THE EFFECT OF SOIL MOISTURE
AND A TRANSPIRATION REDUCING SPRAY ON
TRANSPIRATION AND GROWTH

Thesis for the Degree of Ph. D.

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Oliver M. Neal Jr.

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This is to certify that the

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Reducing Spray on Transpiration
and Growth"

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Oliver M. Neal, Jr.

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A. L. Kenworthy

Major professor

Date February 17, 1956

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THE EFFECT OF SOIL MOISTURE AND A TRANSPIRATION REDUCING SPRAY ON TRANSPIRATION AND GROWTH

By

Oliver M.$^{\text{ader}}$ Neal Jr.

AN ABSTRACT

Submitted to the School of Advanced Graduate Studies
of Michigan State University of Agriculture
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fulfillment of the
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Year 1956

Approved A. L. Kenworthy

ABSTRACT

The object of the investigation was to determine the effect of decreasing soil moisture and transpiration reducing sprays on transpiration and growth of plants. Considerable disagreement appears in the literature concerning the effect of low soil moisture on transpiration and growth.

Transpiration was determined by weight loss of plants growing in soil in containers which were sealed to prevent evaporation. Leaf area increase (the measure of growth used) was determined by daily leaf length - leaf area relationships obtained in this work and from the literature. The different levels of soil moistures were obtained by allowing the treatment plants to remove the soil moisture from the field capacity to the permanent wilting percentage. Changes in growth and transpiration as soil moisture was reduced were determined with respect to plants in soil maintained at field capacity. Four soils, three species and two sprays were used. Both daily and hourly measurements were made. The sprays were made up by the Agricultural Chemistry Department.

There appeared to be less reduction due to low soil moisture, in transpiration rate relative to the controls,

when the environment was not conducive to rapid transpiration, and it might be expected that under very low transpiration conditions that little transpiration reduction would be found as soil moisture was reduced. The hourly measurements showed that the transpiration reduction was much greater in the afternoon than in the morning which indicated that in those cases where transpiration was measured for only a short period during each day the choice of period would influence the amount of reduction indicated.

The most striking difference, however, was found between soils. A compost soil and a sand were at the two extremes. Transpiration of the tomato in compost soil was reduced with the first reduction in available water, while the plants in sand showed no reduction until over 80 percent of available soil moisture had been removed. Clay and muck soils were intermediate and showed a gradual reduction starting when between 40 percent and 50 percent of the available moisture was exhausted.

The transpiration reducing sprays were found to reduce transpiration about 10 percent for each percentage of oil they contained. Growth was proportionately reduced. As the sprayed plants grew the film lost some of its effectiveness. Either the spray was without value after three days or the transpiration of the sprayed and unsprayed plants was reduced together as low soil moisture caused reductions below that caused by the sprays.

Growth was closely related to transpiration.

The data indicated that much of the apparent disagreement in the literature was due to different soils, different transpiring conditions, and different periods of day that measurements were made.

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INTRODUCTION

The total loss to plant industry resulting from water deficits is probably greater than that caused by any other production factor. Irrigation and water conservation are the obvious remedies. While irrigation is a necessity in arid climates it is recently proving to be a remunerative supplement to natural precipitation in humid and sub-humid areas. This has led to a rapid expansion of the irrigated acreage east of the Rocky Mountains and to a more general recognition of the need for additional fundamental information concerning soil-plant-water relations.

The time and rate at which the diminishing soil moisture supply reduces transpiration and growth may determine the effectiveness of both irrigation and conservation practices.

The present work was undertaken as part of the transpiration-reducing-film investigation at the Michigan Agricultural Experiment Station to find the time and rate at which a diminishing soil moisture supply reduces transpiration and how the application of a transpiration-reducing spray might affect this time and rate.

REVIEW OF LITERATURE

The literature pertaining to the effect of decreasing soil moisture supply on plant transpiration and growth has recently been reviewed by Veihmeyer and Hendrickson (1950), and Richards and Wadleigh (1952). A quotation from Veihmeyer and Hendrickson (1950) emphasizes the lack of agreement: "On the one hand it is held that water is equally available to plants throughout the range from the field capacity to the permanent wilting percentage; on the other that plants respond favorably to high soil moisture conditions and that adverse effects will result as the water content decreases."

Although the point in the available range where water first limits growth and transpiration is still in question, it is generally agreed, Briggs and Shantz (1911) (1913), Taylor et al. (1934), Furr and Reeve (1945), Hendrickson and Veihmeyer (1945), that the permanent wilting percentage is the point below which there is essentially no growth. Transpiration, however, continues to remove considerable water at a low rate until the plant dies.

The observation of Briggs and Shantz (1913) and

Shantz (1925), that there appears to be no way of maintaining uniform soil moisture throughout the root zone at percentages below field capacity because of limited water movement, left little or no reliable information on the effects of different soil moisture percentages in the available range on transpiration and growth at the time of Veihmeyer's (1927) first report. Veihmeyer (1927) compared the effects of different but overlapping ranges of soil moisture. Well established two year old French prune trees growing in 1000-2000 pounds of Yolo clay loam (Moisture Equivalent - 22 percent) and Yolo loam (Moisture Equivalent - 22 percent) in sealed containers were allowed to remove moisture to 11.8 percent, the permanent wilting percentage, or to 16 percent before being irrigated to field capacity (22 percent). Thus soil moisture of one set varied between 11.9 percent and 22 percent and the other between 22 percent and 16 percent. The results indicated: "that not only the water use but the trees themselves were not affected by variation in amounts of soil moisture above the wilting coefficient." In later work, with dwarf sunflower in 9,600 gm Yolo clay in small containers, Hendrickson and Veihmeyer (1945) plotted the soil moisture against time as the plants reduced the water from 33 percent to 15 percent in eighteen days, and found that water was extracted at a uniform rate.

Chung (1935) found that the hourly transpiration rate of bean decreased as the soil became drier and that the peak rate fell considerably earlier on the third than it did on the first day.

Change in rate of stem elongation of sunflower with decreasing soil moisture in containers was measured by Blair et al. (1950) and Furr and Reeve (1945). The former showed a decrease when 25 percent to 50 percent of the available moisture of a loamy fine sand was exhausted and there was a downward trend on the first day with the whole series of soils used by the latter.

Schneider and Childers (1941), Allmendinger, et al. (1943), Loustalot (1943), and Upchurch et al. (1955) have used the gas absorption method of Heinicke (1933) to study respiration, photosynthesis and transpiration of individual leaves for short periods as soil moisture was reduced by the plant.

Schneider and Childers (1941) working with young apple trees in a heavy soil in ten gallon containers both in a controlled environment and in the field found a slight increase in photosynthesis for one to four days after termination of irrigation. Before wilting was evident there was a 55 percent reduction in photosynthesis, a 65 percent reduction in transpiration and a 62 percent increase in respiration. When the plants showed definite wilting and the soil moisture was approximately at the wilting percentage there was an 87 percent reduction in transpiration. Similar changes in photosynthesis were obtained in the field.

Allmendinger, Kenworthy and Overholser (1943) selected a made soil which had little shrinkage on drying for growing young apples in containers. Leaves of these trees measured in the morning showed no significant reduction in CO_2 absorption until over 80 percent of the available water had been used.

Loustalot (1945) transplanted six pecan seedlings into five gallon crocks of silty loam and coarse sand. The checks were maintained at 25 percent to 30 percent and 4.5 percent to 6 percent soil moisture respectively. Transpiration ratios were established before treatments and two determinations were made daily, one in the morning and one in the afternoon. It was found that under drought conditions "a marked reduction in the rates of both photosynthesis and transpiration occurred one or two days before the moisture in both sand and soil had reached the wilting point. Transpiration and photosynthesis rates were usually depressed at about the same time and as a rule both processes were depressed in the afternoon periods one or two days before any appreciable reduction was observed in the morning probably owing largely to wide differences in atmospheric conditions that prevail."

Upchurch et al. (1955) modified the gas absorption technique to enable them to make measurements on the entire plant. Ladino clover was grown under controlled conditions in a Yolo loam with moisture equivalent and wilting percentage agreeing closely with the soil Veihmeyer (1927) used for work on prunes in containers. Temperature was 25°C., light 1800 foot candles, and humidity 85 percent to 90 percent during measurements. The curve presented for a nine day run with one irrigation after about 80 percent of the available moisture had been removed, shows there was an increase from 33 - 46 mg CO_2 exchanged per hour during the run. There was very little change in rate either before or after irrigation. "The results of Allmendinger et al. (1943) with apples, Loustalot (1945) with pecan trees, and the present investigation with ladino clover all lead essentially to the same conclusion, namely that the rate of photosynthesis is little affected until the permanent wilting percentage is closely approached." The authors found in unpublished work that vegetative growth of ladino clover was reduced when half the available moisture had been used.

Kenworthy (1949) working on the same experiment as Allmendinger et al. (1943) found significant reductions in terminal growth, total leaf area, and increase in dry weight when the plants were not irrigated until 80 percent of the available moisture had been used.

Martin (1940) raised Russian Mammoth sunflower in 130 pounds of a sandy loam soil in containers and irrigated groups of six plants each when the soil moisture was reduced to 14 percent and to 10 percent. The rate of transpiration per unit leaf surface was ordinarily affected when about two-thirds of the available water had been exhausted, but rate of increase of leaf area was affected long before any change in stomatal opening or transpiration was noted.

Mendel (1945) reported transpiration and stomatal measurements on orange trees growing under different irrigation regimes in the field. Leaves were removed from trees on sandy soil at intervals after irrigating and the rate of change in weight of these leaves was the criteria of transpiration. Transpiration rates and stomatal aperatures decreased before wilting was apparent. A more rapid decrease in the rates of transpiration began as moisture in the main root horizon decreased to the point where soil suction forces rise above 3.5 atmospheres.

Scofield (1945) grew alfalfa in cans 15 inches in diameter and 24 inches deep with 87 kilograms of dry soil with a moisture equivalent of 10 percent to 6 percent with about 14 liters of available water per can. Three treatments were made; irrigated when 50 to 60 percent of the available water was removed, when practically all available water was exhausted and continual sub-irrigation to keep the bottom layer of soil saturated. Dry weight yield of tops decreased with each reduction in soil moisture.

Nutgrass in one gallon pots was irrigated by Davis (1942) to approximately 22 percent soil moisture, 5.1 percent above the moisture equivalent, by allowing the pots to stand in water in pans for 24 hours after the soil moisture was exhausted to 18 percent, 15 percent, 12 percent, 9 percent, and 6 percent. Two of these moisture ranges averaged above the moisture equivalent and the highest never dropped to it. The soil moisture range entirely above the moisture equivalent yielded more tops and tubers on a fresh weight basis than any other treatment and there was a marked decrease in yields with successively lower moisture irrigation regimes.

Ayers et al. (1943) also found reduction in growth of beans with slight reductions of soil moisture of

Fallbrook loam which had 6.2 percent water at 15 atmospheres tension and 14.7 percent at the moisture equivalent. The pots were irrigated to 20 percent when the soil reached 15 percent, 11 percent and 7.5 percent. Bean growth and yield increased as tension decreased.

Haynes (1948) irrigated corn plants growing in soil fluctuating between 0.0 and 0.7, 0.0 and 0.1, and 0.0 and 12 atmospheres tension. The lowest tension resulted in the highest yield and the water used per gram dry matter produced was the same for all treatments.

Went (1944) concluded that as long as water in crushed granite and sand cultures for growing tomatoes was not allowed to reach a low level, it had little effect on growth.

Post and Seely (1947) irrigated greenhouse roses when tensiometers indicated one inch and three inches of water. The lower tension resulted in better but not significantly increased yield.

In greenhouse studies with containers holding 105 pounds of light brown loam with a field capacity of 23.8 percent and a permanent wilting percentage of 10.8 percent, Cyklar (1946) irrigated when 50 percent, 66 2/3 percent and 95 percent of available water was exhausted and found that tuber set and top growth was independent of moisture content as long as available moisture was present for growth. It was thought that the rate of extraction might be the same for all treatments when corrected for evaporation.

Transpiration reducing coatings have been used by a number of workers successfully on roots, and nursery crops. Haller (1947), Mack and Janer (1941), Hitz and Haut (1941), Claypool and King (1941), Tukey and Brase (1931). Comar and Barr (1944) reported that aqueous emulsions of oils gave up to 89 percent reduction in the transpiration rate of sunflower. The work on aqueous emulsions of waxes and oils at Michigan State University was reviewed by Miller et al. (1950).

PROCEDURE

Apparent transpiration was determined by change in weight of potometers consisting of plants growing in soil in cans sealed to prevent evaporation. Leaf area increment was the criteria of growth and was calculated from leaf length measurements according to the length - area relationship determined by Porter (1937) for tomatoes. Similar relationships were determined for castor bean and snap bean (See appendix).

Potometers were made by putting equal weights of moist soil to within an inch of the top of number 10 cans and working to the edge at the surface to prevent irrigations from running to the bottom between the soil and can. The water content of the soil placed in the cans was determined by sampling and drying at 110°C. to a constant weight. Seedlings were started in sand and transplanted to the cans when the first true leaf appeared. When the plant had grown sufficiently not to be damaged, the can top which was cut from the edge to a hole in the center was sealed on with two inch adhesive tape and grafting compound to prevent evaporation. A glass tube for irrigation was put through a second hole in the cover and sealed in a similar manner. Cotton was inserted in the tube and around the stem. By weighing before and after each operation the weight of the potometer with any desired percentage of soil moisture could be calculated.

Weighings were made on a Cenco double beam balance to the nearest tenth gram. Apparent transpiration of unirrigated plants was determined by change in weight whereas the volume of water, added from a burette, to bring the potometer up to weight was the measurement used for irrigated plants. Error due to evaporation was low. Dummies (potometers without plants) seldom lost over a gram per day and usually less than half a gram.

Weighings and irrigations were made daily or twice daily, depending on the transpiration, to keep the soil of the control plants near field capacity.

Field capacity was determined by adding sufficient water to moist soil in graduates to wet part way to the bottom (Loomis and Shull, 1937). After 12 hours samples were taken at a number of levels and the lowest soil moisture of any wetted portion was taken as an approximation of field capacity.

The procedure of Briggs and Shantz (1912), with either dwarf sunflower or tomato, was used for determining the permanent wilting percentage or wilting coefficient.

The experiments were conducted in the greenhouse during the spring and summer of 1940.

The transpiration reducing sprays used on tomatoes and castor beans were oil in water emulsions of drying oils made by the Agricultural Chemistry Department. (Miller et al. 1950).

The difference in transpiration rate and growth of plants at different percentages of soil moisture was obtained by dividing the plants into groups of two or three plants each. One plant of each group was the check and received daily additions of water to bring the potometer to field capacity weight. To obtain relative ratios of transpiration and growth the second and third plants were maintained at field capacity until treated. Transpiration ratios were obtained by dividing the transpiration of the treated plant per unit leaf with that of the control. Transpiration was measured as grams water loss per square decimeter leaf area. When these ratios varied no more than $\pm$ 10 percent for three days the treatments were started and the average of the ratios for the three day period was used as the base for calculating changes. A base ratio for growth was determined similarly.

The effect of the treatment or treatments (diminishing soil moisture, or a transpiration reducing spray followed by diminishing soil moisture) on transpiration rate and leaf area increase was calculated by dividing each of the daily ratios obtained following treatment by the base ratio and multiplying by 100. This gave the percent of the expected rate on the basis of performance before treatment and was plotted on the ordinate axis of Figures 1, 2, 3, and 4. The abscissus are the average soil moistures for the same daily periods.

RESULTS

Experiment I: Large and Small Tomato Plants

On February 27, 1940 24 cans were filled with 1330 grams of compost soil that had a field capacity of 24 percent and a permanent wilting percentage of 9 percent. Small tomato plants weighing two grams were set in 12 and larger plants were set in the other cans. The potometers were sealed to prevent evaporation and the plants grown until March 24. All plants were irrigated to bring the soil to field capacity and measurements were started on March 25. The transpiration ratios were rather uniform the 26th, 27th, and 28th. The means were calculated and no water was added to the container on the 29th. The 30th was the first day differences in the soil moisture between the watered and unwatered plants was determined.

The 29th is the first day shown in Table I and also the date of the first points in the curves of Figure 1 which are the average of four small and eight large plants. The curves were drawn from the relative growth increase and relative transpiration reduction data contained in the table. The average daily transpiration rate of the eight controls which were kept near field capacity, found in column two, is an index of the overall transpiring conditions and is not included in the graphs.

The data (Table I) showed that there was a decrease in the transpiration of the eight large plants but not of the four small on the first day that the soil moisture of the treatments was less than the controls. The large plants had a soil moisture difference of 18 percent and the small 10 percent. At the same time the large plants had exhausted 39 percent of the available water and the small plants 24 percent. The data indicated that 24 percent of the available moisture was equally available for transpiration of the small plants but 39 percent was not equally available for transpiration of the large plants. There appeared to be no difference in the transpiration response of large and small plants to reduced soil moisture. After transpiration was first reduced, further reductions were directly related to the amount of available water. Transpiration was 13 percent and 17 percent of controls for the two plant sizes when the available water was exhausted.

Leaf area increase of both the large and small plants was reduced with the first decrease in available water and growth stopped before the available water was exhausted. Size of plant made little difference in response.

TABLE I

COMPARISON OF THE TRANSPIRATION AND GROWTH REDUCTION OF LARGE AND SMALL PLANTS AS THE AVAILABLE SOIL MOISTURE WAS EXHAUSTED

Days without water	Trans. of controls Gm/Dm^2/Day	Available soil moisture used ...Percent...		Transpiration* ...Percent...		Leaf area increase* ...Percent...	
		Large Plants	Small Plants	Large Plants	Small Plants	Large Plants	Small Plants
1	14.9	16	12	100	102	91	108
2	21.2	39	24	87	104	84	74
3	28.9	68	47	46	70	29	83
4	30.6	84	67	21	45	17	31
5	14.3	91	80	22	36	6	29
6	10.8	101	86	17	32		50
7	7.8		89		26		21
8	22.0		94		17		
9	25.7		99		13		

* Percent of expected rate relative to controls.

The transpiration and growth reductions were effected by the environment. Reductions were least when the transpiration rate of the controls was least and greatest when it was high. Leaf growth was influenced more than transpiration and the marked irregularities in rate of growth (Figure 1) were associated with corresponding changes in transpiration rate of the controls.

Experiment II: Sprayed and Unsprayed Tomato Plants.

Twelve potometers were made up with 1264 grams of compost soil with a field capacity of 25 percent and a permanent wilting percentage of 7 percent thus providing 205 grams of available water per potometer. The plants were set April 18. Three were treated with a transpiration reducing spray (82 A*)(Miller et al. 1950) and six with distilled water on the 29th. Only the three control plants received water after the 30th of April.

The reduction in transpiration the second day following spraying with the transpiration reducing spray averaged 28 percent for three plants. (Table II).

During the four day period when the spray reduced transpiration, growth of the sprayed plants was less than the unsprayed but in the next two days the sprayed plants

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* A spray made up with 3 percent oil by the Agricultural Chemistry Department and closely related to the formula shown on page 19 Miller et al (1950).

TABLE II

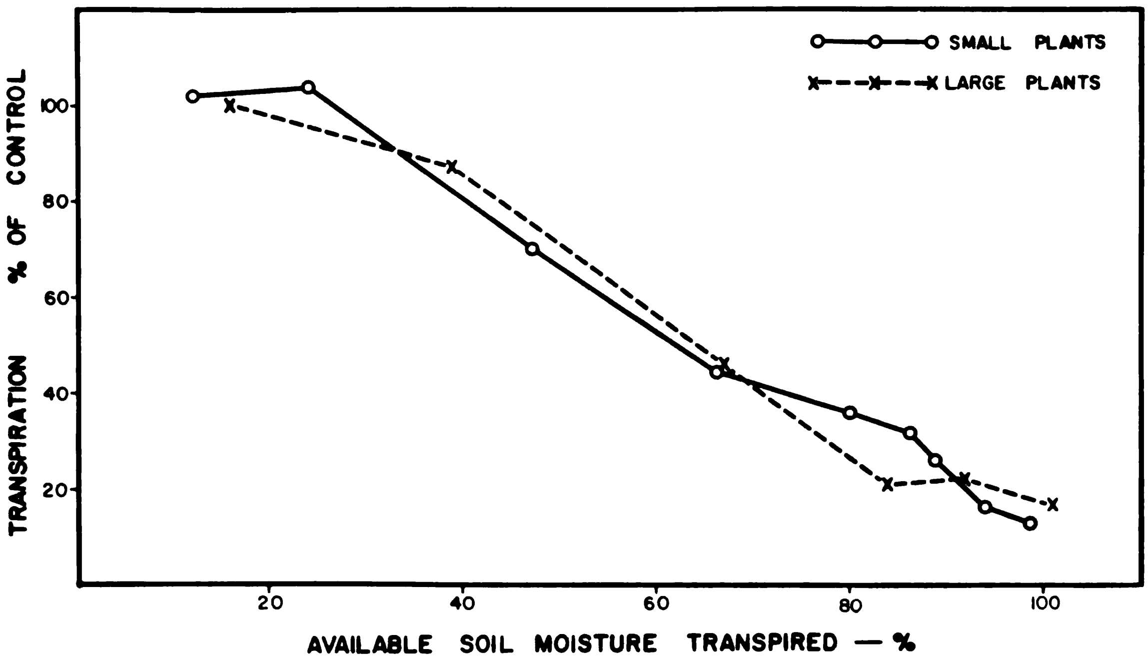
COMPARISON OF THE TRANSPIRATION AND GROWTH REDUCTION OF PLANTS SPRAYED WITH A TRANSPIRATION REDUCING SPRAY WITH UNSPRAYED PLANTS AS THE AVAILABLE SOIL MOISTURE WAS EXHAUSTED

Days without water	Trans. of controls Gm/Dm^2 /Day	Available soil moisture used Percent		Transpiration Percent		Leaf area Percent	
		Sprayed	Unsprayed	Sprayed	Unsprayed	Sprayed	Unsprayed
1	17.2	7	11	72	93	76	88
2	11.1	19	29	69	82	90	155
3	10.2	28	44	63	67	87	40
4	20.9	44	60	62	50	58	25
5	31.8	66	79	37	30	65	41
6	32.1	89	91	25	17	33	-04
7	22.3	92	99	21	14	5	1
8	11.5	98		12		10	
9	21.0	102		11		0	

* Relative transpiration or growth expressed as percentage of controls.

FIGURE 1

Large and small plants. Transpiration reduction (top) and growth reduction (bottom) in relation to depletion of available soil moisture. One day time interval between points.


SMALL PLANTS
LARGE PLANTS
TRANSPIRATION % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

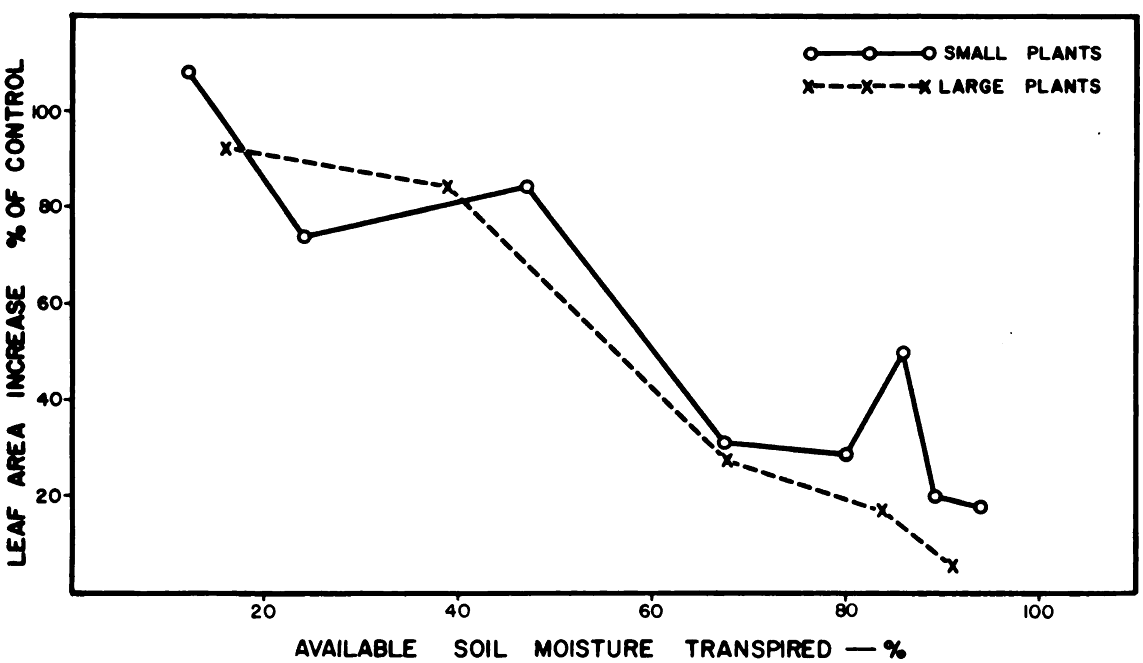
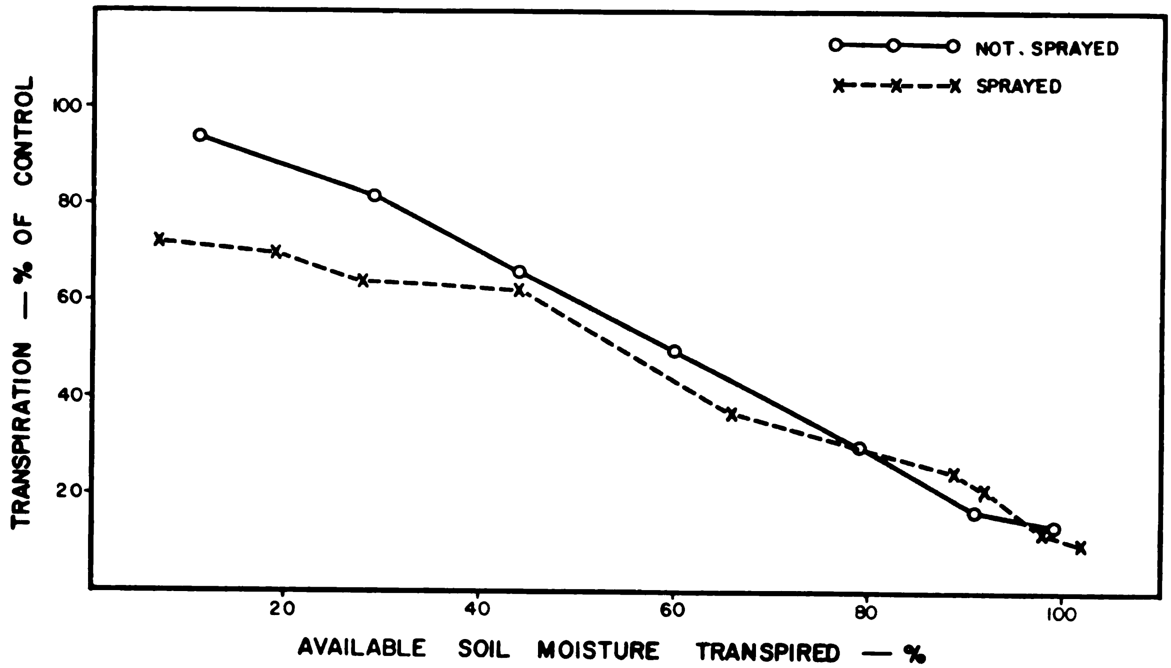
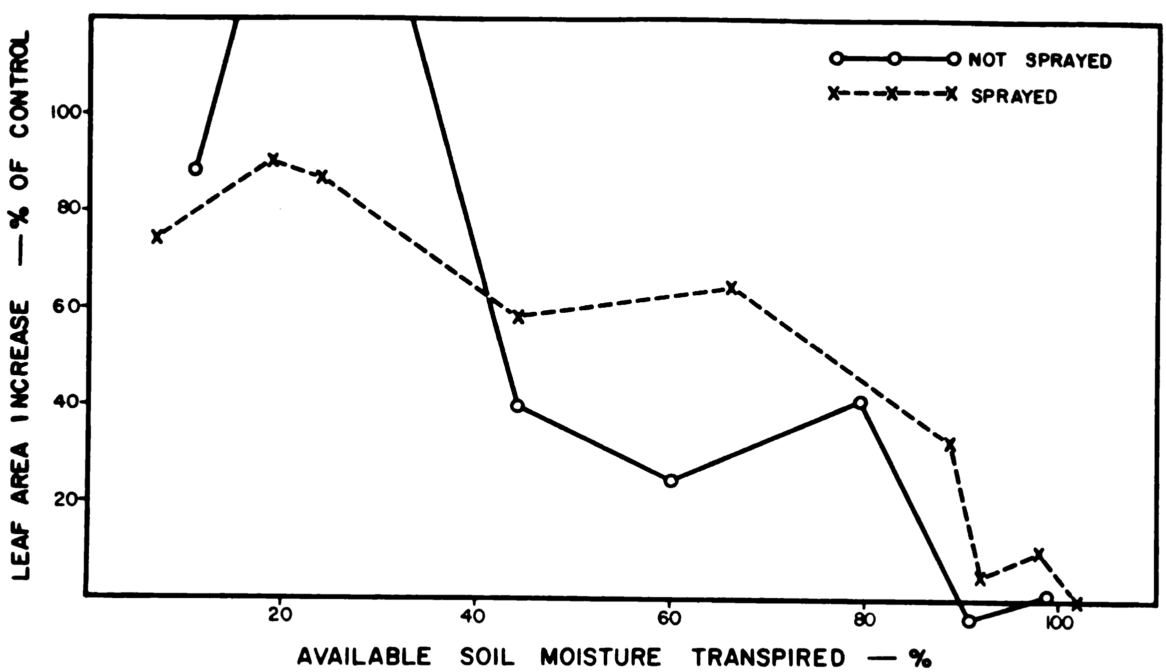

SMALL PLANTS
LARGE PLANTS
LEAF AREA INCREASE % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

FIGURE 2

Sprayed and unsprayed plants. Transpiration reduction (top) and growth reduction (bottom) of sprayed and unsprayed plants with depletion of the available soil moisture. One day time interval between points.


NOT. SPRAYED
SPRAYED
TRANSPIRATION — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %


NOT SPRAYED
SPRAYED
LEAF AREA INCREASE — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

transpired more and grew more. Growth stopped when or before the available water was exhausted but transpiration was still 11 percent and 14 percent. There was an 18 percent reduction in transpiration the first day that there was difference in the soil moisture (second day without water) and an upward trend of growth on the same day. Twenty-nine percent of the available water had been exhausted at this time.

The spray conserved little water under the conditions of this experiment of a rapidly growing plant and a rapid decrease in transpiration rate as soil water was exhausted. However, plants made more growth.

During the eight day period that the available water was being exhausted the leaf area of the controls increased 278 percent, the unsprayed plants 169 percent and the sprayed plants 198 percent. These data indicated a benefit in growth due to the spray of 29 percent, and a sharp decline in growth rate below the controls as the soil moisture of both the sprayed and unsprayed plants was exhausted.

Experiment III: Snap and Castor Beans.

Twenty-four potometers were made up on April 18 with 1273 grams of greenhouse compost. Castor bean seeds were planted in twelve and U.S. Refugee # 5 beans in the other twelve. The field capacity was 25 percent and the permanent wilting percentage 10 percent, thus providing 191 grams of available water in each potometer. Water was withheld from three snap bean plants on the 17th. Three castor bean plants were sprayed with 84 B on the 22nd and these and three additional plants received no water after this date. The spray had a tendency to collect in drops on the leaves but caused very little injury.

Leaf area of both refugee and castor beans was determined daily by measuring the length of the leaflets and length from petiole to the distal end respectively. The relationship was obtained by plotting the leaf area obtained by planimeter measurements against the sum of the leaflet lengths. Sixty-eight refugee bean leaves were used. The curves in Figure 1 of the Appendix were plotted from the length - area data. Table I in the Appendix was made up from the curves.

The data in Table III show that transpiration was reduced with the first reduction of soil moisture below the controls and that transpiration had been reduced to about 3 percent at the permanent wilting percentage. There was no difference between the transpiration response of snap beans and castor beans to reduced soil moisture. Transpiration reduction was proportional to soil moisture reduction.

TABLE III

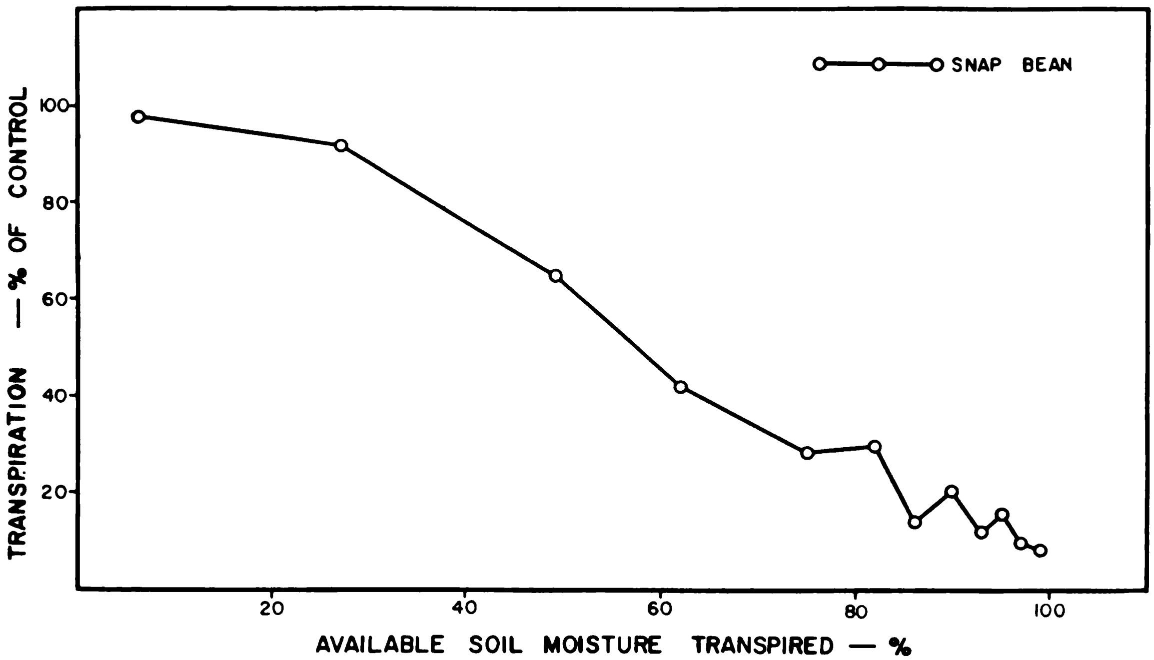
COMPARISON OF THE TRANSPIRATION REDUCTION OF SNAP BEANS AND CASTOR BEANS AS THE AVAILABLE SOIL MOISTURE WAS EXHAUSTED; HALF OF THE CASTOR BEAN PLANTS SPRAYED WITH A TRANSPIRATION REDUCING SPRAY

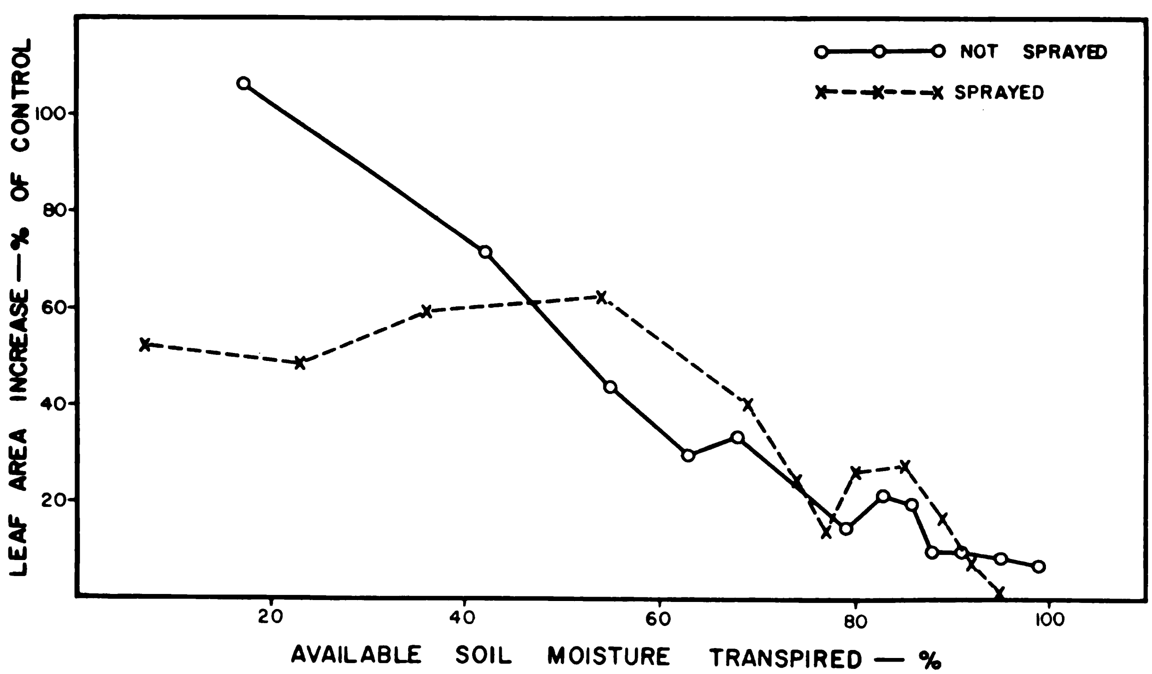
Days without water	Available soil moisture used			Transpiration*		
	Percent			Percent		
	Snap beans	Castor beans		Snap beans	Castor beans	
	Un-sprayed	Sprayed	Un-sprayed	Un-sprayed	Sprayed	Un-sprayed
1	6	7	17	98	52	106
2	27	23	42	94	48	72
3	49	36	55	65	59	44
4	62	54	63	42	61	30
5	75	63	68	49	59	34
6	82	69	76	50	40	24
7	86	77	79	14	14	15
8	90	80	83	21	26	22
9	93	85	86	12	27	20
10	95	89	88	16	16	10
11	97	91	91	10	10	10
12	99	92	95	9	7	9
13		95	99		1	7

* Relative transpiration expressed as percent of controls.

FIGURE 3

Transpiration reduction of snap beans (top) and sprayed and unsprayed castor beans (bottom) with depletion of the available soil moisture. One day time interval between points.


SNAP BEAN
TRANSPIRATION — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %


NOT SPRAYED
SPRAYED
LEAF AREA INCREASE — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

The transpiration reducing spray (84 B*) limited transpiration to 52 percent of the expected rate on the first day after application. Transpiration rose gradually to 40 percent of the expected rate during the next three days while exhausting slightly over 50 percent of the available moisture. When the untreated plants had removed half of the available moisture, transpiration was reduced 40 percent which would indicate that the transpiration reduction of the sprayed plants on the fourth day was due to the decrease in soil moisture rather than to the spray. A gradual breaking of the film by leaf growth during the three day period was indicated.

As available water was reduced the leaves of the snap bean plants turned on edge at the time of day a plant water deficit would be expected. Figure 4 shows the control and a plant only slightly above the permanent wilting percentage at 8:00 a.m. At this time neither plant was affected. However at 4:00 p.m. the leaf turning of the low moisture plant is marked while the control still remains unaffected.

Experiment IV: Soils

The previous experiments indicated that different

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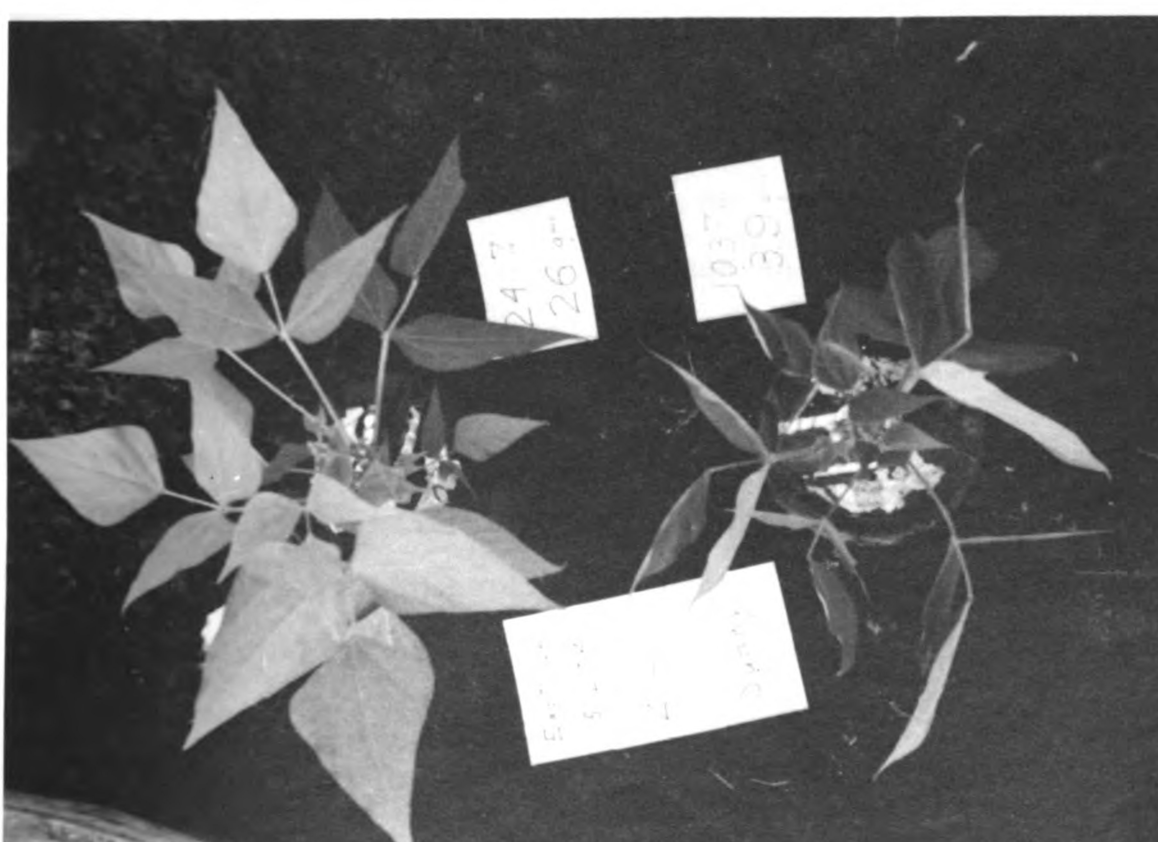
* A spray containing 5 percent oil and other ingredients by the Agricultural Chemistry Department and closely related to the formula shown on page 19 Miller et al (1950).

FIGURE 4

Leaves of bean plants turning away from the sun as the water tension increases during the day.



species and different sized plants in the same size container respond similarly to reductions in soil moisture. The next logical step was to determine the relation of transpiration to soil moisture reduction for soils having widely different soil moisture characteristics.

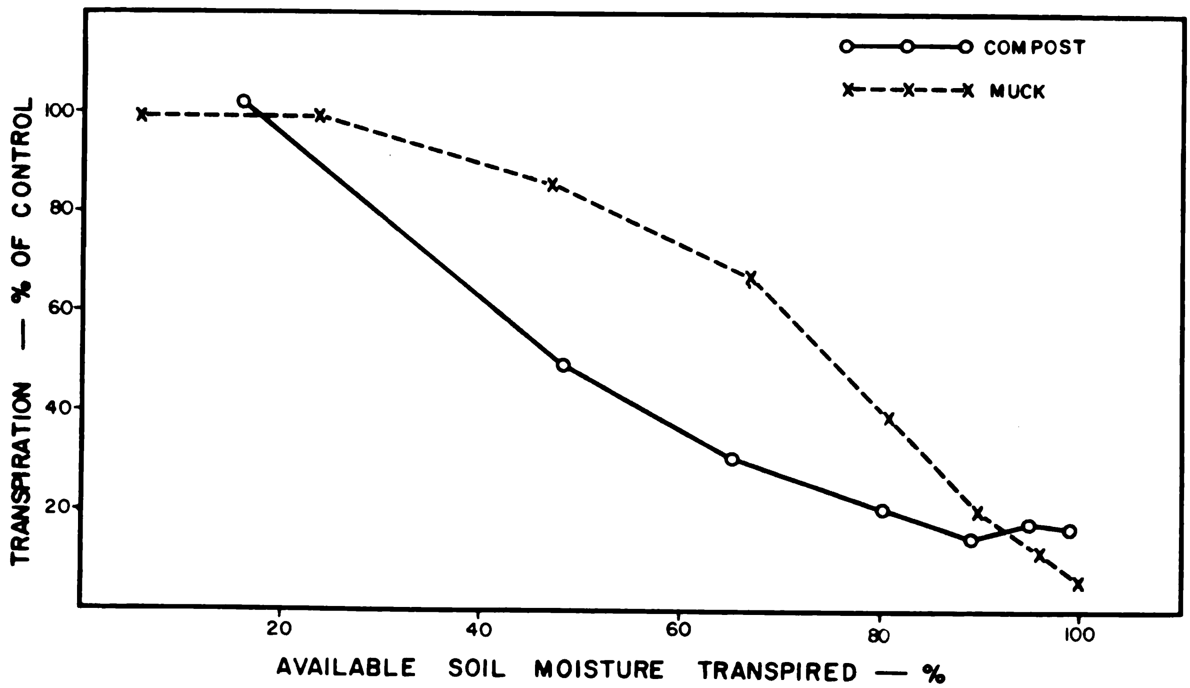
Potometers were made up on June 18. Twelve tomato plants weighing two grams each were set in a muck (field capacity of about 190 percent and a permanent wilting percentage of 65 percent), 12 in a clay soil (field capacity of 30 percent and permanent wilting percentage of 17 percent), 12 in a sand (field capacity 5 percent and permanent wilting percentage 0.25 percent), and 12 in a compost soil (field capacity 35 percent and permanent wilting percentage 22 percent).

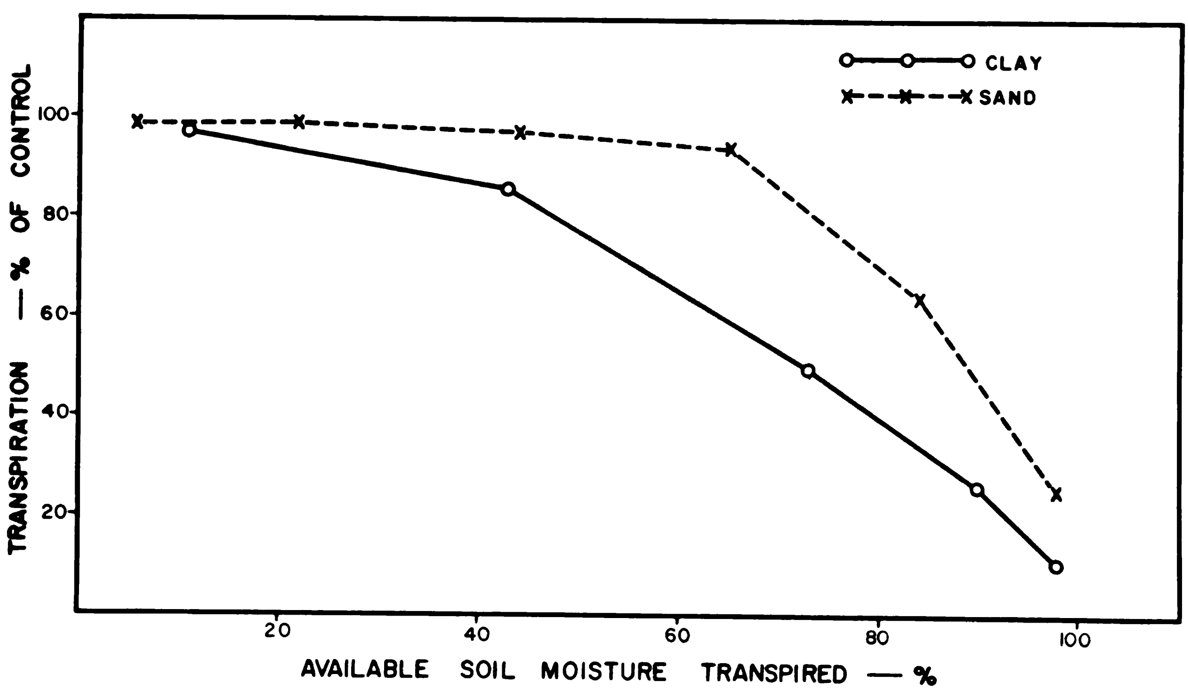
Transpiration reduction in relation to soil moisture was determined for six tomatoes in each of these soils. There was a decrease in transpiration rate as soil moisture was reduced but the response was not exactly the same on any two of these soils (Figure 5). The tomatoes in sand transpired at nearly a uniform rate until an abrupt reduction on the fourth day when 34 percent of the available water had been exhausted.

The first transpiration reduction occurred when 45 percent, 47 percent and 49 percent of the available moisture had been removed from the compost, muck, and clay

FIGURE 5

Transpiration reduction of tomatoes on four soils with depletion of the available soil moisture. One day time interval between points.


COMPOST
MUCK
TRANSPIRATION — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %


CLAY
SAND
TRANSPIRATION — % OF CONTROL
100
80
60
40
20
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

soils respectively. Muck and clay caused a 14 percent transpiration reduction while compost soil caused a 51 percent reduction at approximately the same soil moisture level.

The transpiration reduction of plants on clay and muck was gradual and started at the same soil moisture level. The transpiration reduction of plants on sand was abrupt and occurred only as the permanent wilting percentage was approached. The transpiration reduction of tomatoes on compost was also abrupt but occurred when half of the available soil moisture remained.

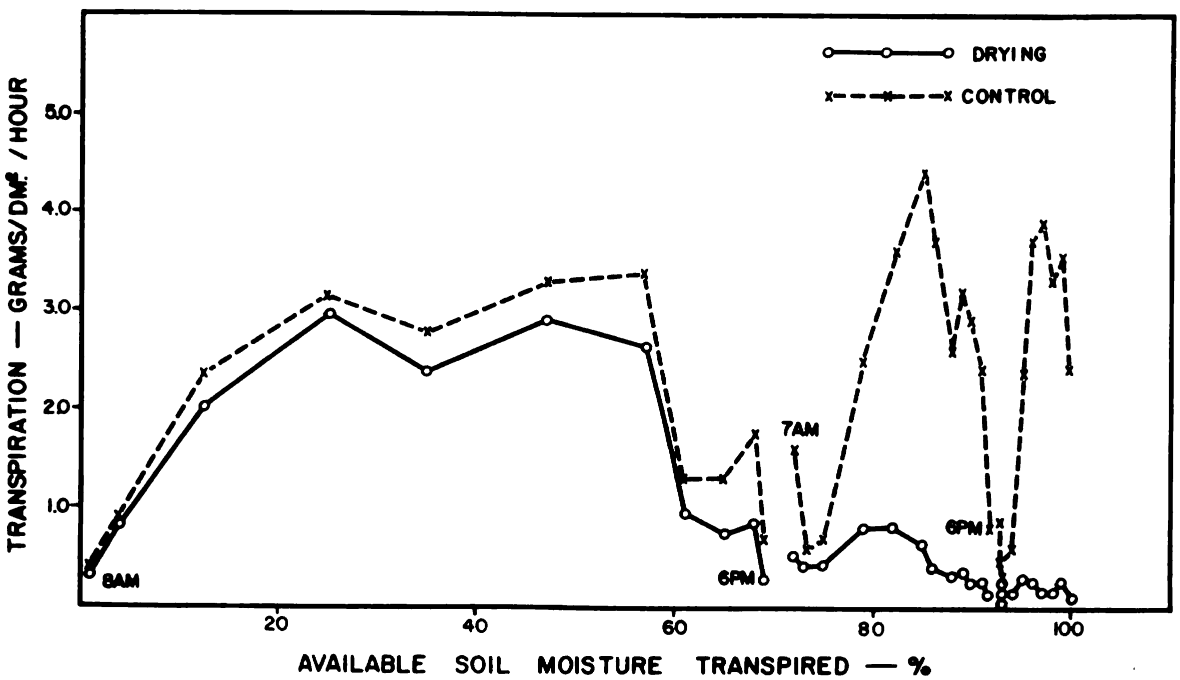
Experiment V: Hourly Transpiration Measurements.

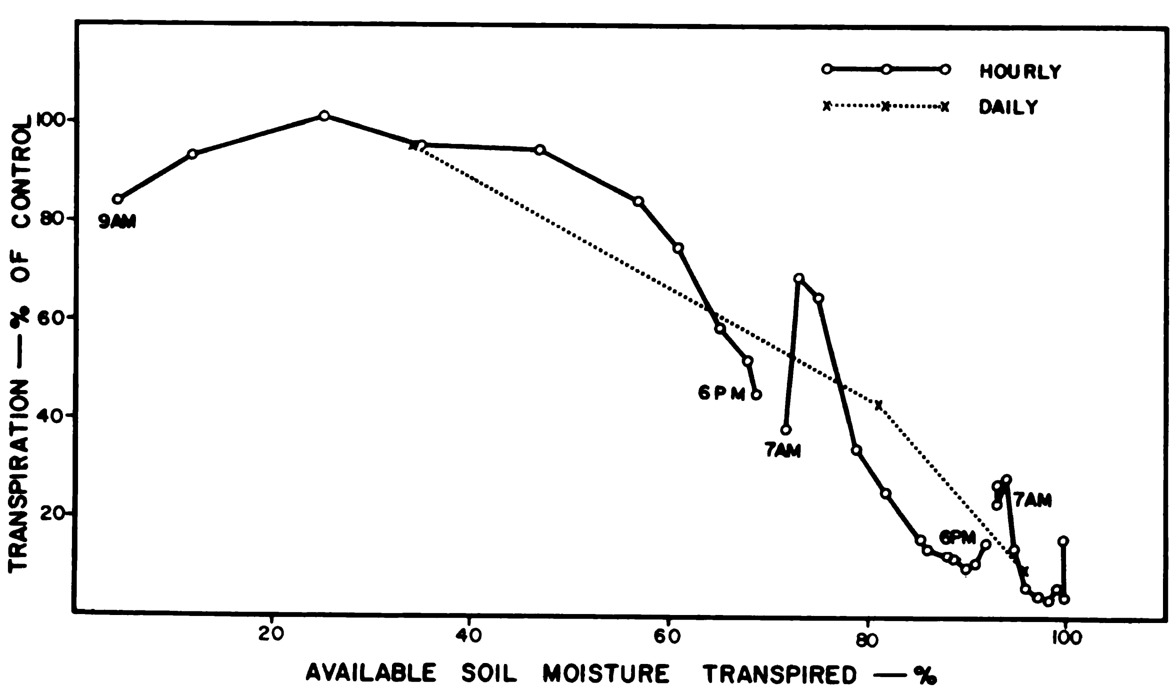
Four containers were filled with 1135 grams of compost soil with a field capacity of approximately 37 percent and a permanent wilting percentage of 17 percent on July 8. The last water was added to bring the soil in these potometers to field capacity at 7:00 a.m. August 3. Transpiration was measured hourly during the next three days from 7:00 a.m. until 6:00 p.m. and the control was watered hourly.

The data showed that this large tomato plant transpired over half of the available water the first day, (Figure 6). A slight reduction in transpiration rate was indicated with the first reduction in soil moisture but it was not marked until 2:00 p.m. or 3:00 p.m. when

FIGURE 6

Hourly transpiration of treatments and controls (top) and reduction of transpiration (bottom) with depletion of available soil moisture. One day time interval between points on broken line (bottom).


DRYING
CONTROL
5.0
4.0
3.0
2.0
1.0
TRANSPIRATION — GRAMS/DM² / HOUR
8AM
6PM
7AM
6PM
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %


HOURLY
DAILY
100
80
60
40
20
TRANSPIRATION — % OF CONTROL
9AM
6PM
7AM
6PM
7AM
20
40
60
80
100
AVAILABLE SOIL MOISTURE TRANSPIRED — %

There was also an abrupt decrease in the transpiration rate of the controls. At 6:00 p.m., 69 percent of the available water had been transpired and transpiration was only 25 percent of the control. At 8:00 the following morning, transpiration of the untreated plants was 69 percent of the controls but fell steadily to 10 percent at 4:00 p.m. when 90 percent of the available soil moisture was exhausted. The transpiration rate for the untreated plants rose only to 28 percent the following day at 9:00 a.m.

The data indicated that there may be less depression of the transpiration rate by low soil moisture, for short periods, when the environment favors rapid transpiration.

DISCUSSION

The data presented here and that of other investigators help to explain some of the differing opinions and apparent discrepencies in the literature concerning the effect of decreasing soil water on transpiration and growth. The data showed that both growth and transpiration decreased as the available moisture was reduced. The reduction occurred before the permanent wilting percentage was reached and before the first wilting of the plant was apparent. The point in the available soil moisture range at which the first depression in growth and transpiration took place varied with the soil (Figure 5), and the time of day the measurements were made (Figure 6). The fundamental causes of the reductions were perhaps less clear.

The effect of decreasing soil moisture on a number of plant or soil processes has been advanced to explain changes in growth or transpiration as the available water was exhausted. (Richards and Wadleigh 1952, Kramer 1949).

Under the conditions of these experiments active transpiration (Kramer 1949) did not appear to be an explanation because the relative transpiration reduction was least at those times of day when it would be expected to be the most because of possible active transpiration of the control (Figure 6).

Another possible explanation for reduction in transpiration would be the exhaustion of water in the soil in contact with the roots and a lesser amount of water becoming available by root growth because of a decrease in rate of root growth or a decrease of available water in the soil into which the roots grew. Kramer and Coile (1940) calculated the amount of water that would become available by daily growth of roots of the winter rye plant of Dittmer (1937) to be 1.6 liters in sand and 2.9 liters in clay at field capacity. This would be approximately the amount of water the plant would transpire and it would appear that as long as roots could grow into soil at field capacity there would be little drop in transpiration. If the soil moisture fell below field capacity or the rate of root growth was decreased by decreasing soil moisture a corresponding decrease in relative transpiration would be expected unless there were a decrease in the transpiration of the controls.

A decrease in rate of water movement through soil to the roots as soil moisture was exhausted would also result in a decrease in transpiration. Veihmeyer (1950) has stated that their experiments indicate that water in soil in contact with the roots is equally available over the range from field capacity to the permanent wilting percentage. Work by Aldrich et al. (1935) indicated that soil moisture not in contact with the roots is not equally available and work by Lewis (1937), Buckingham (1907) and Moore (1939) indicated this water is not available and does not become available unless the roots grow into contact with it. However, Richards and Weaver (1944) found in the pressure membrane apparatus that moisture will move 1 cm. through soil in 24 hours even down to the permanent wilting percentage. Their extraction curves indicate that the rate of movement decreases as the soil moisture decreases and as the diffusion pressure gradient decreases. This decreased rate of soil moisture movement to the roots at higher tensions and decreased pressure gradients could be a partial explanation for some of the changes in transpiration and growth observed in these experiments. If water movement in the soil were the same as water movement in the pressure membrane apparatus water would move toward and become available to the roots at a uniform rate as long as the soil moisture tension and the diffusion pressure gradient remained uniform. As the soil moisture was reduced however, the tension of the water would increase, the rate of movement would decrease, and water would become available to the roots at a slower rate. This could explain a reduction in transpiration with a reduction in soil moisture (Figures 1, 2, 4, 5). It could also explain some of the decreases in transpiration during the daily cycle. The decrease late in the afternoon and the recovery overnight could be due to exhaustion of water near the root and the inability of water to move to the root as fast as it was transpired. During the night the water would move to the root faster than it was transpired resulting in a reservoir in a position to be absorbed during the early morning hours. (Figure 6).

If transpiration exceeded absorption (Kramer 1937, Stoddart 1935) the stress of water in the plant would increase which might be expected to increase the diffusion pressure gradient in the soil resulting in more rapid movement to the root and more rapid absorption by the plant.

A decrease in plant water also results in stomatal closure. Presumably as transpiration exceeds absorption a turgor deficit arises in the epidermal cells resulting in loss of water from the guard cells and closure of the stomata. The degree of turgor deficit will determine the amount of water lost by the guard cells and the degree of closure. Presumably the stomata continue to close until an equilibrium is reached between absorption and transpiration. As absorption decreases turgor deficit increases and stomatal aperture decreases until equilibrium between absorption and transpiration is again established. Increased stress of water in the plant would not be expected to have any appreciable effect on the rate of evaporation because the water stress in the plant at the permanent wilting percentage is of the order of 15 atmospheres while that of the atmosphere at 50 percent relative humidity is between 900 and 1000 atmospheres.

Using nutrient solutions where the complications of water movement through soil to the root and root growth to moisture are eliminated, Haywood and Spurr (1944), Long (1943) and Eaton (1941) found a decrease of absorption proportional to the increase in osmotic pressure of the solution. There seems to be no comparable work for transpiration under known water stress in soils although Wadleigh and Gauch (1948) found a similar relationship existed for cotton leaf elongation. If leaf elongation was a function of soil moisture stress in the present investigation the close relationship between elongation and transpiration (Figures 1 and 2) would support the conclusion that transpiration is also a function of soil moisture stress. To the extent that diffusion pressure gradient determines rate of water absorption a rise in soil moisture stress would decrease absorption and transpiration. There appeared to be a rather close relationship between the soil moisture - tension curves of soils similar to those of Experiment IV (Richards 1949) and the transpiration reduction.

These experiments were set up to minimize the distance between absorbing root surfaces and soil moisture by limiting the soil volume available to the roots. Veihmeyer and Holland (1949) and Dittmer (1938) have found that the soil mass in a container was much more thoroughly permeated by roots than the soil under field conditions. Estimation based on Dittmer's (1937) investigation indicated that tomato root surfaces in these potometers were less than one millimeter apart and the larger the plant the shorter the distance.

If the rate of movement of soil moisture in these containers was of the same order as in similar soils in the pressure membrane apparatus a lag in water movement could hardly explain the decrease in transpiration of these experiments. A similar response after decreasing the distance between roots by using larger plants would support the same conclusion.

The effect of root growth was similarly minimized by the absence of soil masses not permeated by roots.

The hourly changes in relative transpiration data (Figure 6) do not appear to be adequately explained in terms of soil moisture stress alone but soil moisture stress plus diurnal change in weight of the plant may be an adequate explanation.

Availability of water in contact with the roots has been emphasized in recent years. (Veihmeyer and Hendrickson 1950). It would seem that in this work the proximity of the water to the roots was closer than ordinarily occurs in the field and certainly closer than is desirable yet the transpiration of all of the plants of these experiments was reduced before 50 percent of the available water had been transpired except for the tomatoes growing in sand. The average distance between absorbing root surfaces was estimated to be one millimeter. Decreasing this distance by increasing the size of the plant resulted in no appreciable difference in transpiration reduction. There appears to be no other way to explain the data but by the conclusion that water in close proximity to the roots was not equally available for transpiration and growth.

The data from field experiments has been reviewed by Hendrickson and Veihmeyer (1950) and Richards and

Wadleigh (1952). Few of these data have been included in the present discussion because it was felt the variations in root distribution and soil temperature, airation, moisture, structure, and texture to which individual plants are exposed would make the interpretation of the data too complicated to help explain the effect of soil moisture on transpiration and growth.

The data of the present work help explain some of the apparent disagreement in the literature. These data indicated that the soil moisture level at which growth or transpiration was reduced and the amount and rate of reduction varied with the soil, the period during the day when the measurements are made, the plants that are used for the measurements, and the moisture ranges that are compared.

Many workers have used a single soil, made measurements during a short period of the day, compared irrigation regimes which were the same for much of the period, or used perennial plants in which a difference in growth response would tend to be masked by stored food. By proper selection of soil (Experiment IV), period (Experiment V), or range (Experiments I and IV) most of the results in the literature could be matched in these data. The data of Martin (1940) indicated a transpiration reduction similar to that found using compost in these experiments although the first reduction is conservatively reported after two-thirds of the available water is exhausted.

SUMMARY

The object of the investigation was to determine the effect of decreasing soil moisture and transpiration reducing sprays on transpiration and growth of plants. Considerable disagreement appears in the literature concerning the effect of low soil moisture on transpiration and growth.

Transpiration was determined by weight loss of plants growing in soil in containers which were sealed to prevent evaporation. Leaf area increase (the measure of growth used) was determined by daily leaf length - leaf area relationships obtained in this work and from the literature. The different levels of soil moisture were obtained by allowing the treatment plants to remove the soil moisture from the field capacity to the permanent wilting percentage. Changes in growth and transpiration as soil moisture was reduced were determined with respect to plants in soil maintained at field capacity. Four soils, three species and two sprays were used. Both daily and hourly measurements were made. The sprays were made up by the Agricultural Chemistry Department.

The data of these experiments showed that water was

not equally available for transpiration and growth between field capacity and the permanent wilting percentage though the experiments were designed to encourage thorough root permeation of the soil mass and the indicated distance from roots to water was less than would be desired in the field.

There was a close relationship between the reduction in growth and transpiration, and the results indicated that increase in soil moisture stress with decrease in available water was the direct cause of the decrease in transpiration and growth.

There was no appreciable difference in the response of different kinds or sizes of plants on the same soil, but marked differences in response on four different soils. On a compost there was an immediate reduction in relative transpiration and growth with the first difference in soil moisture between the treatments and controls. The relationships between these reductions and available moisture appeared to be linear, while the same relationship with plants on sand, clay and muck appeared to be parabolic. The first reduction with clay and muck occurred when between 40 and 50 percent of the available moisture had been exhausted -- while plants growing in sand showed no decrease until 80 percent of the available moisture was exhausted.

Data from plants weighed hourly showed that there was a continual hourly change in transpiration reduction during three successive 12 hour periods.

Two transpiration reducing sprays reduced transpiration and growth approximately 10 percent for each percent of oil content but whether the effectiveness of the spray was dissapated by growth or the transpiration reductions due to the spray and reduced soil moisture were not additive was not clear.

The leaf - area leaf - length relationships of castor and snap bean were determined.

The data obtained indicated that much of the apparent disagreement in the literature concerning the effect of reductions of soil moisture or transpiration and growth can be explained because of different soils, the comparison of different soil moisture ranges, or measurements during different periods of the day.

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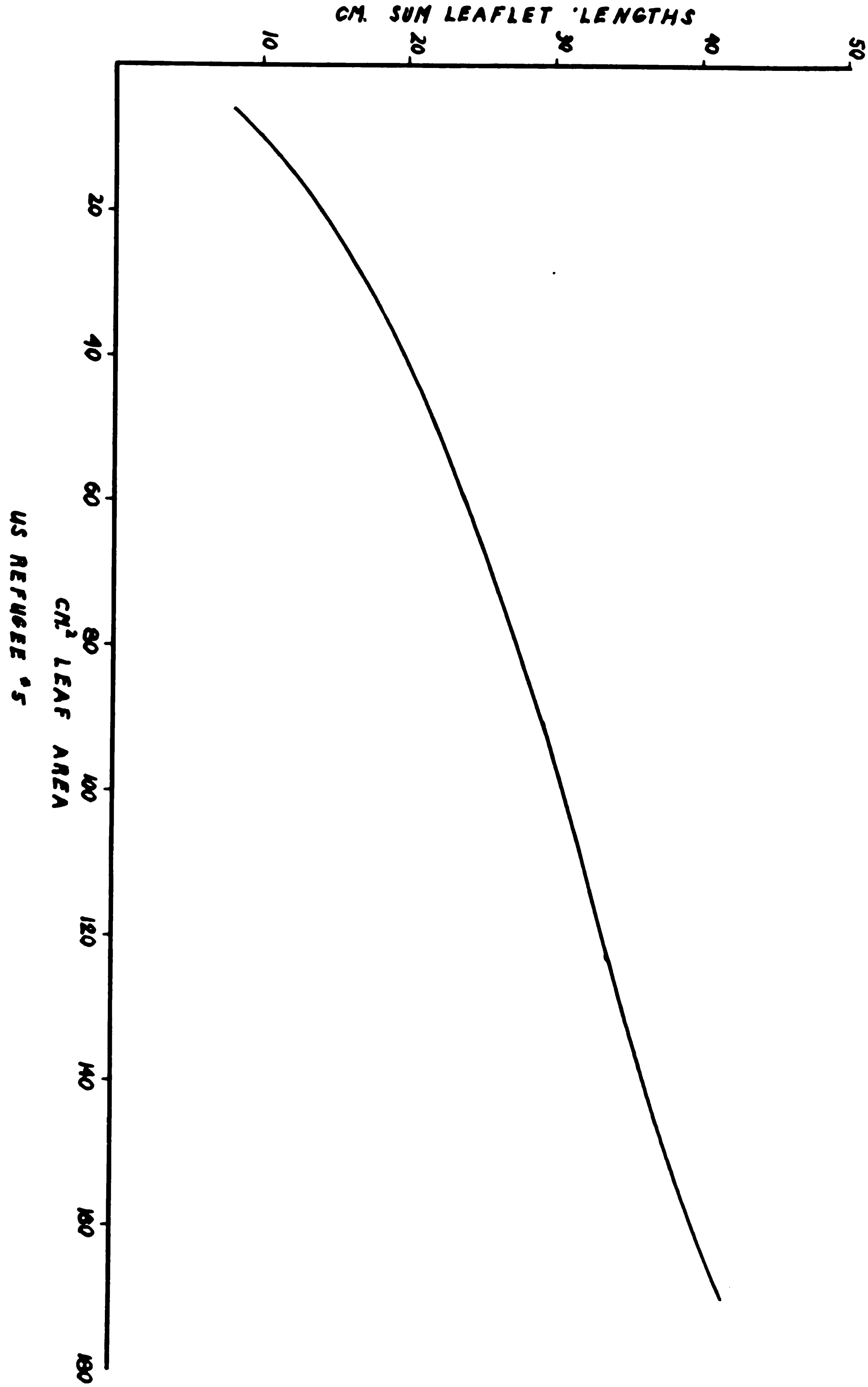
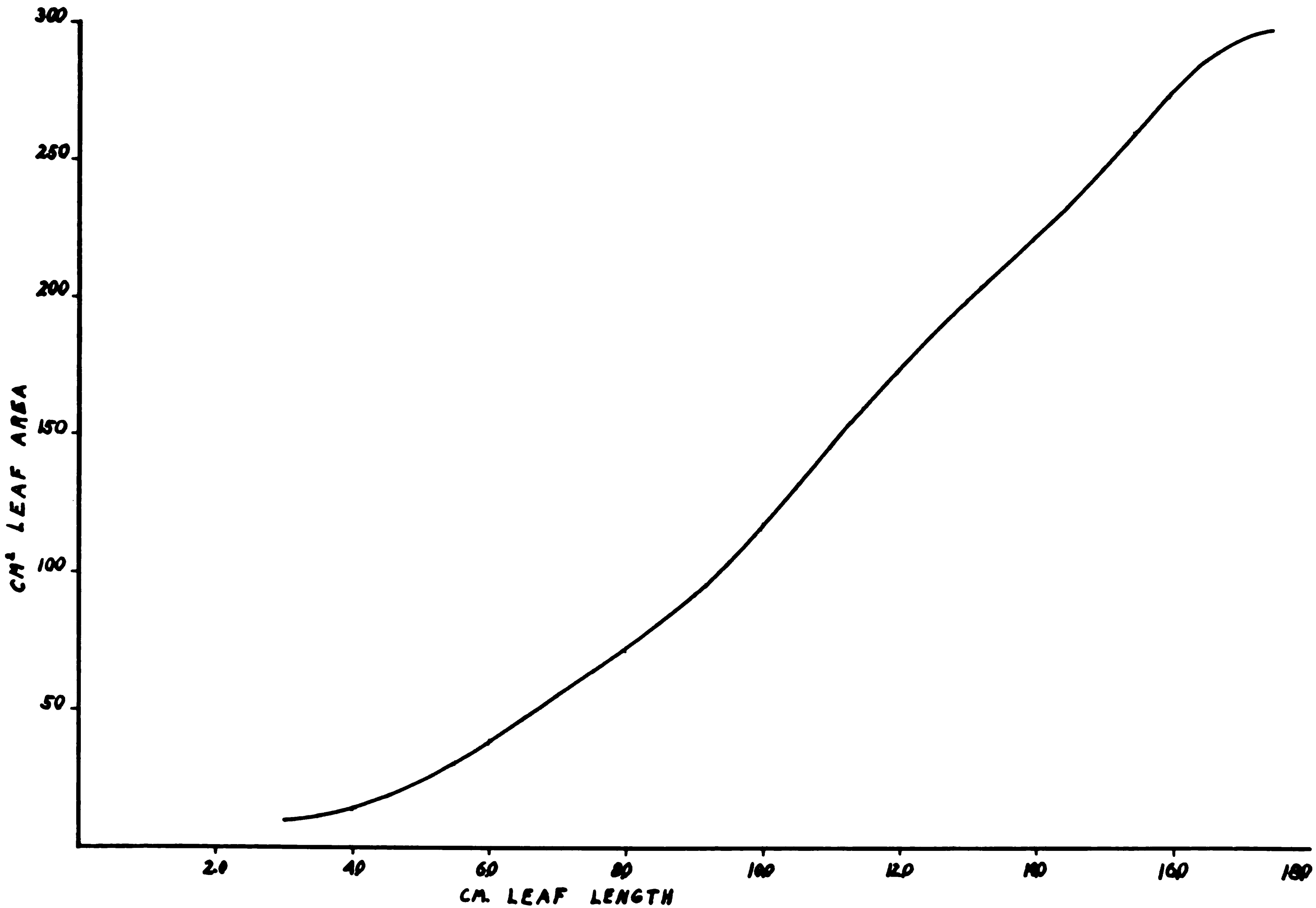
APPENDIX FIGURE I

Leaf length - leaf area curve for U.S. Refugee # 5 Snap beans.


CM. SUM LEAFLET LENGTHS
10
20
30
40
50
20
40
60
80
100
120
140
160
180
CM.² LEAF AREA
US REFUGEE #5

APPENDIX FIGURE II

Leaf length - leaf area curve for Burpee's Castor Bean.



BURPEE'S CASTOR BEANS

APPENDIX TABLE I: RELATION LEAF LENGTH TO AREA

Snap Beans U.S. Refugee #5		Castor Beans (Burpee's)	
Length cm.	Area cm^2.	Length cm.	Area cm^2.
8	6.0	3.0	10
9	7.5	3.5	11
10	9.5	4.0	13
11	12.0	4.5	18
12	14.5	5.0	22
13	17.0	5.5	31
14	20.0	6.0	39
15	23.0	6.5	47
16	26.0	7.0	56
17	29.5	7.5	64
18	33.0	8.0	72
19	37.0	8.5	81
20	41.0	9.0	91
21	45.0	9.5	103
22	50.0	10.0	116
23	55.0	10.5	131
24	60.0	11.0	146
25	64.0	11.5	160
26	70.0	12.0	173
27	76.0	12.5	185
28	82.5	13.0	197
29	89.0	13.5	209
30	95.5	14.0	221
31	102.5	14.5	233
32	109.0	15.0	247
33	116.0	15.5	260
34	123.0	16.0	274
35	129.0	16.5	285
36	136.0	17.0	290
37	143.0	17.5	295
38	149.0		
39	155.0		
40	161.0		
41	167.0		
42	173.0		