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Relationships between Boron Toxicity and Resistance to Two Types of Crown Blight and to Powdery Mildew in Muskmelon

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In greenhouse experiments at Davis, and field experiments at Five Points, California, Western muskmelon varieties and breeding lines were subjected to excess boron in various amounts. External symptoms were noted, and leaf content (dry-weight basis) of boron was determined. Possible relationships were sought between varietal sensitivity to boron and resistance to powdery mildew and to crown blight in Imperial Valley and at Five Points as determined in earlier experiments.

Varieties and breeding lines did not differ in ability to absorb and accumulate boron; none was able to limit the amount absorbed. Some breeding lines, however, were more tolerant, others less so, than standard varieties.

Selection for resistance to crown blight in Imperial Valley and to powdery mildew did not influence boron response in the greenhouse tests nor resistance to crown blight in the field tests.

Crown blight severity at Five Points was closely correlated with an unknown environmental factor that produced intercalary necrotic flecks (freckles) in leaves. Large phenotypic effects of this factor masked boron-toxicity effects, and prevented their measurement.

Long-established commercial varieties, such as 'PMR 45' and 'Honeydew,' are surprisingly tolerant, in the field, to high boron concentration in their leaves and in the soil, and to factors that cause freckles in some muskmelons. Such tolerance may explain, in part, their comparatively wide range of adaptation.

The data suggest that simultaneous or alternate selection in different environments would be more effective than selection in a single environment, in breeding programs designed to produce a widely adapted commercial variety.

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INTRODUCTION

Muskmelon breeding lines resistant to powdery mildew race 2, which were derived from the three-way cross, $P_3 \times$ PMR 45 × PMR 450, performed very well in early spring plantings in Imperial Valley and in midsummer plantings at Davis, California. Some of them, however, suffered crown blight (loss of crown leaves) associated with a necrotic leaf spot, termed "freckles," during midsummer at Five Points, California (figs. 1 and 2). The well water used for irrigation for several years at Five Points was known to contain considerable boron (1.4 ppm). It therefore seemed desirable to determine whether the foliage loss resulted from greater sensitivity to boron or greater accumulation of it in the plant tissues. The breeding lines would be more sensitive to high boron if either resistance to powdery mildew or adaptation to Imperial Valley conditions was linked, genetically or physiologically, with boron absorption or sensitivity.

Scant information is available on boron toxicity to muskmelons, in the literature. From extensive analyses of field-grown plants, Eaton, McCallum, and Mayhugh (1941) reported that boron accumulated in leaves of several crop plants; very little was removed to bark, roots, or fruits. Neither they nor Purvis and Hanna (1938) studied muskmelon, but they reported other cucurbits (squash and cucumber) to be more sensitive to excess boron than were beet, cabbage, carrot, lettuce, turnip, and other tolerant crops. Similarly, Wilcox (1960) failed to include muskmelon in his lists of boron-tolerant and boron-sensitive crops.

Lingle and Carolus (1958) reported that muskmelons grown in boron-treated soils accumulated more boron in their leaves than did any of 13 other vegetable crops. Muskmelon absorption responses to boron applications resembled those of known boron-sensitive crops, such as bean, and contrasted sharply with those of boron-tolerant crops, such as cabbage and carrot. These workers also found that the western 'PMR 45' cantaloup cultivar accumulated more boron than did the eastern 'Honey Rock' cultivar, and suggested that plant breeders might affect boron responses by selecting among plants grown in certain soils. Lingle and Carolus (1958) did not report tolerance limits, but they have stated (personal communication) that boron concentrations exceeding 500 ppm, such as those observed in leaves of muskmelons grown at Five Points, would almost certainly be toxic.

Controlled trials were conducted in pot cultures at Davis, and field trials

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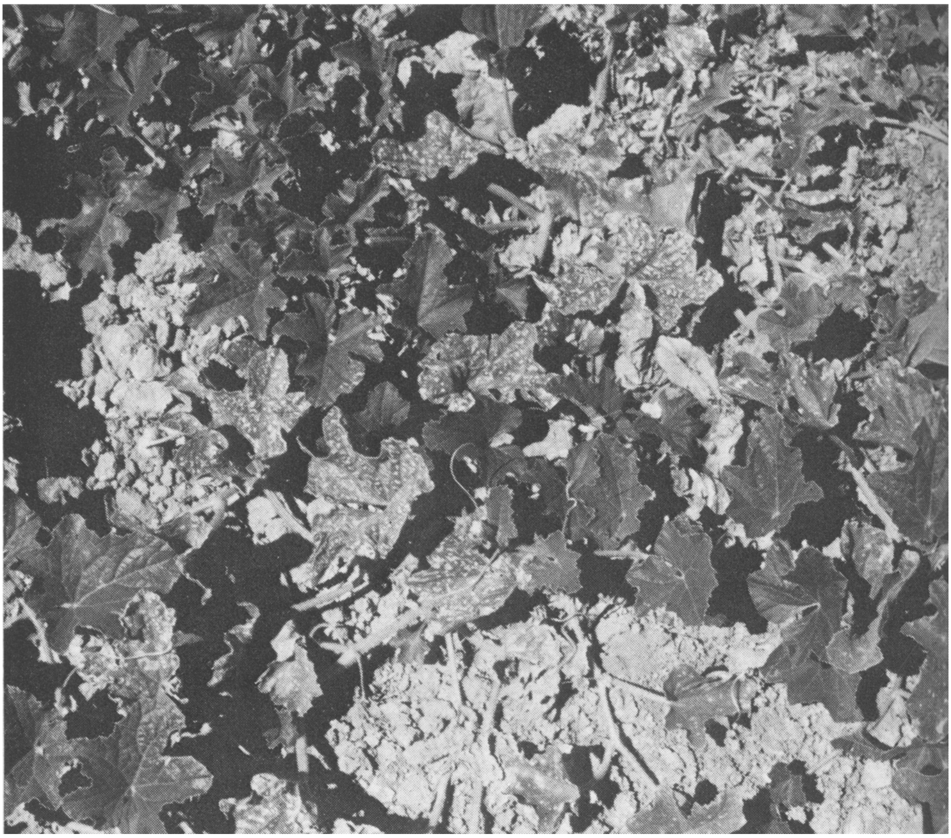

Fig. 1. Freckle and necrotic spot in leaves of crown-blighted muskmelon 'PMR 26.' Numerous spots on older leaves have turned brown. (Five Points, August, 1962.)

were conducted at Five Points. Information on toxic ranges, acquired incidentally in the study, are reported, together with the responses of selected varieties to high boron concentrations in culture media in the greenhouse and in the field. A muskmelon crown blight syndrome, "freckles," is described.

GREENHOUSE TESTS AT DAVIS

Muskmelon breeding lines and varieties susceptible or resistant to powdery mildew race 2, and susceptible or resistant to crown blight in Imperial Valley or at Five Points, were tested for tolerance to boron during 1963 and 1964.

Seeds were germinated in washed sand without nutrients. Seedlings were transplanted to 2-gallon stone jars, and were grown in the greenhouse in washed, fine, white sand, four to six plants in each jar. The cultures were watered daily with Hoagland and Arnon's (1938) nutrient solution (which contained 0.5 ppm boron from the A-Z mixture of minor elements) to which excess boron, as boric acid (H_3BO_3), had been added in various amounts to give concentrations of 1.5 to 10 ppm. After each watering, the excess solution was drained into a separate reservoir for each boron concentration. New solutions were prepared weekly.

Fig. 2. Freckle and necrotic spot in leaves of crown-blighted muskmelon 'PMR 26.' Severely affected leaves become brown and dry from the plant base out along the stems. (Five Points, August, 1962.)

The plants were observed for evidence of boron effects, and scored for severity of leaf necrosis. Samples, including all mature leaves from a plant, were harvested at 33 and 34 days in preliminary experiments in 1963, and at 54 and 74 days in 1964. The samples were oven-dried, and analyzed for boron concentration by James Perdue, in the laboratory of the Department of Vegetable Crops. Boron concentrations in dry leaf tissue are expressed as ppm.

Results

Boron injury. Muskmelons supplied with excess boron developed boron-toxicity symptoms like those described for other plants by Eaton, McCallum, and Mayhugh (1941) and Wilcox (1960). Incipient necrotic spots occurred first at hydathodes (fig. 3), then enlarged along the margin to produce "burning." The adjacent blade tissues were often yellowed. A few large, necrotic spots with broad, diffuse yellow halos occurred irregularly in the leaf blades of plants in media with great excesses of boron. These symptoms contrasted sharply with the necrotic spotting observed in crown-blighted plants in the field at Five Points (figs. 1 and 2).

Symptom-severity ratings and boron-concentration determinations (tables 1, 2, and 3) indicated that boron concen-

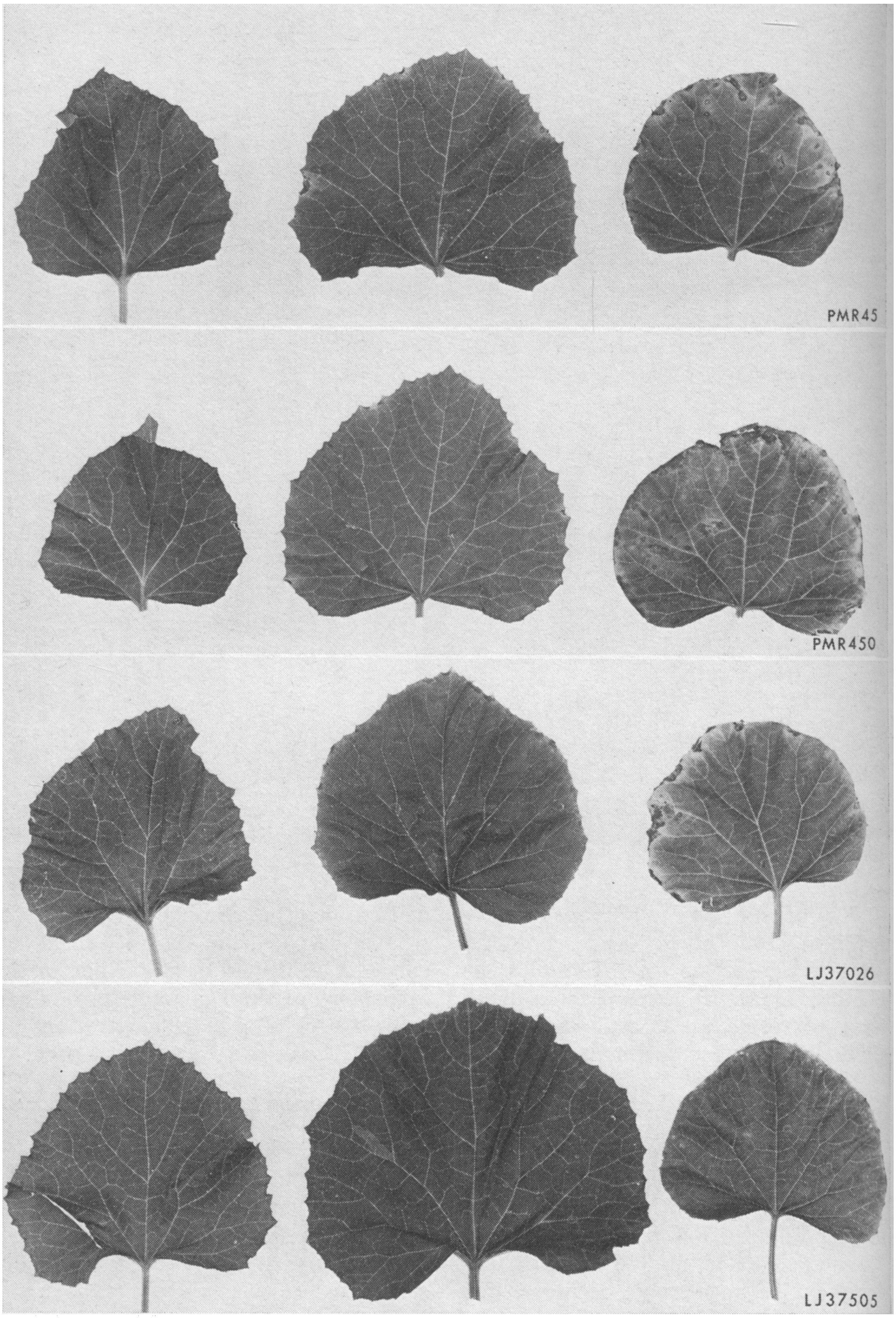

Fig. 3. Leaves of four muskmelon varieties grown in sand culture. Plants received nutrient solution with added boron, as boric acid, for 54 days at the following rates, left to right: 0 (control); 2 ppm; 10 ppm.

TABLE 1

BORON INJURY TO MUSKMELONS, AND BORON CONTENT OF LEAVES, FOLLOWING APPLICATION OF BORON AT VARIOUS CONCENTRATIONS*

(Greenhouse test, Davis, 1963; 34 days; two replications)

Variety	Resistance† to:			Amount of added boron							
				0 ppm		1.5 ppm		3.5 ppm		10 ppm	
	Powdery mildew race 2	Crown blight Imp. Valley	Crown blight Five Points	Injury†	Leaf conc.	Injury†	Leaf conc.	Injury†	Leaf conc.	Injury†	Leaf conc.
					ppm		*ppm*		*ppm*		*ppm*
Honey Dew	1	3	4	5	95	5	151	4	406	3	564
PMR 45	2	2	4	5	97	5	174	4	299	3	762
PMR 26‡	3	4	1	5	104	4	141	4	362	2	737
Campo	4	4	1	5	106	4	140	3	412	2	609
PMR 73	4	4	..	5	78	5	145	3	443	3	746
PMR 75	4	4	..	5	107	4	162	4	446	3	837
PMR 110	4	4	..	5	77	4	168	3	426	2	750
PMR 111	4	4	..	5	136	4	158	4	419	2	726
LJ 43721	4	4	4§	5	103	4	169	4	379	2	805
LJ 43780	4	4	..	5	95	4	165	4	324	3	662
LJ 43787	4	4	4	5	103	4	171	2	355	2	777
Average				5.0	100.1	4.3	158.5	3.5	388.3	2.5	725.0

* Resistance to powdery mildew and crown blight included for comparison.
† Resistance and injury ratings are on a scale as follows: 5 = none; 4 = slight; 3 = moderate; 2 = severe; 1 = very severe.
‡ PMR 26 and following entries are advanced breeding lines for the trihybrid, P_3 × PMR 45 × PMR 450.
§ Response of sib progeny.

trations averaging less than 200 ppm for all leaves on the plant caused trace marginal necrosis in some greenhouse-grown plants (fig. 2). Concentrations of 300 to 500 ppm caused trace to severe symptoms in different varieties; concentrations exceeding 500 ppm caused moderate to severe necrosis in most varieties (tables 1 and 3). The larger size of plants supplied with 1.5 and 2.0 ppm supplementary boron, as compared with those with no supplementary boron (fig. 3), suggested a possible boron deficiency in the base medium although leaves from plants grown in it eventually accumulated 95 to 175 ppm boron (tables 1 and 3). Some trace symptoms of marginal necrosis on such luxuriant plants could have been caused by exudation and resorption of salts, as described by Ivanoff (1961). However, definite symptoms of excess boron on the plants grown in media with 2 ppm supplementary boron (fig. 3) place the muskmelon in Wilcox's (1960) semi-tolerant group.

Powdery mildew resistance. Boron sensitivity was not related to powdery mildew resistance. The greenhouse plantings, with two and three replications of six seedlings each, indicated that many but not all of the resistant derivatives of the three-way cross were more sensitive to excess boron than were the susceptible 'Honey Dew' and 'PMR 45' cultivars (tables 1, 2, and 3). In contrast, inbred LJ37505 and its derivative 37802 were more tolerant than were the controls (table 3). Both inbreds were nearly free of necrosis with 10 ppm boron in the nutrient medium (fig. 3).

The responses of the inbreds demonstrated that boron sensitivity is not a pleiotropic effect of the gene, Pm^2, for powdery mildew race 2 resistance. The frequency of tolerant derivatives indicated that Pm^2 is not closely linked to genes for boron sensitivity. In fact, the resistant parent, P_3, appeared as tolerant to boron as the susceptible parents (table 2). Therefore, selection for resistance could not have caused the ap-

TABLE 2

BORON INJURY TO MUSKMELONS, AND BORON CONTENT OF LEAVES, FOLLOWING APPLICATION OF BORON AT VARIOUS CONCENTRATIONS*
(Greenhouse tests, Davis, 1963; 33 days; three replications)

Variety	Resistance† to:			Amount of added boron					
	Powdery mildew race 2	Crown blight Imp. Valley	Crown blight Five Points	0.5 ppm		3.0 ppm		5.0 ppm	
				Injury†	Leaf conc.	Injury†	Leaf conc.	Injury†	Leaf conc.
					ppm		*ppm*		*ppm*
PMR 45	2	2	4	5	77	4	317	4	447
PMR 450	2	3	4	5	81	5	280	4	411
SR 1463	1	3	4	5	68	4	294	4	388
P_3 36486	4	3	1	5	85	5	149‡	4	358
PMR 6	3	3	2	5	57	4	251	3	329
Average				5.0	73.6	4.4	258.2	3.8	386.6

* Resistance to powdery mildew and crown blight included for comparison.
† Resistance and injury ratings are on a scale as follows: 5 = none; 4 = slight; 3 = moderate; 2 = severe; 1 = very severe.
‡ Quantity based on a single determination.

parent prevalence of boron sensitivity in resistant breeding lines.

Crown blight—Imperial Valley selections. Boron sensitivity was not always associated with resistance to crown blight in Imperial Valley. As compared with the controls, many of the inbreds selected for resistance to crown blight in Imperial Valley were more sensitive to boron injury (table 1); some showed the same reaction; and the inbred LJ37505 and its offspring, 37802, were more tolerant (table 3).

The work of Lorenz (1941), Jones and Scarseth (1944), Reeve and Shive (1944), and others (reviewed by Berger, 1949), indicated a close relationship between calcium and boron nutrition. Those studies and the report of Lingle and Carolus (1958) on work in Michigan suggested that selection for adaptation to the high-calcium, alkaline soils in Imperial Valley could, perhaps, influence absorption of boron or sensitivity to it. The variation in sensitivity and tolerance observed among inbreds resistant to crown blight in Imperial Valley failed to support that hypothesis.

Crown blight—Five Points selections. Boron sensitivity appeared to be partially related to crown blight response at Five Points. Muskmelon breeding line PMR 26 and the cultivar, 'Campo,' which suffered severe crown blight at Five Points, were more sensitive to boron injury than were the controls (table 1). However, their P_3 parent, which was also severely crown blighted at Five Points, was as tolerant to boron as were 'PMR 45' and 'PMR 450' (table 2). The boron-tolerant inbreds, LJ37505 and 37802, were found to be tolerant to crown blight at Five Points as well as in the Imperial Valley (fig. 3 and table 3). Despite the aberrant behavior of P_3, the data and observations did suggest a partial correlation between boron tolerance in sand culture and crown blight resistance at Five Points.

Leaf effects. Boron concetration in muskmelon leaves varied with its concentration in the medium and with time. The basic nutrient solution was believed to contain sufficient boron for normal plant growth. The leaves from plants grown in that medium averaged 100 ppm boron (table 1), well within the accepted "normal" range.

The first leaves of plants grown in the

TABLE 3

BORON INJURY TO MUSKMELONS, AND BORON CONTENT OF LEAVES, FOLLOWING APPLICATION OF BORON AT VARIOUS CONCENTRATIONS*

(Greenhouse tests, Davis, 1964; 54 days; two and three replications)

Variety	Resistance† to:			Amount of added boron					
	Powdery mildew race 2	Crown blight Imp. Valley	Crown blight Five Points	0 ppm		2 ppm		10 ppm	
				Injury†	Leaf conc.	Injury†	Leaf conc.	Injury†	Leaf conc.
					ppm		*ppm*		*ppm*
PMR 45	2	2	4	5	95	4	225	3	855
PMR 450	2	3	4	5	175	4	295	3	1,080
P_3 37026	4	3	2	5	115	4	233	3	763
F_1 21129‡	3	3	3	5	140	4	295	2	945
B_1F_3 37505	4	4	4	5	120	5	223	4	623
B_2F_3 41283	4	4	3	5	115	4	215	2	805
Average 54 days				5.0	126.7	4.2	247.7	2.8	845.2
B_1F_4 37802	4	4	4	5	153§	4	337§	4	940§
B_2F_5 42405	4	4	3	5		4	359§	2	933§
Average 74 days				5.0	153.0	4.0	348.0	3.0	936.5

* Resistance to powdery mildew and crown blight included for comparison.

† Resistance and injury ratings are on a scale as follows: 5 = none; 4 = slight; 3 = moderate; 2 = severe; 1 = very severe.

‡ The F_1 hybrid 21129 was derived from the cross $P_3 \times$ PMR 45; subsequent entries from the three-way cross, $P_3 \times$ PMR 45 $\times$ PMR 450.

§ Analyses on 74-day-old leaves.

basic medium, however, were less luxuriant than those of plants grown with 1.5 and 2.0 ppm boron supplements (fig. 3). It seems likely that the plants started in washed sand initially had inadequate boron. The check plants absorbed boron too slowly to prevent dwarfing of the older leaves. In contrast, plants with small boron supplements absorbed boron fast enough to produce luxuriant first leaves, but continued applications at those levels caused injury.

The different treatments produced great differences in boron concentrations in the leaves. Supplements of 1.5, 3.5, and 10.0 ppm boron increased the average boron concentration from 100 ppm to 159, 388, and 725 ppm, respectively, with 34 days' exposure (table 1). Plants exposed to boron at 2 ppm showed a concentration of 348 ppm at 74 days and of 247.7 ppm at 54 days (table 3). These figures were close to the 258.2 ppm in plants exposed to 3.5 ppm boron for 33 days (table 2). It is obvious that concentration of boron in muskmelon leaves depends mostly on its concentration in the nutrient medium and length of the exposure period. It seems reasonable to expect, therefore, that (1) older leaves would contain more boron and show greater injury than younger leaves on the same plant, and (2) older plants would contain more boron and show greater injury than young plants in the same environment.

Varietal differences. Varieties did not differ significantly from one another in ability to absorb and accumulate boron. With only two replications, the relatively small differences in boron concentration in the different varieties were not significant (table 1). Variation in severity of injury symptoms was not associated with comparable variation in boron concentration (table 1). The highly tolerant LJ37505 accumulated less boron than did its less tolerant parent varieties, but not significantly less (table 3). Its highly tolerant derivative, LJ37802, accumulated quantities of boron comparable with those in the similarly treated, very sensitive LJ42405. The results indicate that more critical tests would be required to demonstrate relatively small varietal differences such as those reported by Lingle and Carolus (1958). The data indicated that a mechanism which limits the absorption and accumulation of boron in certain boron-tolerant crops is lacking in western varieties of cantaloup.

FIELD TRIALS AT FIVE POINTS AND AT DAVIS

Several advanced- and early-generation inbred progenies from the three-way cross, $P_3 \times$ PMR 45 $\times$ PMR 450, were compared with their parent varieties in the field trials at Five Points and at Davis during the period 1963 to 1966. Randomized complete blocks were used in all years except 1965, when Latin squares were used to increase accuracy. Similar information was secured from all field experiments. For brevity, only the 1965 experiment is reported in detail; information from other trials is included when relevant.

1965 Experiments

The powdery mildew race 2-resistant parent P_3, the cultivar 'PMR 45,' their F_1 hybrid, LJ22625, and four trihybrid derivatives that had shown differential crown blight responses in preliminary trials, were planted in 7 × 7 Latin squares in three blocks. One was at Davis, where boron was not a problem; two were at Five Points, one irrigated with high-boron well water (1.4 ppm) and one irrigated with moderate-boron well water (0.6 ppm). Subsequent studies demonstrated that residual boron in the soil at Five Points negated the difference in applied water, so that both blocks at Five Points were actually high-boron blocks.

Seeds were planted in greenhouse flats on April 1, 1965. Seedlings were transplanted, six per plot, at standard spacing, in 7 × 7 Latin squares on April 29, and grown with standard cultural treatment (Davis *et al.*, 1965).

Plot data on plant responses were recorded at maturity on an arbitrary 1-to-5 scale, the numbers increasing with crop quality. Relative plant size, earliness, and resistance to crown blight, freckles, and chlorosis were recorded at peak harvest at Five Points on July 29. Leaf samples were secured the same day for boron determinations. Plant data were not recorded at Davis because all plots there were vigorous and free of leaf defects, and were estimated to rate 4 and 5 on the five-class scale for all plant-condition characters. Leaf samples were harvested at peak maturity for boron analyses.

Results

Plant injury and responses. P_3 and some other breeding lines resistant to sector crown blight in Imperial Valley were severely crown-blighted at Five Points. More than half of the mature leaves were dead at midharvest, and the living leaves exhibited abundant necrotic flecks (fig. 1). Recently-affected leaves contained small, circular, brown, intercalary, interveinal spots with narrow, sharply-defined, water-soaked halos (fig. 2). The number rather than the size of the spots increased with increasing severity and with time. The centers of the spots turned whitish with aging, and irregular portions of the leaf supporting numerous spots turned brown and dry (fig. 1). Severely affected leaves eventually became brown and dry from the base of the plant outward along the

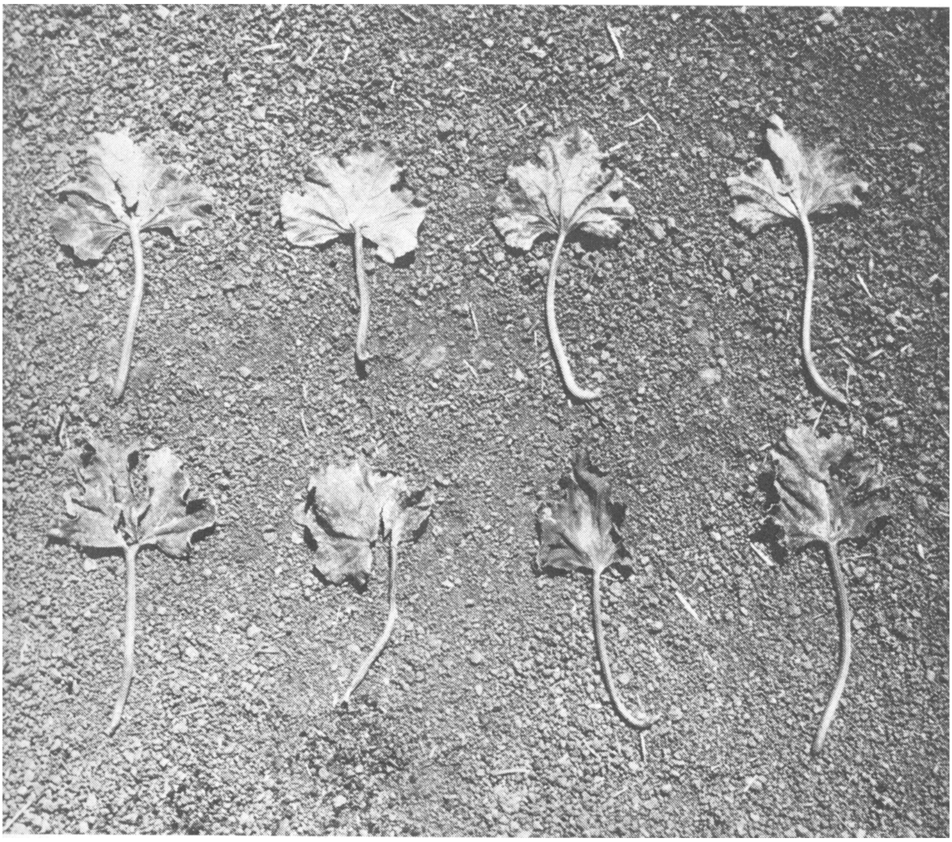

Fig. 4. Crown blight in leaves of muskmelon 'PMR 450,' grown in a commercial field. Sections of brown, dry tissue appeared on veins in green leaves. Petioles were partly brown. (Imperial Valley, 1951.)

stem (fig. 1). The leaf symptom is called freckles; the entire syndrome is termed crown blight, for convenience.

The freckles symptom apparently was not associated with any pathogen or with insect damage. Repeated attempts by University pathologists to isolate viruses, bacteria, and fungi from leaves with similar symptoms, collected at various locations during several years, failed to yield a causal agent. Accordingly, the freckles syndrome is attributed to the effects of an unknown factor, probably physiological in nature.

The crown blight syndrome at Five Points differed sharply from the boron toxicity observed in the greenhouse. It differed, also, from the crown blight syndrome commonly observed in Imperial Valley. At that location, recently affected leaves exhibited pie-shaped or half-leaf sectors of brown and dry tissue centered on veins in otherwise green leaves (fig. 4). Brown discoloration occurred, also, in one or both sides of the petiole. Symptoms were most severe in leaves at the base of the plant, and affected alternate leaves outward along the stem (fig. 5). With aging, entire leaves turned brown and dry, and eventually, the alternating green leaves also succumbed. Finally the whole plant was affected (fig. 6).

For convenience, the Imperial Valley crown blight syndrome associated with necrotic leaf sectors centered on veins is termed "sector crown blight." Its severity is greatly increased by root-rot

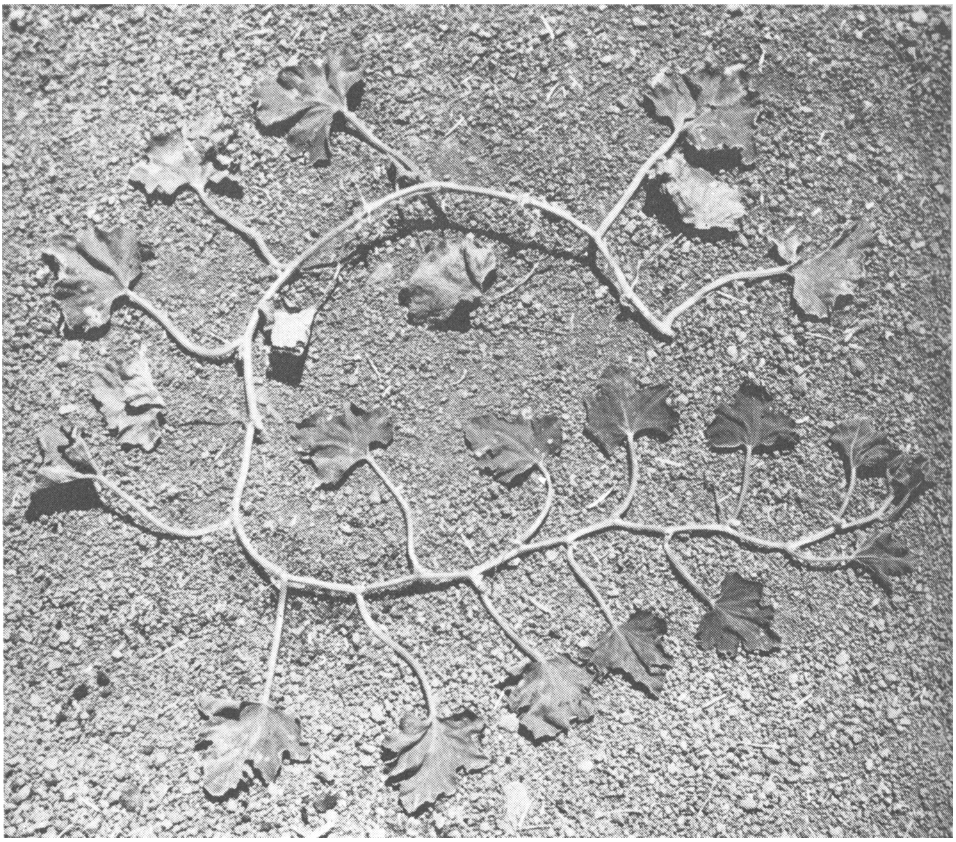

Fig. 5. Crown blight in shoot of muskmelon 'PMR 450,' grown in a commercial field. Alternate leaves along stem showed symptoms, others were green. (Imperial Valley, 1951.)

fungi, by viruses, especially in plants harboring both sorts of pathogens, and by various nonparasitic factors (Kendrick *et al.*, 1957; Wedding *et al.*, 1957; Bohn, 1958). Failure of any single component to cause the leaf-sector and alternate leaf-kill syndrome suggests that crown blight in Imperial Valley is caused either by a complex or by a still undetermined single factor in the environment.

The contrast in symptom patterns of the two types of crown blight in Imperial Valley and at Five Points indicates that the two diseases have different causes. The high frequency of crown blight susceptibility at Five Points among lines selected for crown blight resistance in Imperial Valley suggested that susceptibility at one location might be associated with resistance at the other. The depressant effect of high calcium on boron uptake demonstrated in other plants (Jones and Scarseth, 1944; Reeve and Shive, 1944), together with known high calcium content in Imperial Valley soils and high boron content in soils at the Five Points station, suggests that selection for crown blight resistance in Imperial Valley might increase ability of the plants to absorb boron and other nutrients. Such ability might result in the absorption of excessive amounts of boron by these breeding lines and varieties at Five Points.

In contrast with crown-blighted P_3 at Five Points, 'PMR 45' showed little crown blight injury; most of the plants

Fig. 6. Crown blight in plant of muskmelon 'PMR 450,' grown in a commercial field. Eventually entire leaves turned brown and dry, including the previously unaffected, alternate green leaves. (Imperial Valley, 1951.)

had very few (usually two to four) dead leaves at the crown; the older leaves on some plants contained a few freckle spots but these apparently caused little injury. A few, sporadic plants of 'PMR 45,' as well as some breeding lines, were severely damaged by *Verticillium* wilt, and an occasional group of plants was moderately chlorotic, but the 'PMR 45' plots viewed as units looked vigorous and healthy. 'PMR 45' was very resistant to freckles and crown blight at Five Points although it was only moderately tolerant of boron in the greenhouse, and was susceptible to crown blight in Imperial Valley.

The inbred progenies varied in resistance to crown blight (based on death of oldest leaves) and to freckles; the two characters appeared to be closely but not completely associated with one another. Neither character could be classified into two or three discrete classes, either within or among progenies. Either they were not simply inherited, or interfering environmental effects masked the phenotypes so that they could not be recognized with accuracy.

Severity of crown blight in the field appeared to be partly related to boron resistance as indicated by greenhouse tests, but the relationship was not strong. For example, 'Campo' and LJ-44456 were extremely sensitive to boron in the greenhouse, and to freckles and

TABLE 4

MEAN PERFORMANCE FOR BORON TOLERANCE, BASED ON VARIOUS PLANT SYMPTOMS AND CHARACTERS, AND BORON CONTENT OF LEAVES, IN FIELD-GROWN MUSKMELONS AT FIVE POINTS, COMPARED WITH GREENHOUSE TESTS AT DAVIS AND CROWN BLIGHT TESTS IN IMPERIAL VALLEY

(14 replications; 1965)

Variety	Boron tolerance* (Davis)	Crown blight resistance* (Imp. Valley)	Mean performance†					Boron content of leaves
			Crown blight	Freckles	Chlorosis	Plant size	Earliness	
								ppm
PMR 45	3	2	3.64a	3.93a	2.86a	3.57a	2.93 c	939a
P_3	3	3	2.43 cd	1.79 d	1.43 d	1.79 c	4.21a	988a
Midparent	3	2.5	3.04 b	2.86 c	2.15 bc	2.68 b	3.57 b	964a
F_1(P_3 × PMR 45)	2	..	3.07 b	3.36 b	1.79 cd	3.57a	3.64 b	874a
LJ 42405‡	2	4	2.64 cd	2.43 c	2.43 b	3.79a	3.57 b	942a
Campo	1	4	2.36 d	1.71 d	3.07a	3.50a	3.07 bc	878a
LJ 44456	1	4	2.86 bc	1.86 d	2.86a	3.57a	3.29 bc	852a
Jacumba	2	4	3.50a	2.50 c	3.21a	3.79a	3.00 c	855a

* Tolerance and resistance ratings are on a scale as follows: 5 = none; 4 = slight; 3 = moderate; 2 = severe; 1 = very severe.
† Means not having a letter in common differ at the 0.05 level.
‡ LJ 42405 and subsequent entries were derived from the three-way cross, P_3 × PMR 45 × PMR 450.

crown blight at Five Points; but boron-sensitive 'Jacumba,' LJ42405, and the F_1 (P_3 × 'PMR 45') varied in resistance to crown blight and freckles (table 4). P_3 and 'PMR 45' were equally tolerant to excess boron in the greenhouse, but they differed greatly in resistance to freckles and crown blight (table 4). Finally, LJ37505 was very tolerant to boron in the greenhouse (fig. 2), and also to freckles and crown blight (unreported data). Thus it appears likely that part of the crown blight syndrome at Five Points can be attributed to boron sensitivity, but that the boron effect is masked by some other environmental factor.

The association of freckles and crown blight susceptibility at Five Points with powdery mildew resistance was apparently fortuitous. 'Jacumba' (table 4) and a few other powdery mildew-resistant derivatives of the P_3 × PMR 45 cross were resistant to both defects.

Similarly, the association of freckles and crown blight susceptibility at Five Points with crown blight resistance in Imperial Valley also appeared fortuitous as evidenced by the same varieties. The existence of a breeding line, LJ-37505, that combines tolerance of boron and resistance to crown blight and freckles at Five Points, and to crown blight in Imperial Valley, demonstrates that these characters are not mutually exclusive.

Covariance analyses of the 1965 data at Five Points, with calculations based on 14 randomized blocks, demonstrated that crown blight resistance was significantly correlated with freckles resistance, but not with any other character in inter- and intravariety calculations (table 5). It was significantly correlated with large plant size within varieties. Freckles resistance was very significantly correlated with large plant size, late maturity, and crown blight resistance in intravariety calculations, but only with crown blight resistance between varieties.

The correlation data indicate that crown blight resistance was closely associated with freckles resistance. This correlation, the lack of full agreement between field response and response to boron in the greenhouse, and the dissimilarity between the freckles symptom and boron-induced necrosis in controlled tests all indicate that some factor other than boron, in the environment at Five Points, induced the freckles syndrome and contributed greatly to crown blight there. The relatively large effect of these factors masked those caused by excess boron, *per se,* and prevented their measurement.

The undetermined environmental factor or factors causing the freckles type of crown blight at Five Points apparently is absent from the environments at Davis and in Imperial Valley, where the freckles syndrome has not been observed.

Leaf effects. Boron concentration in leaves of field-grown muskmelons varied with concentration of boron in the soil and with time. Leaf samples collected during midharvest at Davis in 1965 contained 60 to 230 ppm and averaged 145 ppm of boron, based on dry weight of leaf tissue. Leaf samples collected during midharvest at Five Points the same year contained 410 to 1,040 ppm, and averaged 582 and 710 ppm in the two Latin squares. The difference between blocks at Five Points was significant ($F_{blocks} = 24.21^{**}$). That difference and the larger difference between those averages and that at Davis were attributed to differences in available boron in the soil.

The effect of time on boron accumulation was tested in randomized complete blocks at Five Points in 1966. Leaves harvested June 22, prior to fruit setting, on July 13, when the plants supported young fruits, and on August 3 (midharvest), averaged 218, 377, and 544 ppm boron, respectively. The difference was very significant ($F_{dates} = 223.36^{**}$).

TABLE 5

INTER- AND INTRAVARIETAL CORRELATIONS BETWEEN VARIOUS PLANT SYMPTOMS AND CHARACTERS, IN SEVEN VARIETIES OF MUSKMELON

(Five Points, 1965; 14 replications)

Variables		Significance	
		Between varieties (5 *df*)	Within varieties (91 *df*)
Crown blight resistance	Freckles resistance	+.786*	+.331**
	Chlorosis resistance	+.374	+.180
	Boron content	−.263	+.107
	Plant size	+.466	+.469**
	Earliness	−.573	−.191
Freckles resistance	Chlorosis	−.003	+.188
	Boron content	+.058	+.156
	Plant size	+.370	+.339**
	Earliness	−.312	−.308**
Chlorosis resistance	Boron content	−.599	+.168
	Plant size	+.710	+.092
	Earliness	−.936**	−.181
Boron content	Plant size	−.679	+.095
	Earliness	+.594	+.128
Plant size	Earliness	−.773*	−.095

* Significant at the 0.05 level.
** Significant at the 0.01 level.

Varietal differences in amount of boron in the leaves were not significant in any of the field tests. The F value for variety-caused differences at Davis during 1965 was 0.97; at Five Points the same year, 1.18, and during 1966, 1.416.

Thus, the field data confirmed the greenhouse data: the accumulation of boron in muskmelon leaves was dependent on concentration of boron in the culture medium and on length of exposure time. The Western varieties and breeding lines studied in these experiments did not differ in ability to absorb and accumulate boron either in the presence of moderate boron at Davis or of excess boron at Five Points.

DISCUSSION

Muskmelons supplied with excess boron, either naturally or under partly controlled cultural conditions, absorb surprisingly large amounts of this toxic micronutrient element. Western varieties and breeding lines, while unable to limit the amount of boron, do differ in their sensitivity to it. Some breeding lines are more tolerant, others less so than standard varieties.

The field data confirmed the greenhouse data on absorption and accumulation of boron. The Western varieties and breeding lines of muskmelon included in these studies lacked the ability to limit absorption, transport, and accumulation of boron in the leaves. Accordingly, boron accumulation depended on its availability in the nutrient medium and on exposure time.

Tolerance of plants to excess boron in the field differed in degree from that in the greenhouse. 'PMR 45' and some other varieties and breeding lines that were only moderately tolerant in the greenhouse tolerated amazingly large amounts of boron in their leaves, in the field. This was in contrast to other boron-tolerant crops, which limit boron uptake. Tolerance to various adverse conditions, such as excess boron and factors causing freckles, may explain in part the comparatively wide range of adaptation of 'PMR 45' and 'Honey Dew.'

The freckles symptom associated with crown blight at Five Points differed from both marginal necrosis associated with excess boron in the greenhouse and the sector leaf blight associated with crown blight in Imperial Valley. The contrasting symptoms and different associations of resistance indicated that the three types of injury in different varieties are not causally related.

Crown blight susceptibility at Five Points was often but not always associated with resistance to powdery mildew and crown blight in Imperial Valley. A modest amount of screening yielded a line tolerant to excess boron in the greenhouse, resistant to powdery mildew, and resistant to crown blight both in Imperial Valley and at Five Points. It follows that the several characters are independently inherited. A variety with high fruit quality and combined resistance to the several plant defects could therefore be developed by appropriate breeding and selection techniques.

The data confirmed earlier observations that resistance to crown blight in one area does not necessarily indicate such resistance in another. For example, varieties selected for crown blight resistance in one of four very different environments, such as Brawley, California, Phoenix, Arizona, Weslaco, Texas, and Charleston, South Carolina, vary in resistance at each of the other locations, indicating different causes in different areas. The high performance of 'Campo' and some other breeding lines in Imperial Valley and at Davis, and their poor performance at Five Points, show that the performance of a muskmelon variety at one location cannot be predicted from its performance elsewhere.

The comparatively high performance of 'Jacumba' at all three locations in California (and also in Arizona) indicates that it has a wider range of adaptation than does 'Campo.'

Selection for crown blight resistance at one location does not necessarily result in susceptibility at the other, since some breeding lines were resistant at both Five Points and Imperial Valley. The data reported here, together with repeated observations on varieties and breeding lines grown in different areas, suggest that a widely adapted variety resistant to crown blight at many locations can best be secured by alternate or concurrent selection at several locations. The alternative appears to be local selection and subsequent local seed production of numerous ecological subvarieties, one for each area and season.

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