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PRELIMINARY OBSERVATIONS ON THE EFFECT OF
 LIGHT INTENSITY, TEMPERATURE, AND WATER
 SUPPLY ON GROWTH AND TRANSPIRATION OF YOUNG
 BEET PLANTS UNDER CONTROLLED CONDITIONS

by

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I. INTRODUCTION

This paper continues a series concerning the relation between transpiration, growth, and water requirement of higher plants under different environmental conditions (ABD EL RAHMAN *et al.*, 1959). In the previous papers the effect of several environmental factors on growth and transpiration of tomato are discussed; in this paper the effect of light intensity, temperature, and water supply on growth and transpiration of sugar beet will be described.

This plant species was chosen for the following reasons. Under controlled conditions of temperature and humidity the optimum temperature for growth of beets is between 20° and 23° C (ULRICH, 1952), which is lower than that for growth of tomato (WENT, 1957). At temperatures lower than the optimal one, growth of tomato is retarded much more than that of beet. Besides, it is of interest to study the effect of environmental factors on storage of material in roots and stems, and its possible relation to transpiration and water economy.

No experimental data on growth of beet in connection with transpiration under controlled conditions could be found in literature. As an example of field experiments in the Netherlands, the investigations of BOONSTRA (1939, 1942) on the relation between transpiration and production of beet plants in containers should be mentioned. Recently, BOONSTRA's results are reconsidered by DE WIT (1958), who calls attention to the observed linear relation between dry matter production and transpiration under the present field conditions, the curve going through the origin. A water loss of 1 kg by transpiration corresponds with 6.1 g dry matter production. This observation indicates a rather constant value of the water requirement during the growing season. Taking into consideration the variation in temperature and radiation in a temperate climate as in the Netherlands, this is a rather surprising observation.

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II. MATERIAL AND METHODS

Seed clusters of the beet variety "KUHN P" were soaked in water for 24 hours to remove possible germination inhibitors. The clusters were then sown in seed boxes in a cold glass house. The seedlings were transplanted two weeks afterwards in metal pots with a height of 20 cm and a diameter of 10 cm. These pots were filled with 2 kg air-dry loam soil, the pF-curve of which was known. The experiment began three weeks after transplantation.

Before the experiment, the leaf area, the fresh weight, and the dry weight of the shoot and the roots of some plants were determined and considered as initial values. The other plants were transferred to 4 constant temperature rooms. The respective temperatures remained constant during the experiment, with a deviation of less than 1.5°C. The relative air humidity was not controlled, and varied with the outside conditions. Thanks to rather constant weather conditions during the experiment this variation in humidity was at most 15% at 25.8°C. Table 1 summarizes the experimental conditions of temperature and humidity of the air.

TABLE 1. Air temperature and humidity of the air in the experimental compartments.

Air temperature (°C)	Mean rel. humidity of the air (%)	Vapour pressure (mm Hg)	Vapour pressure deficit (mm Hg)
25.8	39	9.7	15.2
20.2	45	8.0	9.8
15.5	58	7.7	5.5
12.2	60	6.4	4.3

The plants were illuminated from above by day light fluorescent tubes, "PHILIPS TL 55", during 14 hours per day. The experimental set-up was surrounded by white curtains to keep light conditions more homogeneous, and the mutual position of the plants was changed every day, at each level of light intensity.

The light intensity was measured with a cos *i*-corrected flat light meter in horizontal position at the height of the plant. Table 2 gives the 4 levels of light intensity at the 4 temperature treatments.

TABLE 2. Levels of light intensity at the four temperature compartments, expressed in $10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$, and measured with a flat cos *i*-corrected light meter in a horizontal position.

Level of light intensity	Air temperature (°C)	25.8	20.2	15.5	12.2
	1		3.75	2.6	2.4
2		1.75	0.95	0.90	1.25
3		1.05	0.70	0.60	0.75
4		0.15	0.20	0.20	0.20

For the light source used (400–700 m μ) and for this leaf type one incident erg corresponds to about 2.6×10^{-18} EINSTEIN absorbed (GAASTRA, 1959). Owing to the position of the leaves, which deviates from horizontal and to mutual shading the actual light absorption of the entire plant certainly is smaller; the complicated problem of the absorption of an entire plant under conditions like those applied here, will not further be considered.

Nine pots were used at each level of light intensity in a constant temperature compartment, and three irrigation treatments were applied (A, B and C). Thus, there were three replicates for each treatment combination. In group A, water was added to bring back the soil to field capacity as soon as 20% of the total available water in the soil was used; in group B and C as soon as 40% and 80% of the available water were used respectively (wilting point is 100% used). Thus respectively A, B and C would correspond to a mean available soil moisture content of 90, 80, and 60%. Under transpiration conditions of low temperature or low light intensity, however, the experimental period of 6 weeks was too short to reach the mean available soil moisture content indicated for B, and C. The real average availability of soil moisture

could be found afterwards for every combination of light intensity and temperature, since water loss by transpiration was determined daily by weighing. Table 3 represents the calculated average available soil moisture content in %.

TABLE 3. Mean availability of soil moisture in % for the different irrigation regimes aimed at. Field capacity is 100% available soil moisture, wilting point is 0% available soil moisture.

Irrigation regime		A	B	C
Air temperature (°C)	Level of light intensity			
25.8	1	90	80	60
	2	90	80	63
	3	90	82	70
	4	92	88	85
20.2	1	90	83	64
	2	92	84	66
	3	92	85	70
	4	93	90	85
15.5	1	92	82	65
	2	92	88	80
	3	95	90	82
	4	100	100	100
12.2	1	95	90	80
	2	95	90	85
	3	97	90	85
	4	100	100	100

A thin dry upper layer of soil was always present, since water was added by way of a funnel at a distance of about 5 cm below the soil surface. On the soil two half rings were put around the plant, made of 1 cm thick white isolating polystyrenedross material, „TEMPEX”, in order to reduce evaporation of the soil. In this experiment, the latter proved to be negligible.

At the end of the experiment the plants were harvested, and fresh weight and dry weight of shoot, dry weight of roots, number of leaves, leaf area, etc., were determined. The dry weight of roots mainly consists of the storage organ, since the small thin roots are easily lost at harvest.

III. EXPERIMENTAL RESULTS

1. TRANSPIRATION

The total water loss by transpiration shows wide variation under different conditions, viz., between 1082 g/plant and 55 g/plant. Table 4 shows that transpiration is affected by temperature, water supply, and light intensity.

Total water loss by transpiration is affected to a large extent by water supply (fig. 1), especially under conditions of high transpiration, such as high light intensity and high air temperature. Under conditions of low transpiration, this influence is less obvious, and more irregular results are obtained, also owing to the smaller number of replicates. This is in agreement with earlier results (KUIPER and BIERHUIZEN, 1958, ABD EL RAHMAN and BIERHUIZEN, 1959). There is a slight indication that at 25.8° C and 20° C (●—●) the effect of the irrigation regime on transpiration is more pronounced between 60 and 80% available water content than above 80%. A possible

TABLE 4. The effect of water supply, temperature, and light intensity on the total water loss in g. The mean availability of soil moisture is given in table 3, the levels of light intensity in table 2.

Irrigation regime		A	B	C
Air temperature (°C)	Level of light intensity			
25.8	1	1082	926	659
	2	818	839	562
	3	437	426	370
	4	177	167	161
20.2	1	561	531	489
	2	344	387	326
	3	318	327	261
	4	103	138	154
15.5	1	372	371	281
	2	196	157	189
	3	236	183	231
	4	100	113	82
12.2	1	271	262	235
	2	197	175	186
	3	158	148	127
	4	64	55	64

explanation is that at a higher level of available soil moisture, the decrease in transpiration with decrease of water supply is low, whereas below a certain level of available water transpiration may be much more affected. As to the mechanism, water supply may variously influence transpiration of beet plants. The water uptake capacity of the root hairs and the extension of the roots system may change, with possible influences on the rate of leaf expansion and the stomatal behaviour.

The effect of light intensity on the integrated water loss is demonstrated in fig. 2 (left side average available soil moisture content 90-100%, right side 60-70%). At each air temperature, slightly idealized curves have been drawn through the experimental points. It is clear that curves of the MITSCHERLICH-type are obtained, the slopes depending on the temperature. At 90-100% of the available soil moisture content the saturation level is only approximated within the range of light intensities studied at 12.2° C, while at higher temperatures the corresponding saturation levels are reached above 3×10^4 or 4×10^4 erg.sec⁻¹.cm⁻² incident energy. These saturation levels decrease with decrease of the mean moisture content to 60-70% (see fig. 2, right side). Explanation of the MITSCHERLICH-curves of fig. 2 is rather premature at the moment. It seems that transpiration of the plant increases with increasing light intensity, its rate depending on factors such as the rate of leaf expansion and the stomatal light response. Both are affected by light intensity and water supply. The saturation levels are mainly determined by the minimum resistance to water flow in the plant; the latter depends on the factors mentioned above, and on others.

Temperature may influence the total water loss by transpiration via an effect on plant growth. Since transpiration is a diffusion process, temperature

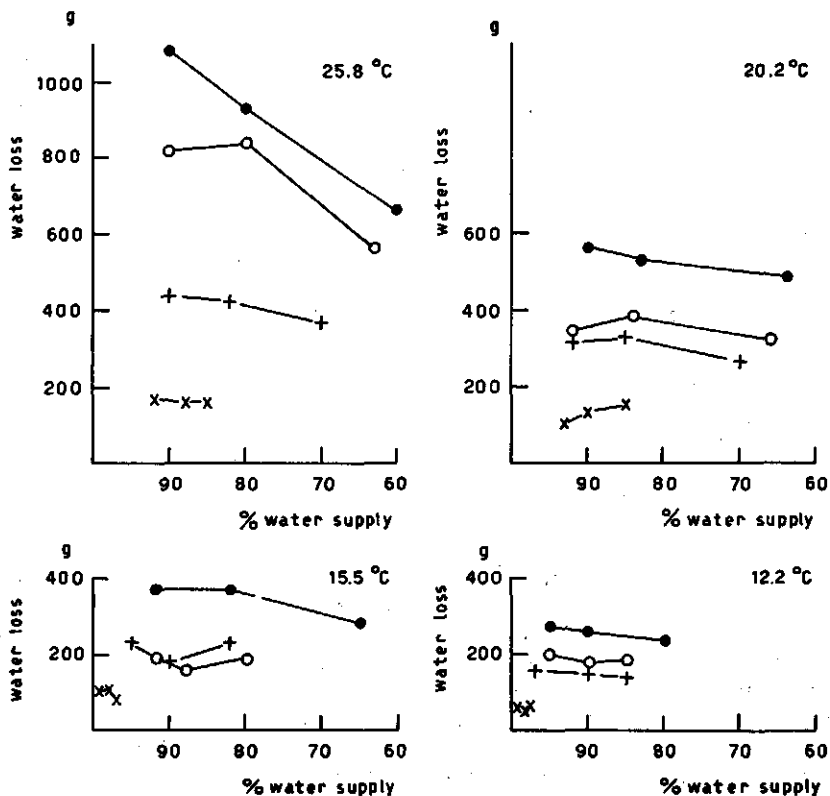


FIG. 1. The effect of air temperature, light intensity, and water supply on total water loss by transpiration. The levels of light intensity, 1: ●—●, 2: ○—○, 3: +—+, and 4: ×—×, are given in table 2. The water supply is expressed as mean available soil moisture content in %.

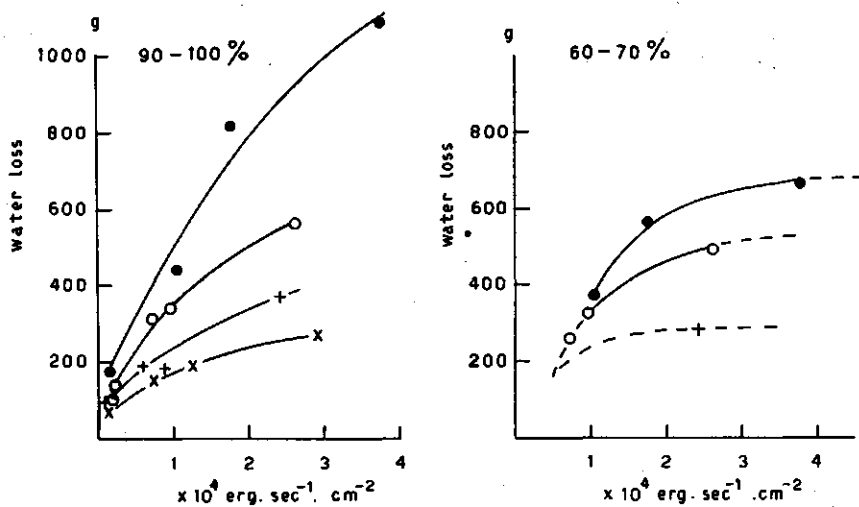


FIG. 2. The effect of light intensity on total water loss by transpiration, at two different irrigation regimes, at 90-100% (left side) and at 60-70% (right side) mean available soil moisture content respectively ●—● 25.8°C, ○—○ 20.2°C, +—+ 15.5°C, ×—× 12.2°C.

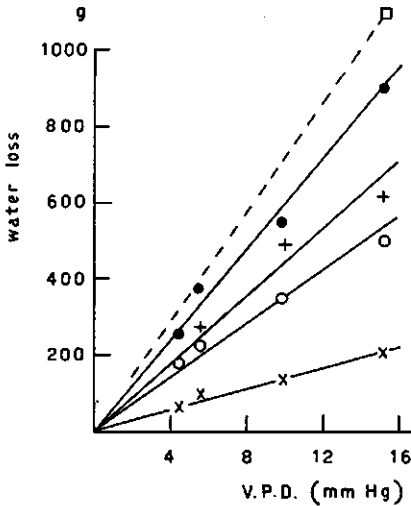


FIG. 3.
The effect of vapour pressure deficit of the air (V.P.D.) on total water loss by transpiration. Mean available soil moisture content 90-100%: □ 3.75×10^4 , ● 2.5×10^4 , ○ 1×10^4 , × 0.25×10^4 erg.sec⁻¹.cm⁻². Mean available soil moisture content 60-70%: + 2.5×10^4 erg.sec⁻¹.cm⁻².

also affects transpiration indirectly via the rate of diffusion of water vapour from the inside of the leaf to the surrounding air.

It is clear from earlier investigations that the differences between leaf and air temperature are small under the present experimental conditions (ABD EL RAHMAN and BIERHUIZEN, 1958). It may thus be assumed that transpiration is directly proportional to the water vapour pressure deficit of the air (as given in table 1), and transpiration can be determined for several levels of light intensity and for different irrigation regimes. The curves of fig. 3 show that the above assumption practically holds true for this experiment. Linear curves, passing through the origin, are obtained. The slopes of these curves depend on light intensity and water supply.

From the curves of fig. 3 and some analogous ones, the two curves of fig. 4 were made. In this figure, transpiration per mm vapour pressure deficit is plotted against light intensity for two irrigation treatments. The curve of the

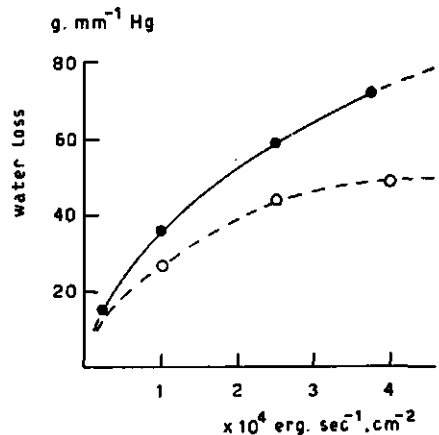


FIG. 4.
The effect of light intensity on transpiration per mm vapour pressure deficit ($T/V.P.D.$) ● $90-100\%$, ○ $60-70\%$ mean available soil moisture content.

lower irrigation treatment (60-70% mean available soil moisture content) is given in broken lines, since some values extrapolated from the curves of fig. 2 were used. Again, two curves of the MITSCHERLICH-type are obtained, showing the effect of light intensity and irrigation treatment on transpiration.

Summarizing the above results, the water loss by transpiration during a growth period of 6 weeks may be described as:

$$T = T_{max} (1 - 10^{-aI})$$

and

$$T_{max} = (f(M)) \cdot (V.P.D.)$$

in which

- T, T_{max} = transpiration (g water),
- a = coefficient,
- I = light intensity (10^4 erg.sec⁻¹.cm⁻²),
- M = mean available soil moisture (%),
- $V.P.D.$ = vapour pressure deficit (mm Hg).

In our experiments we found the following values for $T_{max}/(V.P.D.)$ and a :

Mean available soil moisture (%)	$T_{max}/V.P.D.$ (g.mm ⁻¹ Hg)	a
90-100	90	-0.18
60- 70	50	-0.36

It should be noted that in the formula given above, $V.P.D.$ includes the temperature effect. Since a positive correlation between temperature and $V.P.D.$ exists in our experiments (see table 1), a direct temperature effect is not observed.

2. DEVELOPMENT OF FOLIAGE

Data was also collected on the number of leaves produced by the plants, the total leaf area, and some morphological characters of the leaves. Some of the results obtained will be discussed in the following paragraphs. At the beginning of this experiment, the average number of leaves of the beet plants was 2.5. After 6 weeks it had increased about threefold in most cases (table 5). The number of leaves produced by the plants does not show significant differences at various levels of water supply and temperature, but it is possible that it is slightly higher at the highest water supply and the highest temperature. As regards light intensity, a smaller number of leaves is observed at the lowest level while at higher light intensities the number of leaves reaches a rather constant value. The irregularity of the data presented in table 5 is probably due to the small number of replicates for each treatment.

The initial leaf area was 10.5 cm². Under the conditions of our experiment the total leaf area varied between 15 and 221 cm² after 6 weeks (table 5). It is evident that the increase in leaf area is affected by water supply, light intensity, and temperature.

The effect of the irrigation regime on total leaf area is presented in fig. 5. At air temperatures of 25.8° and 20.2° C leaf area generally decreases with decreasing water supply. At lower air temperatures, viz. 15.5° and 12.2° C, more irregular results are obtained and it is not possible to draw any conclusion about the effect of the water supply. The irregularity at these tem-

TABLE 5. The effect of water supply, temperature, and light intensity on the mean number of leaves and the total leaf area in cm² at the end of the experiment. At the beginning of the experiment the mean number of leaves was 2.5 and the leaf area 10.5 cm². The levels of light intensity are given in table 2, and the mean availability of soil moisture in table 3.

Irrigation regime		Number of leaves			Total leaf area		
		A	B	C	A	B	C
Air temperature (°C)	Level of light intensity						
25.8	1	8	7	7.7	190	179	177
	2	9.7	11.3	9	221	221	159
	3	9.3	8.7	6.7	137	128	77
	4	6.3	6.3	4.3	15	20	16
20.2	1	9	8	7.7	146	156	139
	2	9.7	7.7	7	137	119	109
	3	9	10.3	7.7	123	137	78
	4	4.5	5.3	4.3	16	19	17
15.5	1	7.7	8.7	7	132	161	113
	2	7.7	9	6.7	121	112	93
	3	9	6.7	7	146	91	113
	4	6.7	6.7	6	26	35	31
12.2	1	8	8.7	5.7	80	95	69
	2	7.3	6.7	5.7	76	74	48
	3	7	6.3	7	73	63	67
	4	4.7	5.3	5.3	22	16	23

peratures is probably due to the small number of replicates. The effect of water supply thus is significant only at higher temperatures and at higher light intensities. The rate of leaf expansion probably depends somehow on the water uptake capacity of the root system.

The effect of light intensity and air temperatures on the total leaf area is given for two irrigation treatments, viz., 90-100% average available soil moisture content (fig. 6, left) and 60-70% (fig. 6, right). At 90-100% available moisture, typical curves of the BLACKMAN-type are obtained within the range of light intensities studied. Up to 10^3 erg.sec⁻¹.cm⁻² incident energy, growth of leaves is absent. Above this level, a linear relation between total leaf area and light intensity exists which seems to be practically independent temperature. Light saturation is reached at about 10^4 erg.sec⁻¹.cm⁻² (12.2° C) and at about 1.5×10^4 erg.sec⁻¹.cm⁻² (25.8° C). Because of the small number of data available in the region of 60-70% available moisture, somewhat idealized curves of the BLACKMAN-type have been drawn through the experimental points (fig. 6, right). It appears that the curves at 60-70% and 90-100% are nearly identical in the linear portions. However, at each temperature the saturation level is somewhat lower at the lower water supply. This is demonstrated in fig. 7 which represents the relationship between the total leaf areas at light saturation and temperature for the two different irrigation regimes. A linear relationship appears possible, indicating a complicated influence of temperature on the processes, resulting in leaf expansion.

It may be concluded that under light limiting conditions (below 1×10^4

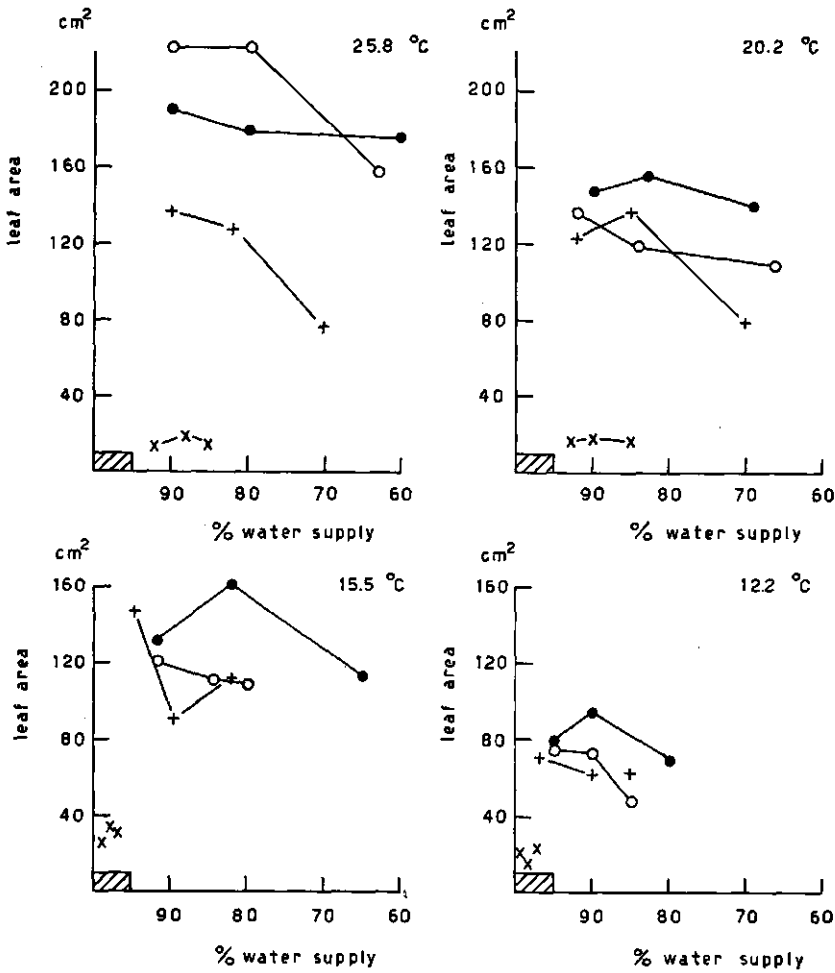


FIG. 5. The effect of water supply on total leaf area at the end of the experiment. Levels of light intensity, 1: ●—●, 2: ○—○, 3: +—+, and 4: ×—×, are given in table 2. The water supply is expressed as mean available soil moisture content in %.

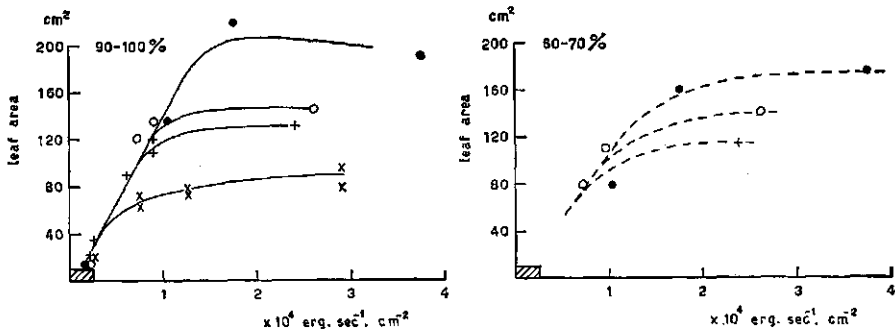


FIG. 6. The effect of light intensity on total leaf area, at two different irrigation regimes, at 90-100% (left side) and 60-70% (right side) mean available soil moisture content respectively. ●—● 25.8°C, ○—○ 20.2°C, +—+ 15.5°C, ×—× 12.2°C.

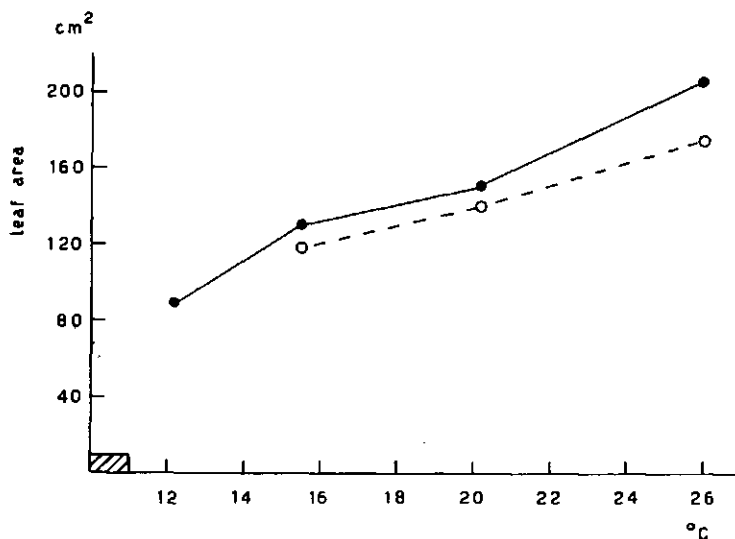


FIG. 7. The effect of air temperature on total leaf area at light saturation (above 1.5×10^4 erg. sec⁻¹.cm⁻²). ●—● 90-100%, ○-----○ 60-70% mean available soil moisture content.

or 1.5×10^4 erg.sec⁻¹.cm⁻²) the rate of leaf expansion will be determined by the input of light quanta (fig. 6). At saturating light intensity the total leaf area is determined by temperature and water supply (fig. 7).

Since water loss by transpiration has been determined every day, the last day of experiment could be used for measuring the transpiration rate per unit leaf area. The data show that it depends on light intensity, temperature, and the availability of soil moisture during this day, but a more quantitative analysis was not possible.

At the end of the experiment, length and width of some leaves was determined for most of the experimental conditions. The results are summarized in table 6. It is apparent from this table that length and width of leaves are rather constant. Only at 12.2° C both length and width are slightly smaller, and this also holds at the lowest light intensity for the other temperature treatments.

In some cases the leaves showed a reddish color, which is probably caused by the formation of anthocyanin. The reddish color was clearly visible at 12.2° C at the higher levels of light intensity, viz. 1 and 2. It was also observed at 15.5° C at the highest intensity.

3. FRESH WEIGHT AND WATER CONTENT OF THE SHOOT

Under the conditions of the experiment, the fresh weight of the combined leaves varies from 0.6 g to 10.0 g (table 7) and depends on the irrigation regime, the light intensity, and the temperature. It is not adequate to present all these figures, but in fact they show a striking resemblance to those obtained for total leaf area in their variation with temperature, light intensity and water supply. For this reason, fresh weight of shoot was plotted against

TABLE 6. Length and width of leaves in cm at the end of the experiment. Initial values: leaf length 4.6 cm, length of the leaf blade 2.7 cm, width of the leaf blade 1.4 cm, L/W ratio 3.3. Levels of light intensity are given in table 2, mean availability of soil moisture in table 3.

Air temperature (°C)	Level of light intensity	Irrigation regime	Length of leaf (L)	Length leaf blade	Width of leaf (W)	L/W ratio
25.8	1	A	15	9	5	3
	1	B	16	8.5	4.5	3.5
	1	C	14.5	8.5	4.5	3.2
	2	A	16.5	10	5.5	3
	3	A	15	8	5	3
20.2	4	A	6	3.5	2	3
	1	A	12	7.5	5	2.4
	2	A	13	8	4	3.2
	3	A	12	7	3.5	3.4
15.5	4	A	9	4	2.5	3.6
	1	A	14	8.5	4.5	3.1
	2	A	14	7.5	5	2.8
	3	A	14	8	4.5	3.1
12.2	4	A	8.5	4.5	2.5	3.4
	1	A	9	7	4	2.3
	2	A	10.5	7.5	4	2.6
	3	A	11	6.7	3.5	3.1
	4	A	6.5	4.5	2.5	2.6

total leaf area (fig. 8). It is rather surprising to observe that the points lie more or less on a straight line passing through the origin which can be described by the equation $y = 0.045x$, in which y represents the fresh weight of the leaves in g and x the leaf area in cm^2 . It may be concluded that under all experimental conditions there is an intimate relationship between leaf area and fresh weight of the leaves. Since dry matter of the leaves is only a small, be it variable part of the fresh weight of the leaves, it is not surprising that under all conditions of the experiment the total amount of water, present in the leaves was fairly proportional to the growth of the leaves.

The water content of the leaves, expressed in g water per g dry matter can be calculated from the data on fresh weight and dry weight (table 7). It decreases rapidly with increasing light intensity to a minimum value. At 25.8°C and 20.2°C it is even higher than at 12.2°C and 15.5°C . This is surprising since transpiration is much stronger at the higher temperatures. Nevertheless, it seems probably that the water percentage of the leaves is determined by the environmental conditions rather than by the actual rates of water uptake and transpiration.

4. DRY MATTER PRODUCTION

In this section, the data on the dry matter production of the shoot (*viz.* the leaves) and of the roots will be presented. Since, at harvest, the thinner roots are easily lost, the dry weight of the roots mainly consists of that of the thicker, storage parts. Dry matter production could be calculated from the data obtained at harvest and the dry weight of the shoot and root at the be-

TABLE 7. The effect of water supply, temperature, and light intensity on the fresh weight of the shoot in g and the water content of the shoot (g water/g dry weight). The levels of light intensity are given in table 2, the mean availability of soil moisture in table 3.

Irrigation regime		Fresh weight of shoot			Water content of shoot		
		A	B	C	A	B	C
Air temperature (°C)	Level of light intensity						
25.8	1	8.52	8.68	8.28	6.8	6.6	8.0
	2	9.67	10.23	7.76	10.6	10.7	10.9
	3	5.94	6.32	3.90	12.8	13.2	12.3
	4	0.80	0.96	0.63	18.2	18.1	16.1
20.2	1	6.38	7.46	6.58	7.0	7.4	5.8
	2	5.38	4.93	4.75	11.5	11.3	11.9
	3	5.36	6.13	3.68	13.9	13.4	11.7
	4	0.83	1.00	0.82	18.4	18.1	15.8
15.5	1	5.63	7.01	4.78	6.3	7.4	7.1
	2	4.86	4.11	3.90	10.1	9.2	7.7
	3	5.65	4.01	4.25	11.9	10.8	8.8
	4	1.38	1.64	1.39	16.0	15.6	11.7
12.2	1	4.21	4.88	3.42	6.3	6.2	5.2
	2	4.02	3.49	2.58	8.6	8.1	5.5
	3	3.05	3.18	3.03	9.6	9.9	9.9
	4	1.07	0.94	1.16	13.9	14.5	15.1

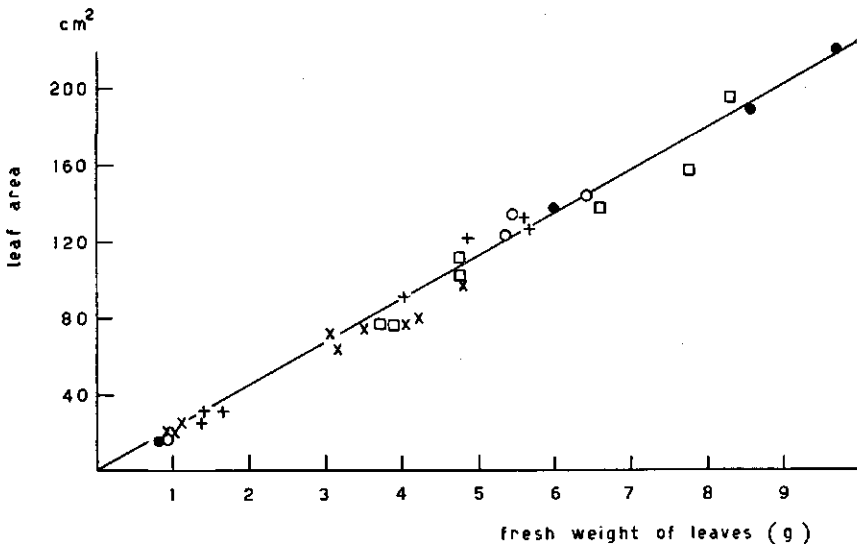


FIG. 8. The relation between fresh weight of the leaves and total leaf area. Mean available soil moisture content 90-100%: ● 25.8°C, ○ 20.2°C, + 15.5°C, × 12.2°C. Mean available soil moisture content 60-70%: □ all temperatures.

TABLE 8. The effect of water supply, temperature, and light intensity on the dry matter production of the shoot (leaves) and of the roots in mg. Initial dry weight of the shoot was 0.036 g and of the roots 0.006 g. Levels of light intensity are given in table 2, mean availability of soil moisture in table 3.

Irrigation regime		Shoot			Roots			Total		
		A	B	C	A	B	C	A	B	C
Air temperature (°C)	Level of light intensity									
25.8	1	1216	1295	989	770	518	289	1986	1813	1278
	2	878	907	779	139	115	111	1017	1022	990
	3	413	441	282	40	35	221	471	476	303
	4	8	17	3	-3	-3	-3	5	14	0
20.2	1	875	977	850	417	363	300	1292	1340	1150
	2	433	400	363	41	35	45	474	435	408
	3	350	424	279	25	23	23	375	447	302
	4	9	19	16	5	-1	3	14	18	19
15.5	1	863	1023	637	450	288	204	1313	1311	841
	2	446	419	475	77	75	70	523	494	545
	3	438	336	447	30	34	46	468	370	493
	4	50	69	49	-2	2	-2	48	71	47
12.2	1	631	745	628	424	424	340	1055	1169	968
	2	429	395	437	152	100	81	581	495	518
	3	281	286	270	34	46	46	315	332	316
	4	41	29	41	1	0	-1	42	29	40

ginning of the experiment, which were 0.036 g and 0.006 g respectively.

It is clear from table 8 that the dry matter production of the shoot is affected by moisture supply, light intensity, and temperature.

The effect of water supply is presented in fig. 9. It is clear from this figure that at a high level of light intensity the gain in dry weight shows a tendency to increase with a reduction of average available soil moisture content from 100% to 80%. However, due to the small number of replicates a clearer statement is impossible. Below 80% average available moisture content a pronounced reduction in gain in dry weight is apparent. At lower levels of light intensity more irregular results are obtained, which is probably also due to the small number of replicates. The observed decrease in dry matter production of the shoot with decreasing water supply is at least partly due to a smaller leaf expansion and consequently to reduced light absorption of the plant. Other influences, e.g. an effect of water supply on the rate of photosynthesis, may also be important for dry matter production of the shoot.

The effect of light intensity on dry matter production of the leaves for two irrigation regimes, is given in fig. 10, i.e. 80-100% and 60-70% mean available soil moisture content respectively. For each level of temperature and water supply a more or less characteristic curve of the MITSCHERLICH-type is found. In this experiment no saturation levels for dry matter production of the shoot are reached, since these levels probably are found at a light intensity higher than 4×10^4 erg.sec⁻¹.cm⁻². The shape of the curve depends on temperature and water supply. It may be assumed that temperature and perhaps also water supply affect the gain in dry weight of the shoot via the

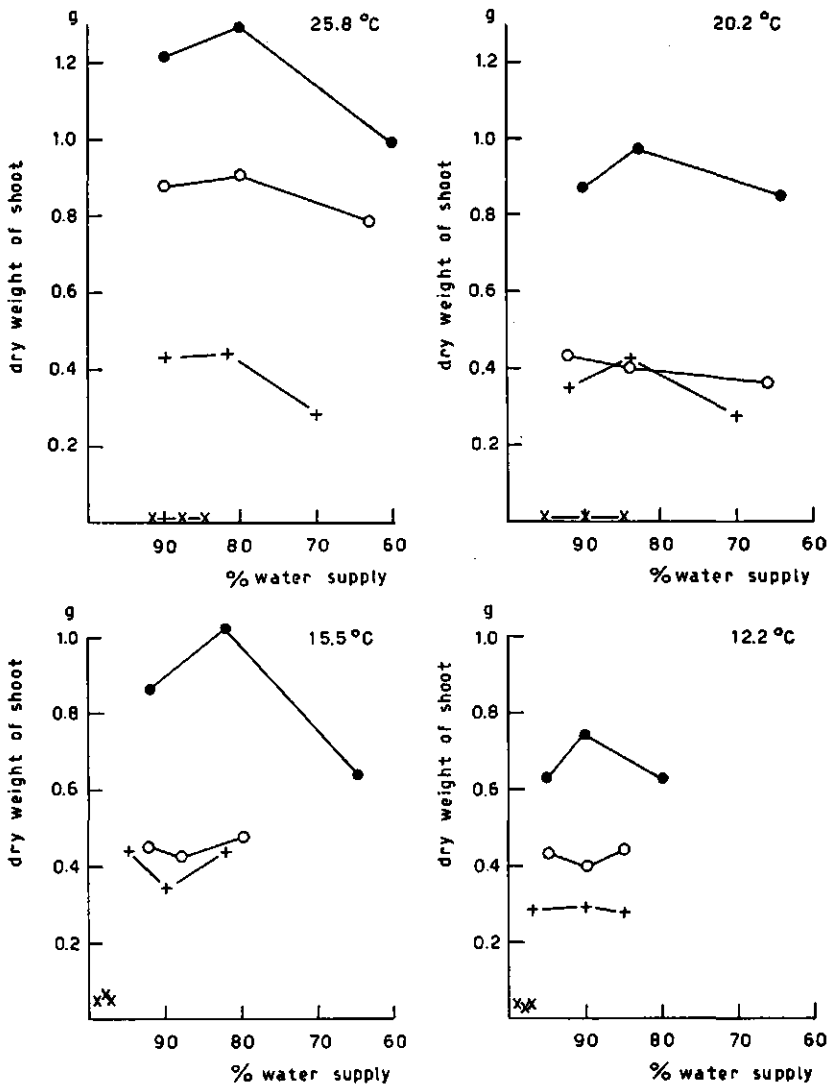


FIG. 9. The effect of water supply on gain in dry weight of the shoot. The levels of light intensity, 1: ●—●, 2: ○—○, 3: +—+, and 4: ×—×, are given in table 2. The water supply is expressed as mean available soil moisture content in %.

rate of leaf expansion producing unequal light absorption in the various cases.

Since the saturation level of the total leaf area was reached at about 1.5×10^4 erg.sec⁻¹.cm⁻² for each temperature and each value of water supply (see fig. 6), the increase in dry weight of the shoot above this light intensity is probably entirely due to the increased rate of photosynthesis. Within the range of light intensities studied, no saturation of photosynthesis by light intensity seems probable. However, it is quite certain that the relation between dry matter production of the shoot and light intensity is complex. For this

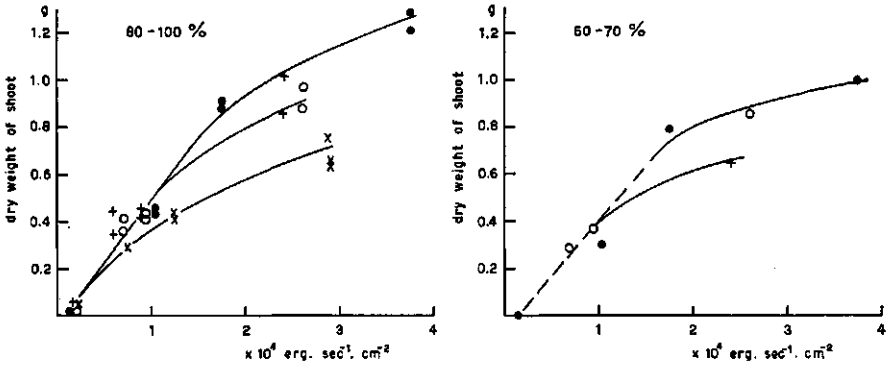


FIG. 10. The effect of light intensity on gain in dry weight of the shoot at two different irrigation regimes, at 90-100% (left side) and 60-70% (right side) mean available soil moisture content respectively. ●—● 25.8°C, ○—○ 20.2°C, +—+ 15.5°C, ×—× 12.2°C.

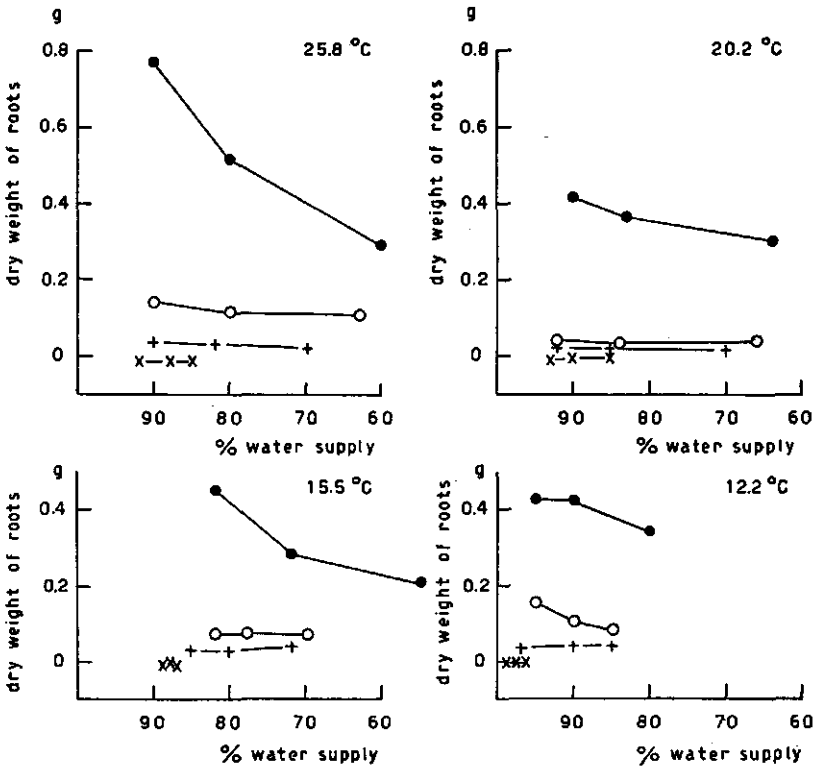


FIG. 11. The effect of water supply on gain in dry weight of roots. The levels of light intensity, 1: ●—●, 2: ○—○, 3: +—+, and 4: ×—×, are given in table 2. The water supply is expressed as mean available soil moisture content in %.

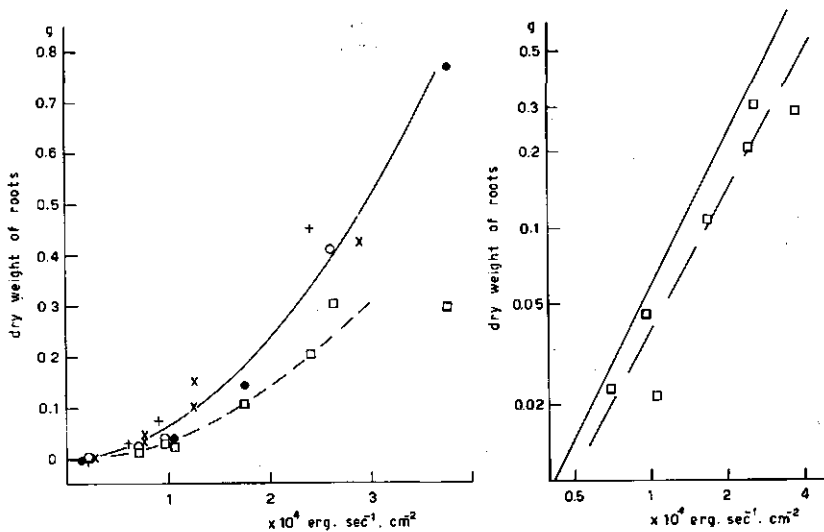


FIG. 12. The effect of light intensity on dry matter production of roots (linear scale on the left side, double logarithmic scale on the right side) at two different irrigation regimes, at 90–100% (full-drawn curves) and 60–70% (broken curves) mean available soil moisture content respectively. 90–100%: ● 25.8°C, ○ 20.2°C, + 15.5°C, × 12.2°C. 60–70%: □ all temperatures.

reason no empirical formula for this relation in connection with temperature and water supply is given.

The gain in dry weight of the roots is influenced by light intensity and water supply. It varies from — 0.003 g to + 0.770 g (table 8). A large effect of water supply on dry matter production of the roots is apparent at all temperatures, especially at high light intensity (fig. 11). It is surprising that water supply affects dry weight of the roots much more than it affects dry weight of the shoot. It seems therefore that water stress limits downwards transport of sugar.

In weak light, an effect of water supply is nearly absent, indicating another limiting factor. It seems that under these conditions the photosynthetic products are mainly used for growth of new leaves, while only a small amount of sugar is transported to the roots.

The effect of light intensity on the gain in dry weight of the roots is given in fig. 12 for two irrigation regimes, viz., 90–100% and 60–70% mean available soil moisture content. In the right hand figure the data are plotted on a double logarithmic scale. It is surprising that no temperature effect is detectable (see the full-drawn curve). Since in dry matter production of the shoot a clear temperature effect was observed, it is remarkable that dry matter production of the roots is determined quantitatively by a temperature independent process. Considering the gain in dry weight of the roots as a resultant of many chemical and physical processes, it may be assumed that a process with a Q_{10} of about 1.2 or lower limits dry weight of the roots. This small temperature effect can easily escape attention, especially where the number of replicates is small. This limiting process may be the sugar transport through the sieve tubes.

With decreased water supply, the effect of light intensity on the dry weight of roots is reduced. The point on the graph at $3.75 \times 10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$ (average of 3 closely similar values) may indicate a tendency towards light saturation under these conditions.

From the curves of fig. 12 a formula was derived $P = aI^b$, in which P represents dry matter production of roots in g and I the light intensity in $10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$. Since the curves of this figure run about parallel, nearly identical values for b were found. Values of a and b are given below, P and I expressed in the units mentioned above.

Mean available moisture content	a	b
90-100%	0.058	1.95
60-70%	0.039	1.85

Assuming that the sugar transport through the sieve tubes is the limiting process in dry matter production of the roots, some reasons for increased sugar transport with increasing light intensity may be suggested. In plants grown in strong light more sieve tubes are present, while the sugar transport capacity of each sieve tube may be larger. Besides this, the rate of photosynthesis increases so that more sugar is available for transport. At present, however, it cannot be visualized in detail, how these factors cooperate in producing the relationship expressed by the above formula.

It is clear from the foregoing considerations that there is most probably a rather complex relationship between total dry weight of the plants and the environmental factors. It is therefore interesting to plot the total dry matter production against light intensity for two irrigation regimes (table 8, fig. 13). A linear relationship between the total gain in dry weight and the light intensity seems evident, the slope of the curves depending on water supply. Since

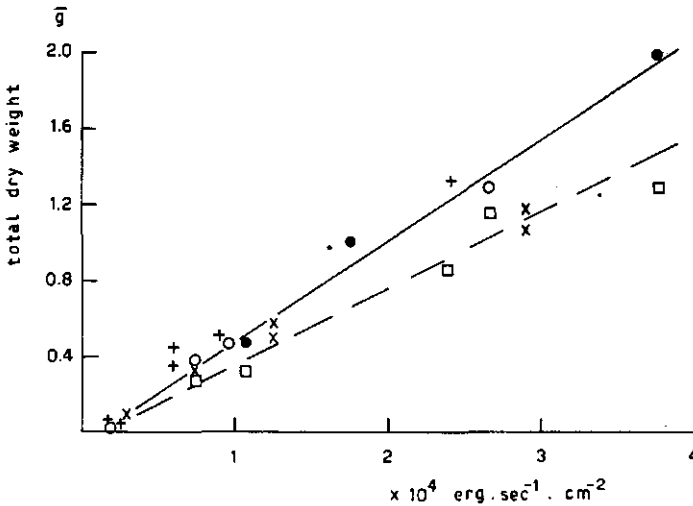


FIG. 13. The effect of light intensity on total gain in dry weight at two different irrigation regimes, at 90-100% (full-drawn curve) and 60-70% (broken curve) mean available soil moisture content respectively. 90-100%: ● 25.8°C, ○ 20.2°C, + 15.5°C, × 12.2°C. 60-70%: □ all temperatures.

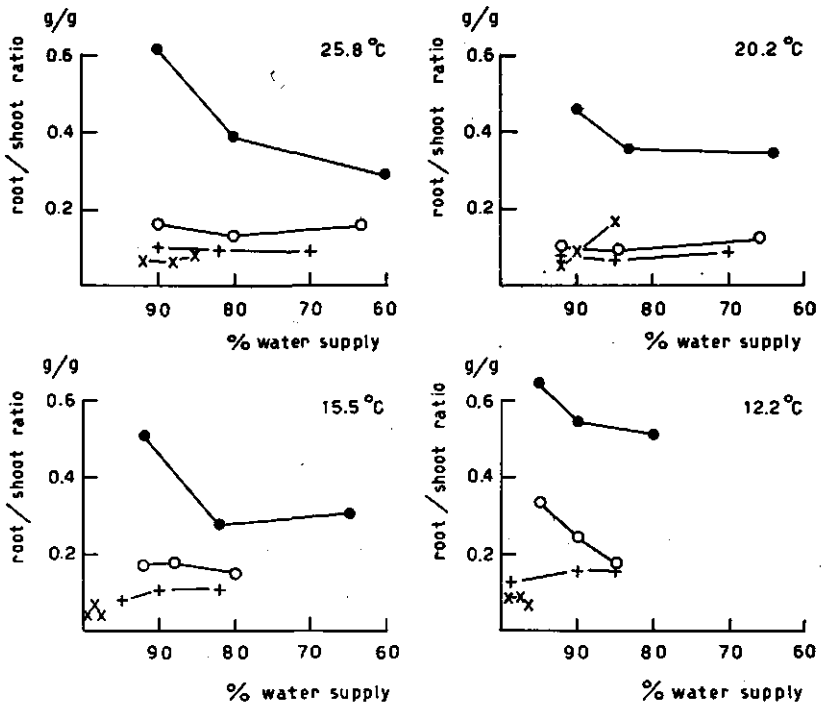


FIG. 14. The effect of water supply on root/shoot ratio (dry weight of roots/dry weight of shoot). The levels of light intensity 1: ●—●, 2: ○—○, 3: +—+, 4: ×—×, are given in table 2. The water supply is expressed as mean available soil moisture content in %.

only at 12.2° C, and 2.9×10^4 erg.sec⁻¹.cm⁻² a small deviation from the curve is observed, the temperature effect on dry weight is of minor importance. However, since this apparent linear relation is made up of two more complex curves, *i.e.* dry matter production of shoot and roots (fig. 10 and 12), no conclusions may be drawn from the "linearity" of this curve.

In this connection it should be observed that the relation between total dry weight of the plant and light intensity may neither be presented as a substitute for the photosynthesis — light intensity curve.

To conclude this section some remarks will be made on the root/shoot ratio (g/g *) at the end of the experiment. The root/shoot ratio may be calculated from the data on dry matter production of shoot and root (table 8) and the initial dry weight of shoot and root, as given at the beginning of this section.

The root/shoot ratio decreases regularly with a decreasing water supply at all temperatures and especially at a high level of light intensity (fig. 14). This decrease in root/shoot ratio is mainly caused by the observed decrease in dry matter production of the roots with decreasing water supply.

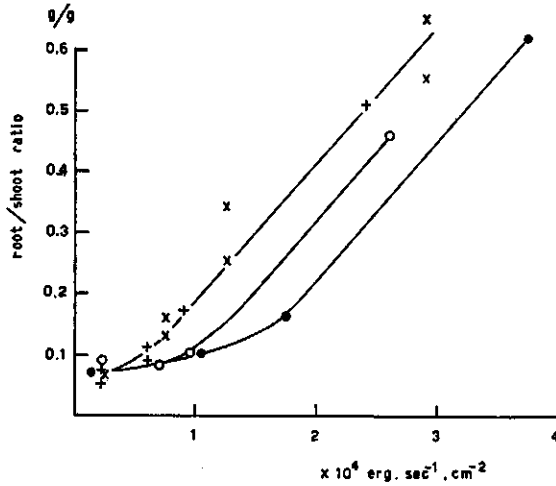
Under favourable irrigation conditions (90-100% mean available moisture

*) It should be observed that this ratio may well behave fundamentally different from a root/shoot ratio in cases of the root system that does not fulfill primarily a storage function.

FIG. 15.

The effect of light intensity on root/shoot ratio (dry weight of roots/dry weight of shoot) at 90-100% mean available soil moisture content.

- 25.8°C,
- 20.2°C,
- +—+ 15.5°C,
- ×—× 12.2°C.



content) the root/shoot ratio increases with increasing light intensity, while also a temperature effect is present (fig. 15). It may be assumed that only above a certain level of light intensity, viz. about $10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$, noticeable amounts of photosynthetic products are transported for storage in the roots. Above this level of light intensity the increase in dry weight of the shoot per unit light intensity is reduced, whereas the opposite occurs with regard to dry weight of the roots (see fig. 10 and 12).

The temperature effect on the root/shoot ratio is mainly due to the observed effect of temperature on the gain in dry weight of the shoot.

5. TRANSPIRATION AND DRY MATTER PRODUCTION

In this section, the water requirement (or the transpiration ratio) is considered in relation to the environmental factors. It is expressed as the ratio of total water loss/gain in dry weight (g/g).

As discussed in the previous paragraph, the dry matter production of the shoot and that of the roots showed a different behaviour with regard to water supply, temperature, and light intensity. A separation of the water requirement of shoot and roots must therefore be made in order to arrive at an understanding of the problem in physiological terms.

Under all experimental conditions, the water requirement of the roots exceeds that of the shoot (table 9). Both water requirements are affected by light intensity, temperature, and water supply.

The effect of light intensity on the water requirement is presented in fig. 16 (mean available soil moisture content 90-100%). The water requirement of the shoot is high at low light intensity, and decreases rapidly with increasing light intensity. This decrease in water requirement is due to the fact that dry matter production of the shoot rises more rapidly than transpiration. Since the curves of fig. 2 (total water loss *versus* light intensity) and of fig. 10 (gain in dry weight of shoot *versus* light intensity) are of the MITSCHERLICH-type the existence of minimum levels of water requirement are to be expected. Indeed such minimum levels are found at higher light intensities (fig. 16).

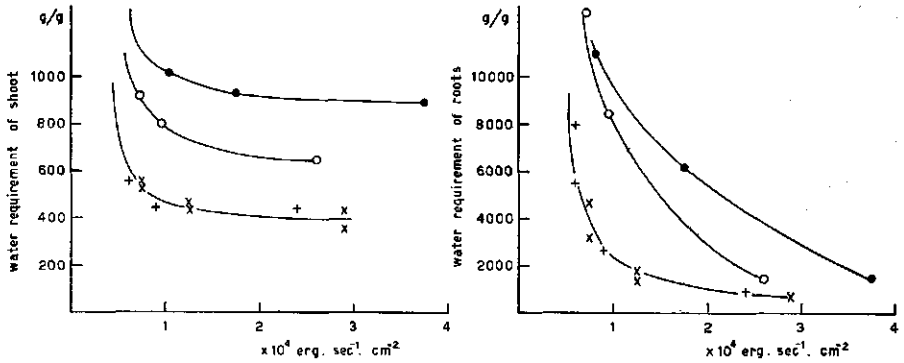


FIG. 16. The effect of light intensity on water requirement of the shoot (transpiration/dry matter production of shoot) and on water requirement of the roots (transpiration/dry matter production of roots) at 90-100% mean available soil moisture content. ●—● 25.8°C, ○—○ 20.2°C, +—+ 15.5°C, ×—× 12.2°C.

The water requirement of the roots shows more or less similar curves at all temperatures. It decreases rapidly with increasing light intensity which is also due to the fact that dry matter production of roots increases much more rapidly than transpiration. The initial part of all the water requirement curves points to $+\infty$ at zero gain in dry weight of shoot and roots. Negative values of the water requirement of roots are obtained at very low light intensities (see table 9).

TABLE 9. The effect of water supply, temperature, and light intensity on the water requirement of the shoot and of the roots, expressed as total water loss by transpiration/dry matter production of shoot (or roots), in g/g. The levels of light intensity are given in table 2, the mean available soil moisture content in table 3. neg. = negative.

Irrigation regime		Shoot			Roots		
		A	B	C	A	B	C
Air temperature (°C)	Level of light intensity						
25.8	1	890	715	665	1410	1780	2280
	2	930	925	720	6100	7300	5050
	3	1015	965	1310	10900	12200	17600
	4	22000	9800	54000	neg.	neg.	neg.
20.2	1	640	545	575	1340	1460	1630
	2	795	965	900	8400	11100	7250
	3	910	775	945	12700	14200	11400
	4	11400	7250	9650	20600	neg.	51500
15.5	1	430	360	440	825	1290	1380
	2	440	375	400	2540	2100	2700
	3	540	545	520	7900	5400	5050
	4	2000	1640	1670	neg.	56500	neg.
12.2	1	430	350	370	640	620	690
	2	460	440	425	1295	1750	2300
	3	555	520	470	4650	3100	2750
	4	1560	1900	1560	64000	∞	neg.

The effect of water supply on the water requirement of the shoot is clear under high transpiration conditions, viz., at 25.8° C air temperature, and high light intensity (table 9). Under low transpiration conditions such an effect of water supply is not found, since in this case the water supply by the roots does not limit transpiration. In order to compare the results obtained at different temperatures, the important influence of light intensity should be excluded. It is clear from fig. 16 that such a comparison is only possible at the highest level of light intensity. Thus, in fig. 17, the water requirement of the shoot is plotted against water supply. A reliable effect of the irrigation regime is only found at 25.8° C. The levels of water requirement roughly coincide with the V.P.D.-values of table 1, making the 20.2 value fit with 600 g/g, the

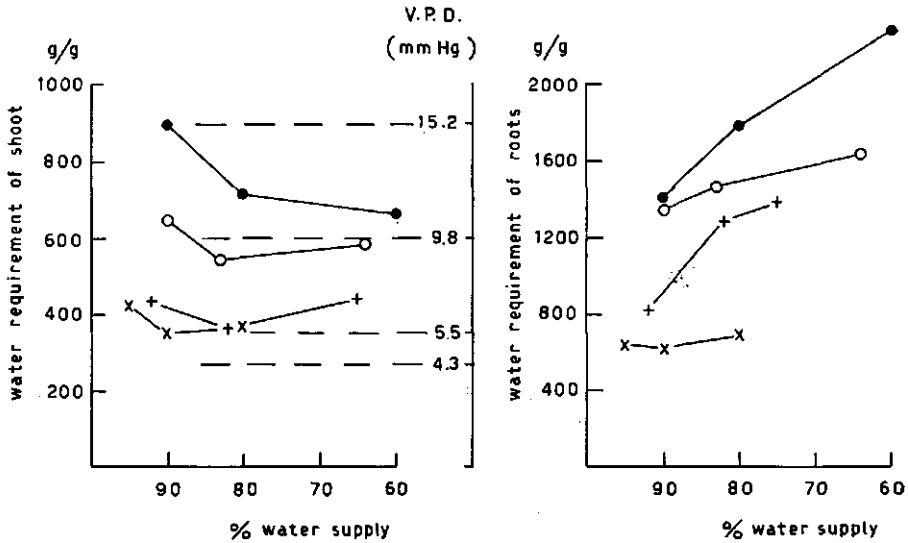


FIG. 17. The effect of water supply on water requirement of the shoot (transpiration/dry matter production of shoot) and on water requirement of the roots (transpiration/dry matter production of roots) at the highest level of light intensity, 1 (given in table 2). ●—● 25.8° C, ○—○ 20.2° C, +—+ 15.5° C, ×—× 12.2° C.

water requirement at 20.2° C. The V.P.D.-value at 25.8° C corresponds with the water requirement at 90% mean available moisture content. The water requirement levels at 15.5° C and 12.2° C are higher than the corresponding V.P.D.-values. A possible explanation is that the difference in vapour pressure between the leaves and the air is higher than the observed vapour pressure deficit of the air owing to increased leaf temperature. This may especially be true under low evaporation conditions and in strong light. However, more experiments are needed to test this assumption.

The water requirement of the roots is quite different with regard to water supply (table 9, fig. 17, right side). The table shows that if light intensity is high, the water requirement of the roots increases with decreasing water supply at all temperatures. The increase in water requirement is due to the fact that dry matter production of roots decreases more rapidly than transpiration at reduced water supply. At low light intensities this effect of the irrigation regime is not observed, indicating another limiting factor. In this

case the calculated data on water requirement of the roots, moreover, are less reliable.

Since no temperature effect on dry matter production of the roots was observed, the effect of temperature on the water requirement is similar to that on transpiration.

Besides the discussion on the water requirement, a direct comparison between dry matter production and transpiration seems interesting. This relation, however, was found to be complex. The data on gain in dry weight scatter when plotted against transpiration. Some general trends are visible, however. At 12.2° C and 15.5° C, the data on total gain in dry weight scatter around linear curves. At higher temperatures a similar picture was obtained,

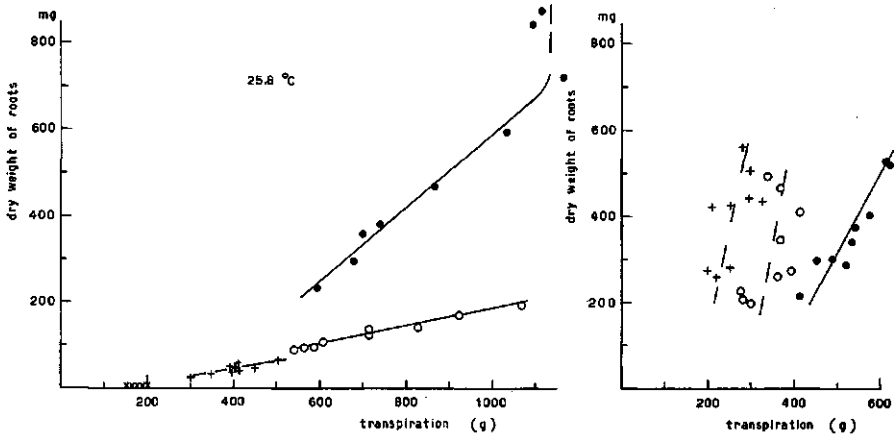


FIG. 18. The relation between total water loss by transpiration and gain in dry weight of the roots at 25.8° C (left side) and at the other temperatures (right side). Left side: air temperature 25.8° C, ●—● 3.75×10^4 , ○—○ 1.75×10^4 , +—+ 1.05×10^4 , ×—× 0.15×10^4 erg.sec⁻¹.cm⁻². Right side: ● 20.2° C 2.6×10^4 erg.sec⁻¹.cm⁻², ○ 15.5° C 2.4×10^4 erg.sec⁻¹.cm⁻², + 12.2° C 2.9×10^4 erg.sec⁻¹.cm⁻².

when total gain in dry weight was plotted against transpiration per mm vapour pressure deficit.

Some interesting results were obtained when the dry matter production of the roots was plotted against transpiration (fig. 18). The figure represents the data from the individual plants. At 25.8° C, linear relationships were obtained, the slopes depending on light intensity. This relation with transpiration is pronounced at high light intensity, whereas transpiration shows only a weak, or no relation with dry weight production at low light intensities. It is evident that, in weak light, dry matter production is limited by light intensity, whereas in stronger light transpiration somehow interferes with synthesis of organic substances in the roots. Since root weight increase depends more upon water stress than total dry weight increase, it seems that under these conditions the sugar transport through the phloem vessels is limited by water stress.

The right side of fig. 18 shows the experimental data, obtained at the highest level of light intensity at 20.2°, 15.5°, and 12.2° C. At these lower temperatures the relation between transpiration and dry matter production

of the roots is decreasingly evident. Transpiration is increasingly limited by the vapour pressure deficit of the air and effects of the water supply are scarcely noticeable any more. Thus the experimental points in this type of graph scatter more.

It may be concluded that only under high transpiration conditions of the air and at high light intensity a linear relation between transpiration and dry matter production of the roots exists. Under these conditions the water supply exerts a large influence on transpiration and on dry matter production of the roots, which led to the suggestion that transpiration limits the downward sugar transport.

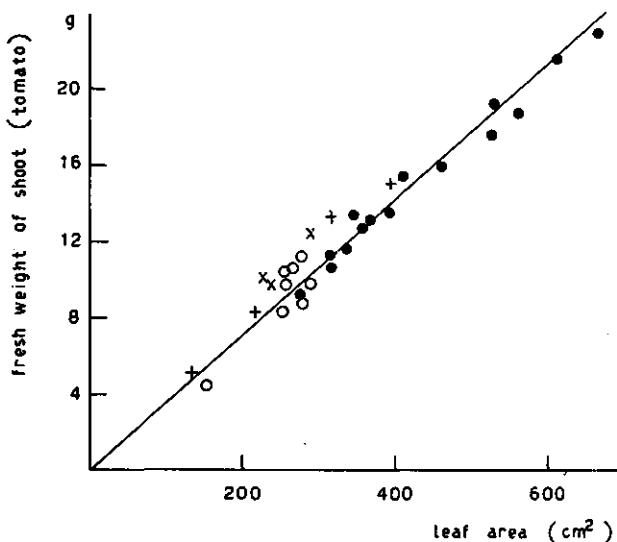


FIG. 19. The relation between fresh weight of the shoot and total leaf area in tomato from experiments of ABD EL RAHMAN *et al* (1959). ● the effect of water supply and nitrogen application, ○ effect of light intensity and photoperiod, + effect of soil temperature (air temperature 25.3°C). × effect of soil temperature (air temperature 16.8°C), derived from an unpublished experiment of the author.

IV. DISCUSSION

The experimental results have shown that the effect of external factors on growth and transpiration of beet plants is complicated. Since water supply, temperature, and light intensity may affect the plant in different ways, a complete analysis of growth and transpiration is not possible. Some of the results, however, suggest further research.

The water supply exerts hardly any effect on growth and transpiration at low light intensities and/or low temperatures, in other words under low transpiration conditions. Under high transpiration conditions remarkable effects of the irrigation regime on nearly all aspects of growth and transpiration are observed.

NEZGOVOROVA (1957) found that carbohydrates produced by photosynthesis are incorporated more rapidly into cellulose and other cell wall materials under conditions of insufficient water supply. ORDIN (1958, 1960) studying incorporation of C¹⁴-glucose into the cell wall, suggests that the turgor is the

chief component of the diffusion pressure deficit, affecting the incorporation.

Assuming that under the conditions of our experiment, turgor of the cells depends on the water content, several growth aspects may be related to water uptake and transpiration. During a period of rapid growth, water uptake should exceed transpiration. Since dry weight of the leaves contributes only little to the fresh weight of the shoot, the latter is indicative for the water content of the plant. In this way it is found that the relation between total leaf area and fresh weight of the leaves is a straight line through the origin.

A similar relation between fresh weight and leaf area was observed in tomato by BIERHUIZEN, ABD EL RAHMAN and KUIPER (1959) under a variety of irrigation regimes and nitrogen applications. This data is given in fig. 19, together with the data of experiments on the effect of light intensity, photo-period, and soil temperature (ABD EL RAHMAN, KUIPER and BIERHUIZEN, 1959, together with unpublished data of KUIPER, 1961). All data tends to fall on one straight line, and no additional effects of the different environmental factors are found, just as in the beet experiment (fig. 8).

One may connect the observed relation between fresh weight and area of the leaves with the suggestion that turgor determines expansion of the leaf cells by way of synthesis of cell wall material. Fresh weight of leaves corresponds to their water content, influences the turgor of the cells which may affect synthesis of cell wall material, and thus expansion of leaf cells and total leaf area. However, the curves of fig. 8 and 19 represent complex relations with several physical and chemical factors, one of them probably limiting the overall process. For this reason it appears unwise to lay too much stress on the apparent linear relationship obtained. In this connection, the reader may be referred to the so-called linear relationship between total gain in dry weight and light intensity which also was the result of a complicated situation (see fig. 10, 12 and 13).

The effect of water supply on leaf area and dry matter production of the shoot is rather small in beets; it was found much larger in tomato (ABD EL RAHMAN and BIERHUIZEN, 1959). The effect of water supply on the water requirement of the shoot is also much more pronounced in tomato than in beets (WASSINK and KUIPER, 1959). The fresh weight per unit leaf area of beets is higher than that of tomato (see fig. 19). It may be that growth of plants with a high water content of the leaves, such as beets, does not decrease so much during a short period of drought as does growth of plants with a low water content of the leaves. Many xerophytes, however, have a comparatively high percentage dry weight, and can stand long periods of drought.

At high temperatures, the water requirement of tomato was found to depend on the availability of water from the soil within a wide range of water supply. At lower temperatures, saturation levels of water requirement were observed which agreed with the corresponding levels of vapour pressure deficit of the air (WASSINK and KUIPER, 1959). The data of the beet experiment more or less confirm the results obtained with tomato. If we consider the water requirement of separate parts of a plant, (total water consumption over dry weight increase of the respective parts) at 25.8° C, the water requirement of the shoot decreases with decreasing water supply, though this decrease is smaller than in tomato. The saturation levels of the water requirement of the shoot roughly coincide with the levels of vapour pressure deficit of the air (fig. 17). The water requirement of the roots follows a different

pattern. At high light intensities, water requirement increases with decreasing water supply at all temperatures.

Under high transpiration conditions of the air and at high light intensity a linear relation between transpiration and dry matter production of the roots is found. There are some indications that under certain conditions synthesis of root material is limited by the sugar transport from the shoot, and the hypothesis is put forward that, under high transpiration conditions of the air and at high light intensity, the water uptake by the roots limits the sugar transport through the phloem. In this connection it is of interest to note that, according to PRISTUPA and KURSANOV (1957), the flow of assimilates from the leaves to the roots strongly depends on the activity of the root cells. BIDDULPH and CORY (1957) measured the rate of transport, including uptake into the sieve tubes in bean plants for THO (tritiated water), P^{32} , and C^{14} . They found a rate of 87 cm per hour for THO and P^{32} , and a rate of 107 cm/hour for C^{14} . Since the mechanism of transport of sugar through the sieve tubes is still unknown, no definite conclusions can be drawn from the assumed influence of transpiration on the sugar transport or from the observed relation between transpiration and dry matter production of the roots. Studying the effect of water supply on the translocation of assimilants ZHOLKEVICH, PRUSAKOVA and LIZANDR (1958) observed a decreased rate of photosynthesis, and a decreased rate of sugar transport to the roots under conditions of water stress. Besides, under conditions of optimal water supply the phloem was better developed. ZIMMERMAN (1960) recently discussed the solute transport in the phloem, including the mass-flow theory of MÜNCH.

In this connection the observed linear relationship between dry matter production and transpiration of beets in field experiments (DE WIT, 1958) still is a puzzle. Assuming that total dry weight of the plants at harvest mainly consists of the storage root, similar linear relations can be reproduced in our experiments under controlled conditions. It still then is a problem why the weather conditions do not affect the linearity of the curve and why the experimental dots do not scatter more.

With regard to the effect of light intensity on growth and transpiration, we have observed curves of the MITSCHERLICH-type (e.g. total water loss by transpiration dry matter production of the shoot), curves of the BLACKMAN-type (e.g. total leaf area), and exponential curves (e.g. dry matter production of roots). The saturation levels of the curves of the MITSCHERLICH-type and of the BLACKMAN-type are determined by temperature and water regime.

A linear, temperature-independent relation between total leaf area and light intensity is found between 10^3 and 10^4 erg.sec⁻¹.cm⁻². Since photosynthesis of sugar beet leaves in normal air is saturated at about 10×10^4 erg.sec⁻¹.cm⁻², (high pressure mercury vapour tubes, GAASTRA, 1959) the effect of light on growth of leaves is different from that on photosynthesis.

In good agreement with GAASTRA's results, the gain in dry weight of the shoot does not reach saturation in the range of light intensities applied. The curves differ strongly from the exponential curves of the gain in dry weight of the roots; above 10^4 erg.sec⁻¹.cm⁻² more products of photosynthesis are obviously used in synthesis of root materials. It seems probable that, under these conditions, more sugars are available for transport, while also the transport capacity of the phloem may be larger. Since no direct evidence as to the nature of the regulating mechanism of the transport exists, it can only

be said that $10^4 \text{ erg}\cdot\text{sec}^{-1}\cdot\text{cm}^{-2}$ represents a critical level of light intensity for sugar transport to the roots, as well as for expansion of the leaves.

The relation between water requirement and light intensity is the same as found in tomato by ABD EL RAHMAN, KUIPER and BIERHUIZEN (1959).

Temperature was found to exert an appreciable influence on nearly all growth aspects of beets, though this effect is not as great as found in tomato. Since in this experiment no attempt was made to maintain a temperature difference between the air and the soil, the root temperature as well as the shoot temperature may have affected growth. The observed effect of air temperature on transpiration is indirect and results from changes in the vapour pressure deficit of the air. Dry matter production of the shoot and increase in total leaf area show more complex relations with temperature. No temperature effect on the gain in dry weight of the roots was found. Assuming that dry matter production of the roots is limited by sugar supply (see above), this would mean that under our experimental conditions this supply is practically temperature independent. This is in agreement with observations of HULL (1952), who found equal or greater translocation of sugar after cooling the petioles of beet leaves.

V. SUMMARY

Young beet plants are grown for a period of 6 weeks at different temperatures, light intensities, and irrigation regimes.

Transpiration and the vapour pressure deficit of the air are related by linear curves, the slopes of which depend on light intensity and water supply. Applying the MITSCHERLICH-equation to these results a formula for the effect of light intensity, vapour pressure deficit of the air, and water supply was derived (see p. 7).

Leaf area at the end of the experiment shows a relation of the BLACKMAN-type with light intensity. The linear, temperature-independent part is due to a relation between total leaf area and light intensity, while the saturation levels are determined by temperature and water supply. Fresh weight of the shoot has a linear relation to leaf area, indicating an intimate relationship between the water content of the leaves and growth of the leaves.

The dry matter production of the shoot is affected by temperature, light intensity, and, to a smaller extent, by water supply. The effect of a factor is most pronounced under optimal conditions of the others. The gain in dry weight of the shoot is related to light intensity by curves of the MITSCHERLICH-type. The dry matter production of the roots increases exponentially with increase in light intensity, while no temperature effect is detectable. It is suggested from many indications that the sugar transport to the roots limits their dry matter production. Under high transpiration conditions, especially at high light intensity, a linear relation between transpiration and the gain in dry weight of the roots is observed, indicating limitation of dry matter of roots by the water uptake.

Under high transpiration conditions the water requirement of the shoot (total water consumption/dry matter of shoot) decreases with decreasing water supply, while under lower transpiration conditions the levels of water requirement coincide with the values of vapour pressure deficit of the air. On

the other hand, the water requirement of the roots (total water consumption/dry matter of roots) increase considerably with decreasing water supply at high light intensities and at all temperatures.

ACKNOWLEDGEMENTS

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