope for ${}^{L}\psi_t$ was greater than that for ${}^{L}\psi_o$ for both barley and wheat and explains the decrease in ${}^{L}\psi_p$ as ${}^{S}\psi_o$ decreases (Table 4). ${}^{L}\psi_p$ was consistently higher at 90% than at 45% RH. The results of Aceves-N. et al. (1975) for wheat, however, indicated that ${}^{L}\psi_p$ remained constant as ${}^{S}\psi_o$ decreases, but their data, unlike our's and Bernstein's (1961), did not indicate complete osmotic adjustment.

Effect of Leaf Water Potential on Yield

The relationship between ${}^{L}\psi_t$ and yield for barley and wheat at two RH's is shown in Fig. 3. The yields were normalized by assigning the highest yield for each crop a value of 1.00. For example, the -0.04 MPa yield of wheat at 90% RH is 1.00, while the -0.04 MPa yield at 45% RH is 0.81. Similar conversions may be made from the yields given in Table 1. The ${}^{L}\psi_t$ values are identical to those in Fig. 2. Although the ${}^{L}\psi_t$'s are not for the entire growing period, they do represent the time period when the plants were growing rapidly.

The relationship between ${}^{L}\psi_t$ and yield is linear for both barley and wheat. This linear relationship agrees with the data presented by Hoffman and Rawlins (1971) for root crops and by Cerda, Bingham, and Hoffman (in press) for sesame (*Sesamum indicum* L.). The parameters for the linear regression lines shown in Fig. 3 are given in Table 5. All of the lines of regression have correlation coefficients above 0.95.

The slope for wheat is steeper than that for barley, indicating that wheat is more sensitive to ${}^{L}\psi_t$.

Relative humidity had little influence on the relationship between ${}^{L}\psi_t$ and wheat yield. For barley the relationship, unlike the results from other crops, was most favorable for 45% as compared with 90% RH.

Also evident in Fig. 3 is the relatively narrow range of ${}^{L}\psi_t$ in which barley and wheat will grow and yield. The difference in ${}^{L}\psi_t$ between full and almost no yield is 2.0 MPa. This range in ${}^{L}\psi_t$ is slightly larger than that reported for root crops (Hoffman and Rawlins, 1971), but our results support the hypothesis that plants make physiological and morphological adaptations to maintain their ${}^{L}\psi_t$ above a certain minimum. In general, these adaptations have a negative effect on yield.

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Table 1. Influence of atmospheric relative humidity (RH) and root medium salinity (${}^{S}\psi_o$) on dry weight and height of barley, wheat, and sweet corn. Also reported are the number of heads per plant and grain weight for barley and wheat.

	${}^{S}\psi_o$	Relative humidity	Dry Weights				Plant height	Heads	Grain weight
			Yield*	Stover	Root	Total plant			
ECe	MPa	%	g/plant				m	no./plant	g/100 seeds
			BARLEY						
1.1	-0.04	90	8.6ab**	27.0a	2.5a	38.1a	0.77a	15.6a	4.5ab
		45	10.2a	27.4a	2.2a	39.8a	0.84a	15.0a	4.7a
13.9	-0.50	90	8.2bc	16.3b	1.2b	25.7b	0.54b	10.7b	4.1bc
		45	6.6c	13.2c	1.0bc	20.8c	0.61b	10.3b	3.8c
27.8	-1.00	90	3.1d	8.3d	0.5cd	11.9d	0.34c	6.8c	3.1d
		45	2.1de	7.0d	0.3d	9.4d	0.42c	5.4c	3.0d
41.7	-1.50	90	0.8e	3.4e	0.2d	4.4e	0.28d	2.4d	--
		45	0.5e	3.7e	0.2d	4.4e	0.26d	2.3d	--
			WHEAT						
1.1	-0.04	90	9.4a	14.5a	1.2a	25.1a	0.79a	8.2b	3.2a
		45	7.6bc	10.4b	1.1a	19.1b	0.79a	9.4a	3.1a
8.3	-0.30	90	8.3ab	10.8b	0.6b	19.7b	0.73b	7.1c	3.3a
		45	6.5c	8.2c	0.6b	15.3c	0.70b	5.4d	3.2a
16.7	-0.60	90	2.0d	4.2d	0.2c	6.4d	0.66c	2.5e	2.2b
		45	1.9d	4.0d	0.2c	6.1d	0.60d	2.6e	2.4b
25.0	-0.90	90	0.5e	1.7e	0.1c	2.3e	0.56d	0.9f	2.2b
		45	0.4e	1.7e	0.1c	2.2e	0.49e	0.7f	2.4b
ECe			CORN						
1.1	-0.04	90	52.2a	103b	12.6a	168b	2.02a		
		45	51.3a	133a	13.4a	197a	1.88b		
5.6	-0.20	90	48.4a	80c	9.9b	138c	1.84b		
		45	34.2b	82c	9.9b	126c	1.60c		
9.6	-0.35	90	26.2c	46d	6.3c	79d	1.55c		
		45	12.7d	37de	4.9cd	55e	1.15d		
13.9	-0.50	90	6.4e	30e	3.9de	40ef	1.13d		
		45	2.1e	25e	3.0e	30f	0.94e		

*Yield for barley and wheat is grain; for corn, it is ear weight.

**Values followed by the same letter in each column for each crop are not significantly different at the 5% level (Duncan's Multiple Range Test).

Table 2. Effects of relative humidity (RH) and root medium salinity ($^S\psi_o$) on transpiration and transpiration ratio.

ECe	$^S\psi_o$	Relative humidity	Total transpiration	Peak transpiration rate	Transpiration ratio
	MPa	%	ℓ/plant	ℓ/plant/day	ℓ H_2O/g yield
			BARLEY		
1.1	-0.04	90	14.8	0.17	1.72
		45	17.9	0.22	1.75
13.9	-0.50	90	7.2	0.10	0.88
		45	8.3	0.10	1.26
27.8	-1.00	90	2.8	0.04	0.90
		45	3.2	0.05	1.52
41.7	-1.50	90	1.1	0.02	1.38
		45	1.3	0.02	2.60
			WHEAT		
1.1	-0.04	90	11.6	0.16	1.23
		45	18.5	0.26	2.43
8.3	-0.30	90	6.9	0.10	0.83
		45	8.1	0.11	1.25
16.7	-0.60	90	2.4	0.04	1.20
		45	3.0	0.05	1.58
25.0	-0.90	90	1.0	0.01	2.00
		45	1.2	0.01	3.00
			CORN		
1.1	-0.04	90	40.9	0.99	0.78
		45	58.9	1.35	1.15
5.6	-0.20	90	33.1	0.79	0.68
		45	40.0	0.95	1.17
9.6	-0.35	90	20.9	0.54	0.80
		45	24.7	0.56	1.94
13.9	-0.50	90	12.1	0.32	1.89
		45	14.3	0.35	6.81

Table 3. Equation of linear regression lines relating osmotic potential of the root medium ($^{S}\psi_{o}$) to leaf total water ($^{L}\psi_{t}$) and osmotic ($^{L}\psi_{o}$) potentials where $^{L}\psi_{t} = a + b\ ^{S}\psi_{o}$ and $^{L}\psi_{o} = c + d\ ^{S}\psi_{o}$.

Relative humidity	Leaf Total Water Potential ($^{L}\psi_{t}$)			Leaf Osmotic Potential ($^{L}\psi_{o}$)		
	Intercept	Slope	Correl. coeff.	Intercept	Slope	Correl. coeff.
%	MPa	MPa/MPa		Mpa	MPa/MPa	
			BARLEY			
	a	b		c	d	
90	-0.43	1.37	0.99	-1.68	0.96	0.99
45	-0.59	1.54	0.99	-1.79	1.03	0.99
			WHEAT			
	a	b		c	d	
90	-0.30	2.09	0.99	-1.40	1.29	0.99
45	-0.58	1.86	0.99	-1.55	0.96	0.97

Table 4. Influence of root medium salinity $({}^{S'}\psi_{o})$ and relative humidity (RH) on leaf pressure potential $({}^{L}\psi_{p})$.

Crop		${}^{S}\psi_{o}$	Leaf Pressure Potential	
			At 90% RH	At 45% RH
		MPa	MPa	MPa
	ECe			
Barley	1.1	-0.04	+1.13	+1.12
	13.9	-0.5	+1.16	+1.07
	27.8	-1.0	+0.87	+0.62
	41.7	-1.5	+0.56	+0.45
	ECe			
Wheat	1.1	-0.04	+1.01	+0.87
	8.3	-0.3	+0.92	+0.74
	16.7	-0.6	+0.67	+0.55
	25.0	-0.9	+0.33	+0.08

Table 5. Equations of linear regression lines relating leaf total water potential (${}^{L}\psi_t$) to relative yield (Y) where $Y = a + b\,{}^{L}\psi_t$.

Relative humidity	Intercept	Slope	Correlation coefficient
%	a	b	
	BARLEY		
90	1.12	0.42	.98
45	1.24	0.44	.99
	WHEAT		
90	1.27	0.58	.96
45	1.19	0.52	.97

FIGURE LEGENDS

Figure 1.--The influence of relative humidity on the salt tolerance of barley, wheat, and sweet corn based on commercial yield. The dashed line is the concensus salt tolerance of each crop from Maas and Hoffman (1977).

Figure 2.--The influence of relative humidity (RH) and salinity (${}^{S}\psi_{o}$) on leaf total water (${}^{L}\psi_{t}$) and osmotic (${}^{L}\psi_{o}$) potentials for barley and wheat.

Figure 3.--The effect of leaf total water potential (${}^{L}\psi_{t}$) on the yield of barley and wheat.

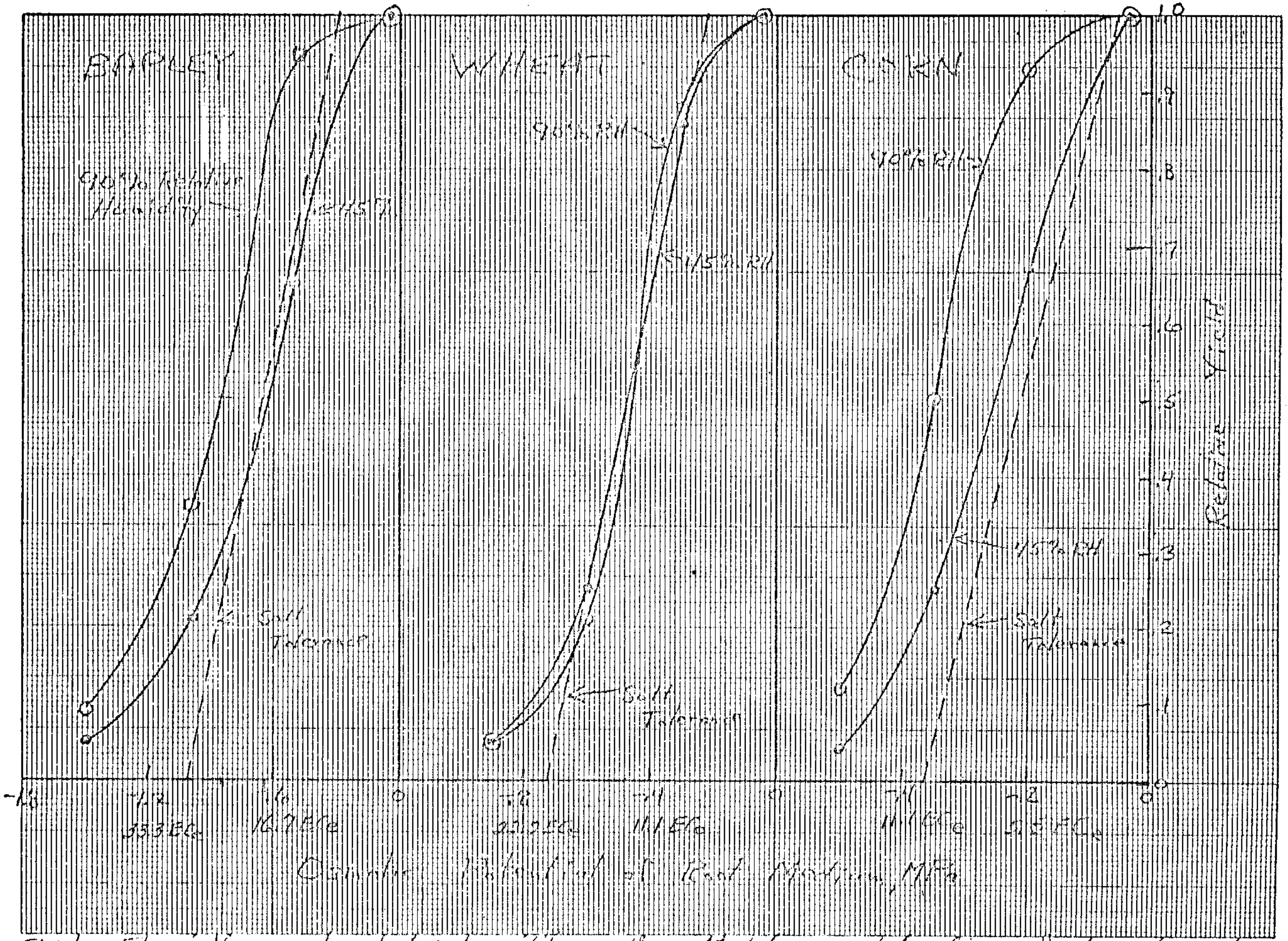

Fig. 1. The influence of relative humidity on the salt tolerance of barley, wheat, and sweet

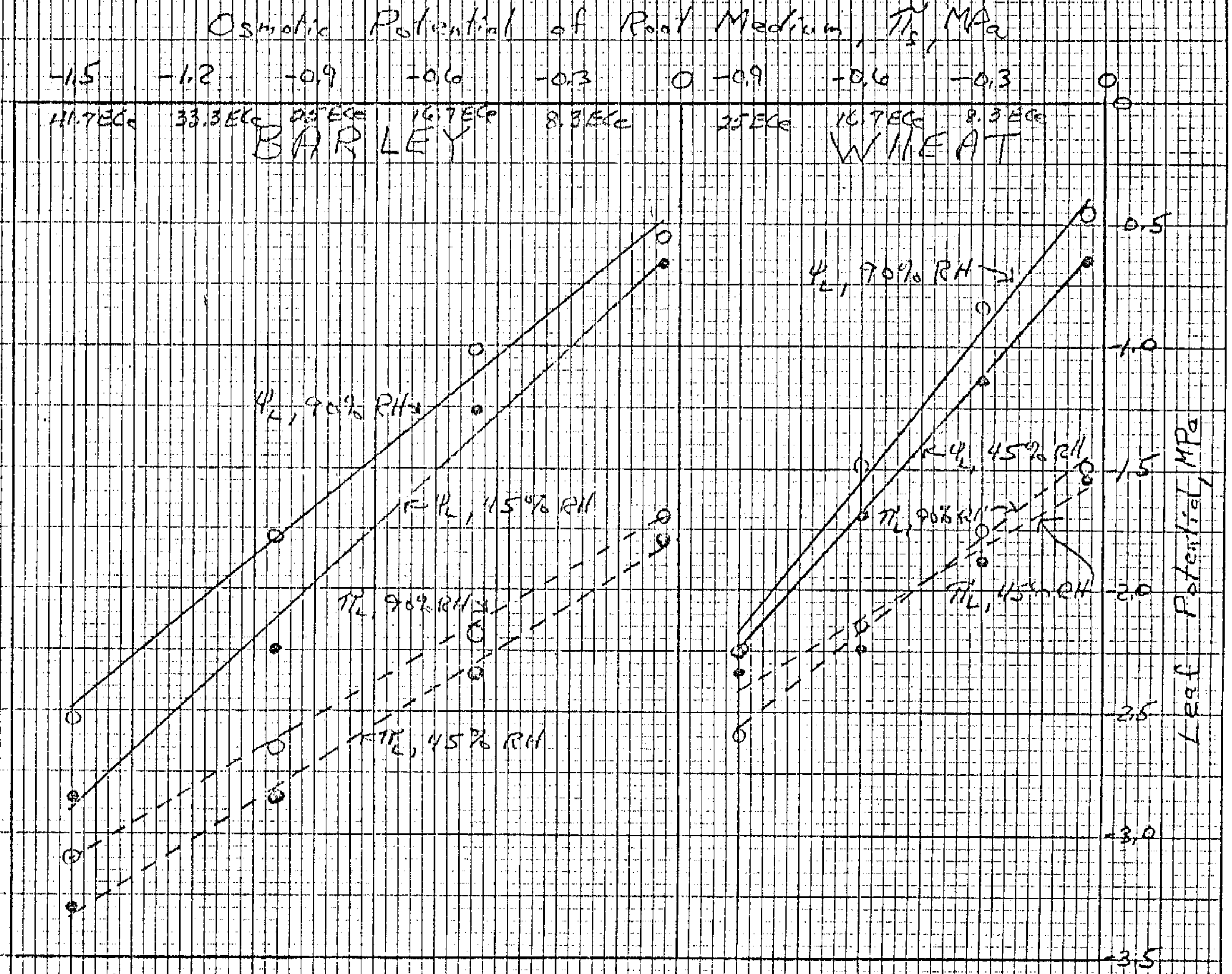

Fig. 2. The influence of relative humidity (RH) and salinity (π_s) on leaf water (ψ_L) and osmotic (π_L) potentials for barley and wheat.

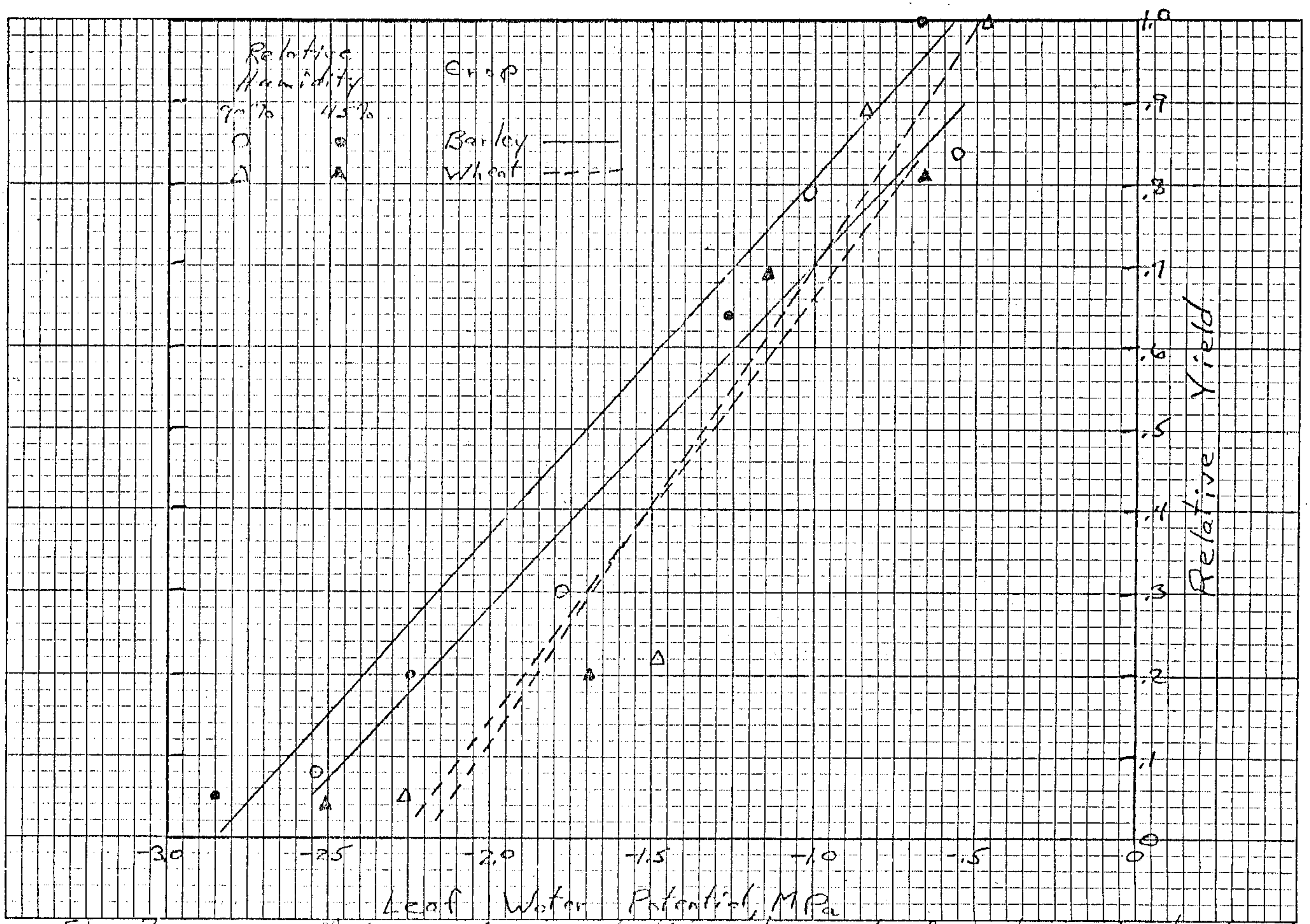

Fig. 3. The effect of leaf water potential on the yield of barley and wheat.