

Variety Climate Interactions of Sugar Beet Varieties in Simulated Climates¹

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The question is often asked, will a sugar beet variety that is superior in one climate be superior in all climates, or just in one climate and not in another? Ordinarily, this question is answered by growing a series of sugar beet varieties in test plots in several locations during the same year and in different years. If some variety is found to be outstanding the first year, the tests are continued until the relative superiority of a variety is definitely established.

In conducting variety tests, the varieties are actually tested for an entire array of factors that include not only climate, but also disease, pest, soil and management factors as well. In a sense the answer to the question about the effect of climate on a variety is not a definitive one, but is confounded by factors not directly related to climate. Confounding of climate and disease factors can be clearly shown for resistant and non-resistant varieties in diseased areas, where all resistant varieties do better than non-resistant varieties and where their superiority is to a large extent independent of climate.

The real effects of climate on resistant and non-resistant varieties can be studied only by having disease-free conditions. An ideal place for such a study is in a phytotron (8)³. Here the environment can be kept free of diseases and insects, and in addition, the kind of climate can be controlled at will, an obvious advantage over waiting for nature to present the right climatic conditions necessary for making the proper experimental comparisons.

Procedure

The present experiments were conducted in the phytotron of the Earhart Plant Research Laboratory, California Institute of Technology, Pasadena 4, California (8). Four sugar beet varieties, US 22/3, US 35/2, European Kleinwanzleben E and ZZ, were compared in four simulated climates, cold, cool, warm and hot. The simulated climates were provided for in green-

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³ Numbers in parentheses refer to literature cited.

house units that were illuminated by sunlight for natural day lengths of 9.9 to 13.1 hours. The greenhouse temperatures were kept at pre-set values from 8 AM to 4 PM and from 4 PM to 8 AM. These were for the "cold" climate, 17° C and 12° C; for the "cool" climate, 20° and 14° C; for the "warm" climate, 26° C and 20° C; and for the "hot" climate, 30° C and 22° C, respectively. The U.S. varieties 22/3 and 35/2 are resistant to curly top and the European varieties Klein E and Klein ZZ are non-resistant to curly top. Of these, the US 22/3 and the European Klein E are yield-type varieties and the US 35/2 and Klein ZZ varieties are sugar-type varieties, with the ZZ being an extreme sugar-type variety. The original selections for the US 22/3, US 35/2 and ZZ varieties were made to a large extent from the European Klein E, which in itself originated from many selections. Because of this common origin of genetic material it is of interest to compare the European Klein E with its "progeny" US 22/3, US 35/2 and ZZ as to performance in different simulated climates.

The seeds of the four sugar beet varieties were treated before planting with Phygon XI at the rate of 1% by weight. The pots were 4 gallons in capacity (25 cm in diameter and 30 cm deep), protected on the inside by a sanitary lacquer, and were provided with four small holes on the side at the bottom for drainage. The pots were filled with number 2 expanded vermiculite by adding successively small increments of the material to each pot in rotation. The vermiculite was moistened thoroughly with water and then settled firmly by jarring each pot several times on the floor. Four pots to a wheeled truck, 51 cm x 51 cm, were planted at random to the four sugar beet varieties, with one variety to a pot.

The seeds were planted on October 15, 1951, by placing 10 seedballs per pot in a circle 13.0 cm in diameter and forcing the seeds into the vermiculite to a depth of 2 cm. The seeds, and later the plants, were watered daily with Hoagland's culture solution (8); the excess solution drained off by gravity through the four drainage holes. During seed germination and early seedling development all trucks were kept in a greenhouse maintained at a temperature of 23° C from 8 AM to 4 PM and at 17° C from 4 PM to 8 AM. The seedlings, after 2 weeks, had developed to the early 2-leaf stage of growth and were then thinned to 1 seedling per seedball. On November 8, when the seedlings had progressed to the early 4-leaf stage they were thinned to 4 plants per pot. The following day the plants were moved to 4 simulated climates (Tables 1-6). In this move there

were 8 replications of each variety or a total of 8 trucks per climatic condition. The 8 trucks were randomized weekly within a climatic condition so as to minimize the variability due to greenhouse position. On November 23, 14 days after starting the differential climatic treatment, the plants were thinned to 2 plants per pot. The tops of the plants, which were removed by thinning, were dried at 80° C and then weighed. Old leaves, more than 50% necrotic, were removed and collected weekly beginning from January 7 until harvest on April 17, 1952.

The tops of the plants at harvest were separated from the roots just below the oldest living leaf. The crown material between the oldest living leaf and the first leaf scar was relatively small in amount and was included with the root for root weight and for sucrose analysis. The tops were separated into petioles and blades of "recently matured" leaves, blades of all remaining leaves and residue. Fresh weights were immediately recorded after the plants were harvested and dry weights were taken after the plant parts were dried in a forced draft oven at 80° C. All harvest weights were recorded on a pot basis. The beet roots were washed and wiped free of excess moisture, weighed and analyzed for sucrose by the hot water lead acetate extraction technique (1).

Differences between varieties and simulated climates were tested for significance by the method of analysis of variance. Pooled error variances were found to be uniform by Bartlett's test for only the sucrose percentages and leaf counts. For all other measurements the error variances were calculated from the replicates of the two treatments compared. Significance of the difference was estimated by the F-test, which in this instance is equivalent to the t-test, where $t = \sqrt{F}$ (5).

Results

Beet root weights. The beet root weights for the four varieties and four climates are given in Table 1. Here the beet root weights may be seen to be very uniform within the hot, warm and cool climates for the yield-type E and US 22/3 varieties, even though the weights doubled for the two varieties in going from the hot to the cool climates. However, in the cold climate the roots of the US 22/3 variety weighed only one-half of the European type E variety, indicating a variety-climate interaction in going from the cool to cold climates. Apparently, during the breeding program for curly-top resistance the ability to grow well in cold climates had been lost by the US 22/3 variety. This loss in ability to grow well in cold weather was not detected

in the field under curly-top conditions of the Salinas Valley, where spring weather is often as cold as in the simulated "cold climate."

The beet root weights of the sugar-type US 35/2 variety followed the same pattern as the yield-type US 22/3 variety (Table 1). It too produced only half the beet root weight of the E variety in the "cold climate." This again indicates a loss in ability to grow well in "cold climates" after breeding for curly-top resistance. As expected, the beet root weights for the sugar-type US 35/2 variety were in all instances less than for the yield-type US 22/3 variety but none of the differences within a climate were significant statistically. For the ZZ variety there was again a variety-climate interaction for a comparison of the ZZ to the E or of a U.S. variety in the cold and cool climates. The ratio of root weight for the E, US 22/3 or US 35/2 varieties to the ZZ variety within the cool climate is approximately 3 to 1. Whereas within the cold climate the ratio of E to ZZ is approximately 10 to 1 and for the U.S. to ZZ varieties, 5 to 1. The best climate for beet root growth is the "cool" climate (20° C days and 14° C nights) and the poorest is the "hot" climate (30° C days and 22° C nights.). On the average the E variety made the best beet root growth and the ZZ variety the poorest.

Table 1.—Effects of climate on root weight of yield- and sugar-type curly-top resistant non-resistant sugar beet varieties (Mean of 8 values expressed in counts per pot).

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	US 22/3	US 35/2	ZZ	
Cold	17° C	12° C	497 **	253 **	247 **	49	261
Cool	20° C	14° C	621	637	558 **	199	504
Warm	26° C	20° C	466 *	480 *	381 *	225	388
Hot	30° C	22° C	304	303	213	121	235
Variety mean			472	418	350	149	

The symbols * and ** indicate significant differences between the adjacent means at the 5% and 1% levels, respectively, calculated from the t-test for paired means (5).

Sucrose percentage. The sucrose percentages of the four sugar beet varieties followed the same general pattern that has been discovered in earlier work (6) namely, sucrose concentrations are higher in cold to cool climates and lower in warm to hot climates. The present values (Table 2) dropped from 11.71 to

Table 2.—Effects of climate on sucrose percentage of yield- and sugar-type curly-top resistant and non-resistant sugar beet varieties (Mean of 8 values).

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	US 22/3	US 35/2	ZZ	
Cold	17° C	12° C	11.3	10.8	11.0 **	13.7 **	11.71
Cool	20° C	14° C	10.3	10.0	10.9	11.9	10.76
Warm	26° C	20° C	9.2	9.1	9.8 **	11.6	9.94
Hot	30° C	22° C	8.1	9.4	9.4 **	12.0	9.81
Variety mean			9.81	9.83	10.27 **	12.31	

The least significant difference between climate or variety means equals 0.53% and 0.70% and between variety-climate means equals 1.1% and 1.4% at the 5% and 1% levels, respectively. The symbols * and ** indicate significant differences between the adjacent means at the 5% and 1% levels, respectively, calculated from the t-test for paired means (5).

9.81 from the cold to the hot climate. The yield- and sugar-type varieties performed as expected, i.e. the sugar-types tended to be higher in sucrose concentration than the corresponding yield-type. The differences, however, were relatively small and were not significant statistically for the U.S. varieties, but for the ZZ variety, which is an extreme sugar-type, the sucrose values were significantly higher than the E and U.S. varieties in all climates.

There was no significant variety climate interaction for sucrose concentration for the US 22/3, US 35/2 and E varieties, but for the ZZ variety, there was a significant variety-climate interaction for the cold and cool climate comparisons. The ZZ variety in the cold climate was relatively higher in sucrose concentration than in the cool climate, thus indicating that varieties may differ in relation to each other in different climates in sucrose concentration as well as in beet root size.

Sucrose weights. The sucrose weights for the four beet varieties in the four simulated climates are tabulated in Table 3. The variety-climate interaction is again significant for the yield-type varieties E and US 22/3, for sugar produced in the cold and cool climates. The sugar produced in the "cold" climate by the US 22/3 variety and also for the US 35/2 variety, is only one half of the E variety, whereas in the other climates there is no appreciable difference among the three varieties. The ZZ variety in comparison with the other varieties also seems to have produced proportionately less sugar in the "cold" climate than in the other climates. Maximum sugar production, as in beet root

weight, also occurred in the "cool" climate. The "fall off" in sugar produced by all varieties is quite appreciable in the "hot" climate and this loss should be studied in detail for the fundamental reasons why beet plants do poorly in hot weather.

Fresh weight of tops. The fresh weight of the tops (Table 4) offers no clue as to the reason for the poor growth of the roots of the U.S. curly-top resistant varieties in the cold climate. In fact, the tops of the U.S. varieties weigh as much as or even more than those of the E variety. This might imply that less

Table 3.—Effects of climate on *sucrose weight* of yield- and sugar-type curly-top resistant and non-resistant sugar beet varieties (Mean of 8 values expressed in grams per pot).

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	US 22/3	US 35/2	ZZ	
	Cold	17° C	12° C	56.8	* 27.8	27.2	
Cool	20° C	14° C	64.7	64.3	61.8	** 23.6	53.6
Warm	26° C	20° C	44.3	44.1	37.8	26.3	38.1
Hot	30° C	22° C	25.8	28.9	21.1	14.6	22.6
Variety mean			47.9	41.3	37.0	17.8	36.0

The symbols * and ** indicate significant differences between the adjacent means at the 5% and 1% levels, respectively, calculated from the t-test for paired means (5).

Table 4.—Effects of climate on *fresh weight of tops* of yield- and sugar-type curly-top resistant and non-resistant sugar beet varieties (Mean of 8 values expressed in grams per pot).

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	US 22/3	US 35/2	ZZ	
	Cold	17° C	12° C	861	842	922	
Cool	20° C	14° C	813	834	890	** 518	761
Warm	26° C	20° C	479	617	595	103	523
Hot	30° C	22° C	346	365	302	294	319
Variety mean			617	664	677	344	

The symbols * and ** indicate significant differences between the adjacent means at the 5% and 1% levels, respectively, calculated from the t-test for paired means (5).

sugar is produced by the leaves or translocated from the leaves to the roots by the resistant U.S. varieties than by the non-resistant E variety.

The tops of the ZZ variety, in sharp contrast to those of the US 22/3, US 35/2 and E varieties, weigh only one-third as much in the cold climate as in the cool climate (Table 4). This pronounced decrease in top weight for the ZZ variety results in a significant variety-climate interaction for top weight. The smaller tops for ZZ can account for the relatively smaller beet root weight for this variety (Table 1) but not for its higher sucrose concentration in the cold climate (Table 2).

The fresh weight of the tops dropped off appreciably in the warm climate and still more in the hot climate. These decreases in top weight are typical for sugar beet plants in warm climates (7). There were no significant variety-climate interactions in proceeding from the cool to the hot climate except possibly for the ZZ variety, which held up better in the hot climate than the other varieties (Table 4).

Dry weight of leaves. The amount and relative proportion of living, dead and combined living and dead leaves produced by the sugar beet plants differed considerably for the four varieties in the four simulated climates (Table 5). In the cold climate the dry weight of the living leaves made up about 75% of the total dry weight of living plus dead leaves produced, whereas in the cool climate the corresponding value for the living leaves was approximately 60%, in the warm climate 48% and in the hot climate 44%. In terms of living and dead leaves the living in the cold climate weighed approximately 3 times as much as the dead leaves, whereas in the hot climate the dead leaves weighed 30% more than the living leaves. The longer life expectancy of sugar beet leaves in the cold climate compensates for a slightly slower leaf initiation (Table 6), so that the living leaves in the cold climate weighed nearly as much as in the cool climate. Total leaf production (Table 5) and leaf count (Table 6) is greatest, however, in the cool climate.

An interaction of variety and climate is evident for the living leaf weight of the ZZ variety in the cold climate. The living leaf weight decreases sharply in the cold climate for this variety, whereas the weights increase appreciably for the other varieties. A similar interaction of variety and climate appears to exist for dead leaves formed by the ZZ variety in the cold climate. The dead leaf weight falls off much faster for the ZZ variety than for the other varieties.

Leaf counts. In terms of leaf counts (Table 6), the values are quite similar to those of total leaf weight. The total number of leaves produced to harvest did not differ greatly among climates. The lowest average value was 112 for the cold climate and the highest, 148, in the cool and warm climates. Again there were larger differences in numbers of living and dead leaves in relation to climate. In the cold climate the number of living leaves made up 61% of the total number of leaves produced

Table 5.—Effects of climate on leaf weight of yield- and sugar-type curly-top resistant and non-resistant sugar beet varieties (Mean of 8 values expressed in grams per pot on dry basis).

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	US 22/3	US 35/2	ZZ	
	Living Leaves						
Cold	17° C	12° C	91	85	97 **	21 **	73.6
Cool	20° C	14° C	76	78	88 *	58 **	77.9
Warm	26° C	20° C	47	59 *	61 *	46	53.2
Hot	30° C	22° C	33	35	30	35	33.5
Variety mean	63	61	69	40	58.8
Dead Leaves							
Cold	17° C	12° C	32 *	30 **	32 **	12 **	25.2
Cool	20° C	14° C	54	53	62 **	33 *	50.4
Warm	26° C	20° C	55	62	61 *	47	56.3
Hot	30° C	22° C	47	50	43	35	43.7
Variety mean	47	49	32	50	44.2
Total Leaves							
Cold	17° C	12° C	123	115	129 **	34 **	100.0
Cool	20° C	14° C	130	131	150 **	91 **	125.0
Warm	26° C	20° C	102	121	122 **	93	110.0
Hot	30° C	22° C	80	85	73	70	77.0
Variety mean	109	113	119	72	103.0

The symbols * and ** indicate significant differences between the adjacent means at the 5% and 1% levels, respectively, calculated from the t-test for paired means (5).

whereas in the hot climate the corresponding value was only 41%, a drop of nearly 50% in living leaf number relative to the total number of leaves produced.

Table 6.—Effects of climate on leaf count of yield- and sugar-type curly-top resistant and non-resistant sugar beet varieties (Mean of 8 values expressed in counts per pot.)

Simulated climate	Temperature		Yield-type		Sugar-type		Climate mean
	8 AM to 4 PM	4 PM to 8 AM	E	U.S. 22/3	US 35/2	ZZ	
	Living Leaves						
Cold	17° C	12° C	68 *	80	69 *	55 **	68
Cool	20° C	14° C	70 *	84 *	75 **	76 **	76
Warm	26° C	20° C	65 *	70 **	54	65	63
Hot	30° C	22° C	51	51	49 *	61	54
Variety mean	64	71	62	65	65
Dead Leaves							
Cold	17° C	12° C	43 **	51 **	50 **	32 **	44
Cool	20° C	14° C	77 **	76 **	80 **	59 *	71
Warm	26° C	20° C	83	93	89 *	74	81
Hot	30° C	22° C	78	89	80 **	64	78
Variety mean	69	77	75	57	70
Total Leaves							
Cold	17° C	12° C	111 **	131 **	119 **	87 **	112
Cool	20° C	14° C	141 *	160 **	155 *	135 **	148
Warm	26° C	20° C	148 *	162 *	143	139	148
Hot	30° C	22° C	129	140	129	128	131
Variety mean	132	149	136	122	135

The error variances within groups were found to be homogeneous for living, old and total leaf counts by Bartlett's test (3). The corresponding error variances are 146, 143 and 364 and the least significant ranges for $p = 2$ at the 5% and 1% levels of significance for variety-climate means with eight replications and 112 degrees of freedom for error are 12, 12 and 19 and 16, 16 and 25, respectively. For the variety or climate means the least significant ranges for $p = 2$ at the 5% and 1% levels of significance are 6, 6 and 9 and 8, 8 and 13, respectively. The symbols * and ** indicate significant differences between adjacent means at the 5% and 1% levels, respectively.

Discussion

The results of the present experiment with four sugar beet varieties, resistant and non-resistant yield- and sugar-types, grown in four simulated climates, "cold," "cool," "warm" and "hot," suggest that the practice of comparing varieties at more than one location for more than one year is a good one if a sound evaluation of variety performance for sugar content and root size is to be made effectively. Varieties may parallel each other in performance for a fairly wide range of climates and then suddenly one or more of the varieties may fail to grow satisfactorily when the temperatures become slightly lower on the low side or slightly higher on the high side of the temperature scale. Under these conditions segregation of varieties, otherwise uniform, becomes immediately apparent. This phenomenon has been known of course for many genetic characters, but only recently appreciated for climatic factors as it influences genetic expression.

Recent germination studies at low temperatures also attest to the importance of getting sugar beet plants off to a good start during cold spring weather (4, 9, 10). That subsequent growth, particularly root growth, may also be retarded greatly in cold weather is not as well known. This reduction in root growth by one half is rather surprising since top growth, as measured by fresh weight, was not reduced at all. Apparently, the sugar produced by the leaves was either just sufficient to maintain top growth but not sufficient for maximum root growth, or perhaps the sugar synthesized in the tops failed to move out of the leaves into the roots for root growth.

What brought about the decline in ability of curly-top resistant varieties to form large roots during "cold" weather? One possible answer, although an unlikely one here, is that resistance and lack of ability to grow in "cold" weather are linked genetically. The present results provide no specific answer to this question. However, if we assume there is no genetic linkage or at least very little linkage between resistance and ability to grow in cold weather, one might postulate how this ability to form large roots in cold weather was lost. A review of the research program adopted for developing the curly-top resistant variety (2) indicates that the sugar beet seeds were planted, quite appropriately, at a time when the plants would be small and infestation by leaf hoppers would be high. Such a time is early summer, during warm weather. Under these conditions, however, it is not possible to select simultaneously for ability to grow in cold weather and disease resistance but only for disease re-

sistance. The ability to grow in cold weather just happened to be lost in warm weather, unless we are willing to assume that resistant varieties do not grow well in cold weather. This is a point in need of further study.

The failure to detect a loss of growth by resistant varieties in relatively cold weather from field experiments could well have been associated with two situations, one being that curly-top disease depressed the growth of the non-resistant varieties so much that their better growth in cold weather could not be detected and the other being that the duration of the cold weather was not always sufficiently long to cause a detectable loss of yield. A loss in yield of only 5% or even of 10% would be difficult to detect experimentally in the field even under disease-free conditions, but of course with curly-top disease present, the loss in cold weather could be masked completely. In the Salinas Valley a loss of only 5% would be approximately equivalent to 20,000 tons of beets per annum, which when translated to dollars would make it desirable to test "disease" resistant varieties for growth potential under "disease-free" conditions before the variety is released commercially.

Summary

Two yield-type sugar beet varieties curly-top resistant US 22/3 and non-resistant Kleinwanzleben E and two sugar-types, resistant US 35/2 and non-resistant Kleinwanzleben ZZ, were compared in four simulated climates by the open pot culture technique, using vermiculite flushed daily with complete Hoagland's nutrient solution. The greenhouse temperatures from 8 AM to 4 PM and 4 PM to 8 AM were kept for the "cold" climate at 17° C and 12° C; for the "cool" climate, 20° C and 14° C; for the "warm" climate, 26° C and 20° C; and for the "hot" climate 30° C and 22° C, respectively.

In the "cold" climate the US 22/3 and US 35/2 varieties produced only one-half as much storage root and sugar as Klein E, whereas in the "cool," "warm" and "hot" climates, there were no significant differences among the three varieties. Consequently, in the selection for curly-top resistance, ability for storage root growth in a "cold" climate had been lost by the US 22/3 and US 35/2 varieties. This variety-climate interaction for root growth and sugar produced by the three varieties did not carry over to top growth or to sucrose concentration. However, for the ZZ variety there was a variety-climate interaction for sucrose concentration and top size as well as for root size. Variety-climate interactions were also observed for leaf growth and leaf counts.

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