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INTRODUCTION

During the past a large number of pot experiments were carried out in which dry matter production and transpiration were measured during the period of growth of the plants.

Figure 1 gives the relationship thus obtained from experiments with oats, carried out in the Netherlands. Considering that these experiments differ in years and places and also in the availability of water and nutrients, the scattering around the straight line relationship is remarkably small. This was explained by DE WIT (8) in the following way.

The dry matter production equals the net assimilation rate and the transpired amount of water, transpiration rate, both integrated over the whole period of growth. In the Netherlands, the assimilation rate is more or less proportional to the intercepted radiation (2, 9) and to a large extent unaffected by temperature (4). The transpiration rate is also more or less proportional to the intercepted radiation. The effect of wind, temperature and humidity is accounted for in the proportionality factor because this effect is linearly and positively correlated with radiation (5).

Since assimilation and transpiration are governed by the same leaf surface and, since the effect of availability of water and fertility is mainly reflected in this leaf surface, there must be a linear relation between transpiration and production of single plants (8). Of course, there is some effect of the growing conditions on this relation and the scattering of observations, as found in figure 1, is due to this, rather than to experimental errors.

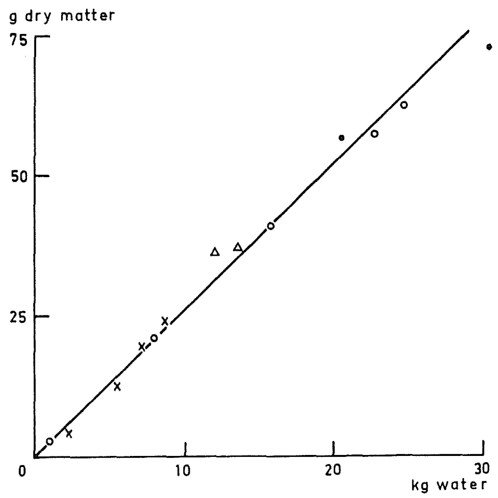

FIG. 1.
The relation between dry matter production and transpired amount of water of oats, grown in containers.

Author	year	treatments
× MASCHHAUPT	1915	4 fertility levels
O MASCHHAUPT	1922	5 fertility levels
△ VERHOEVEN	1939	2 fertility levels
• VAN DER PAAUW	1947	2 moisture levels

Details and references are given by DE WIT (8).

In other climatic regions there may exist another proportionality between transpiration and radiation, so that another relation between transpiration and production may be found. It was shown (8) that in arid climates, as prevail in the Midwestern States of the U.S.A., assimilation to a small extent is affected by radiation so that it is of advantage there, to correlate production with the quotient of the transpired amount of water and the free water evaporation during growth.

The transpiration coefficient, i.e. the ratio of the transpired amount of water to the dry matter production, depends on the plant species. The relation between assimilation and radiation is not strikingly different for different agricultural crops(3). Hence, different transpiration coefficients between plant species must be mainly due to different transpiration rates per unit leaf area or unit leaf weight.

To confirm this an experiment was carried out with three plant species grown in growth chambers, in which light intensity, temperature and humidity of the air were kept more or less constant during growth. Dry matter production and transpiration were determined at two relative humidities.

Experimental procedure

Seeds of maize (var. Pioneer), oats (var. Abed minor) and summer barley (var. Vinesco) were sown in moist gravel. About one week after germination the seedlings were transferred to one litre glass jars filled with a Hoagland nutrient solution of half strength, in which iron was given as Fe-EDTA. Each jar contained four seedlings fixed into holes in a hardboard cover. 56 jars of each species were equally divided over two growth chambers with relative humidities of 55 and 93 %. For a detailed description of these chambers see (1). The temperature in both rooms was 19 °C and the light intensity was 4.5×10^4 ergs $cm^{-2}sec^{-1}$ at the height of the pots. The water loss from the jars was determined at regular intervals, after which the solution was renewed. This occurred two times a week at the beginning and about every other day as the plants matured.

One half of the jars was harvested after 20 days and the other half 5 days later. The fresh and dry weights of roots and shoots were determined for each jar and of some plants the leaf surface was also measured. These data enable to calculate the transpiration coefficient.

It was supposed that a relative value for the transpiration rate could be obtained by determining the water loss from detached leaves. Both the experimental procedure and the results of these measurements are given in the last section.

Although the experiment was not designed as such, the transpiration rate of the plants during the last two days in relation to the weight of the shoots at the time of harvest was used to estimate the transpiration rate per unit of leaf weight.

Calculated for the individual jars, the transpiration coefficient as well as the transpiration rate per unit of top dry weight varied considerably. These differences are mainly caused by the fact that the linear correlation between radiation on the one hand and wind velocity, temperature and humidity on the other hand, which exists in the field, does not hold in a growth room, where these factors are controlled independently If a plant, by individual variation, grows faster than another plant, it will also grow into a different climatic condition, since the light intensity increases here without correspondent changes in the other factors. It thus appears that, for calculating the transpiration coefficient, pot experiments in the open give less variable results than similar experiments under controlled conditions.

The present experiments could not be carried out in the open or in a greenhouse be-

TABLE 1. Average yield data (S% calculated from total fresh weight data).

Growth period (days)	20				25				
Relative humidity (%)	55 low	93 high	difference (high-low)	P%	55 low	93 high	difference (high-low)	P%	
Maize									
Number of pots	12	12			14	14			–
S% of mean	5.55	3.27			4.53	3.72			%
Dry wt. at start	0.79	0.79			0.79	0.79			g/pot
Fresh wt. total	56.4	67.3	+10.9	0.5–1	81.2	95.4	+14.2	0.5–1	g/pot
Dry wt. total	5.03	4.93	– 0.10	50–80	6.72	7.55	+ 0.83	5–10	g/pot
Fresh wt. shoots	35.6	43.9	+ 8.3	0.2–0.5	51.0	67.0	+16.0	<0.1	g/pot
Dry wt. shoots	3.24	3.43	+ 0.19	20–50	4.54	5.56	+ 1.02	0.1–0.2	g/pot
Leaf area	745	980	+235	<0.1	1040	1580	+540	<0.1	cm^2 leaf/pot
Barley									
Number of pots	11	12			14	12			–
S% of mean	5.50	3.82			7.09	6.33			%
Dry wt. at start	0.16	0.16			0.16	0.16			g/pot
Fresh wt. total	21.3	24.8	+ 3.5	2–5	35.3	36.2	+ 0.9	50–80	g/pot
Dry wt. total	2.14	2.58	+ 0.44	0.5–1	4.12	3.76	– 0.36	20–50	g/pot
Fresh wt. shoots	14.3	18.3	+ 4.0	0.1–0.2	24.8	27.2	+ 2.4	20–50	g/pot
Dry wt. shoots	1.77	2.16	+ 0.39	0.5–1	3.30	3.18	– 0.12	50–80	g/pot
Leaf area	425	595	+170	<0.1	790	875	+85	20–50	cm^2 leaf/pot
Oats									
Number of pots	12	12			14	14			–
S% of mean	3.82	4.71			2.75	2.32			%
Dry wt. at start	0.09	0.09			0.09	0.09			g/pot
Fresh wt. total	27.8	26.3	+ 1.5	20–50	47.0	43.5	– 3.5	2–5	g/pot
Dry wt. total	2.56	2.20	– 0.36	1–2	4.53	3.72	– 0.81	<0.1	g/pot
Fresh wt. shoots	17.3	17.4	+ 0.1	>80	29.7	29.6	– 0.1	>80	g/pot
Dry wt. shoots	2.01	1.78	– 0.23	5–10	3.77	2.98	– 0.79	<0.1	g/pot
Leaf area	441	463	+22	>80	830	775	–55	5–10	cm^2 leaf/pot

cause the growing conditions would vary too much in time and humidity cannot be controlled.

Yields at low and high humidity

The yield data of the three species after 20 and 25 days of growth at high and low humidity are given in table 1.

The total dry weight of maize appears to be the same at both humidities. However, the fresh weights of the total plants and of the shoots and the dry weight of the shoots after 20 days are significantly and considerably higher at high humidity. This effect of humidity appears also in the data on leaf area.

The same holds for barley grown during 20 days. The differences in fresh weight and leaf area for the plants harvested after 25 days are distinctly smaller, and, also due to the high standard deviation, not significant.

As for oats, it appears that the dry weight data for the shoots and the whole plants are significantly higher at low humidities.

From the 20th to 25th day growth was so fast that the leaves were pressed against the glass partition between plants and lamps. This affected the transpiration coefficient and transpiration rate during the last few days before the second harvest to such an extent that in the following only the results of the harvest at the 20th day are considered.

Transpiration coefficient and transpiration rate

The dry matter production and the transpired amount of water during 20 days of growth of maize, oats and barley at dry and humid conditions are given in figure 2a and c. The lines drawn through the individual observations do not go through the origin because some water is lost by direct evaporation out of the jars, especially during the first days of growth. The transpiration coefficients as read from the slopes of the lines are given in the second column of table 2. There is a large difference between maize and the small grains as well as between dry and humid air.

The transpiration during the last two days of the experiment is plotted against the dry weight of the shoots at the end of the experiment in figure 2b and d. The scattering of the observations is considerable and probably for the greater part due to differences in climatic conditions as discussed before. The direct evaporation from the jars during these last two days is supposed to be negligible because the jars were almost completely shaded. Hence the slope of the lines, given in the third column of table 2, represents an estimate of the transpiration rate in g water (g dry shoots)$^{-1}$ day^{-1}.

Division of this transpiration rate by the transpiration coefficient in g water (g dry matter)$^{-1}$ gives a value with the dimension of an assimilation rate. These quotients, in g dry matter (g dry shoots)$^{-1}$ day^{-1} are given in the fourth column of the table.

The assimilation rate, calculated in this way, differs systematically from the assimilation rate during the growth period because (1) the transpiration during the last two days is compared with the leaf weight at the time of harvest, (2) during the last two days, the leaves are closer to the lamps, and at a lower humidity than before and, (3) the assimilation rate per unit leaf weight during the growing period is anyhow not constant, due to a systematic variation in the degree of mutual shading.

The calculated assimilation rate of maize at both low and high humidity is practically equal to the calculated assimilation rate of the two small grains at both humidities. Hence these calculated assimilation rates also prove that the difference between the transpiration coefficient of maize and the two small grain species is mainly due to the different transpiration rate per unit leaf weight.

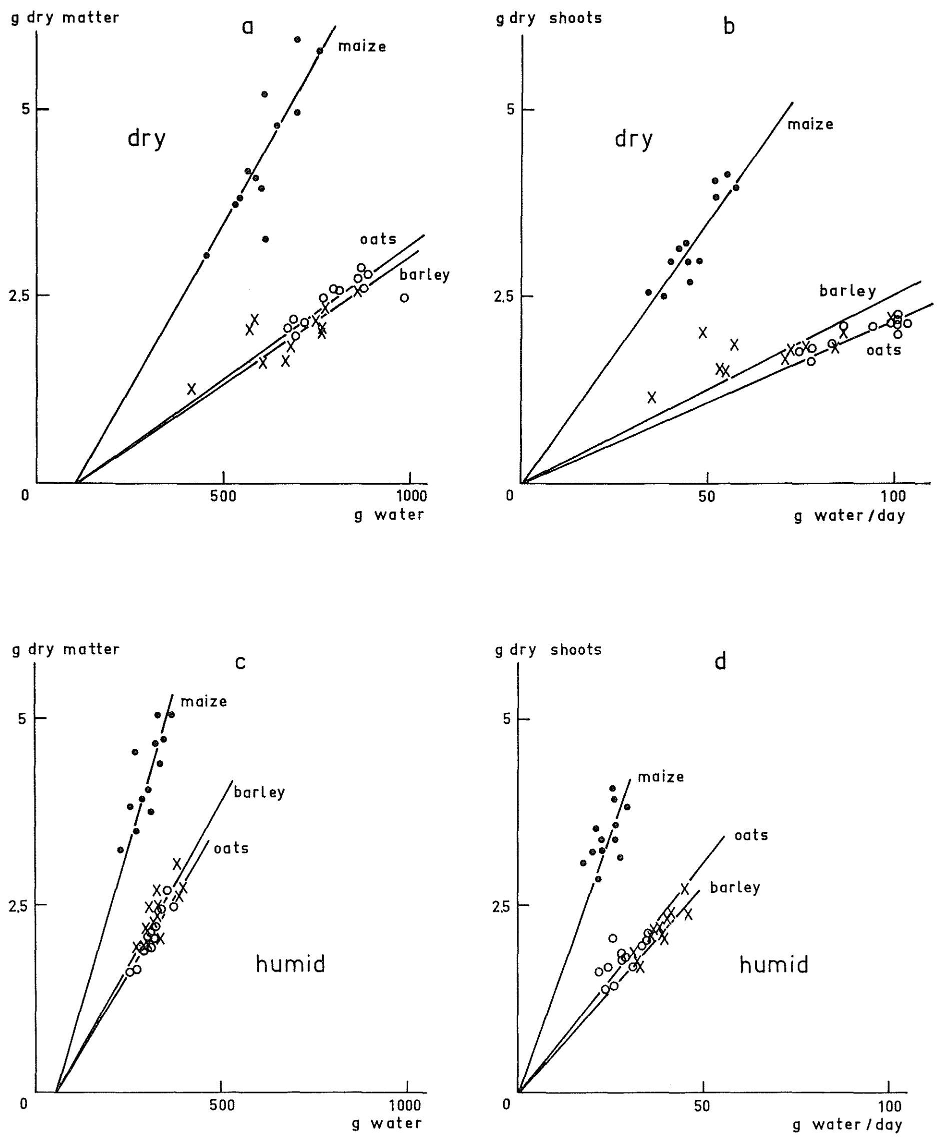

FIG. 2. *a.* The relation between the total dry matter production and the total amount of water transpired during 20 days at low humidity.
b. The relation between the dry weight of the shoots at the time of harvest and the transpiration rate, averaged over the last two days of growth at low humidity.
c. The same at high humidity.
d. The same at high humidity.

Maize manages in some way or another to combine a low transpiration rate with a normal assimilation rate.

The over-all average assimilation rate in this experiment equals 5.10^{-7} mg dry matter (cm^2 leaf)$^{-1}$min^{-1}. This is about 1/6 of the maximum assimilation rate of some agricultural plant species (3, 4). This small value is undoubtedly due to the comparatively

TABLE 2. Transpiration and production data, calculated from the observations in figure 2.

	g water / g d.m.	g water / g shoots day	g d.m. / g shoots day
Dry			
Maize	110	14.2	0.13
Oats	300	45.8	0.15
Barley	290	37.8	0.13
Humid			
Maize	70	7.0	0.10
Oats	140	15.8	0.11
Barley	140	17.7	0.13

low light intensity in the growth chambers and the non-horizontal position and the mutual shading of the leaves.

TRANSPIRATION RATE AND FREE WATER EVAPORATION

The calculated relation between the evaporation rate from both sides of a horizontal wet, black paper and the humidity in the rooms is given in figure 3, the method of estimation being explained in the caption to the figure.

The two humidities which were maintained during the experiments are marked by arrows on the horizontal axis, the corresponding evaporation rates being 0.18 and 0.40 mg water $(cm^2 \text{ paper})^{-1} \min^{-1}$.

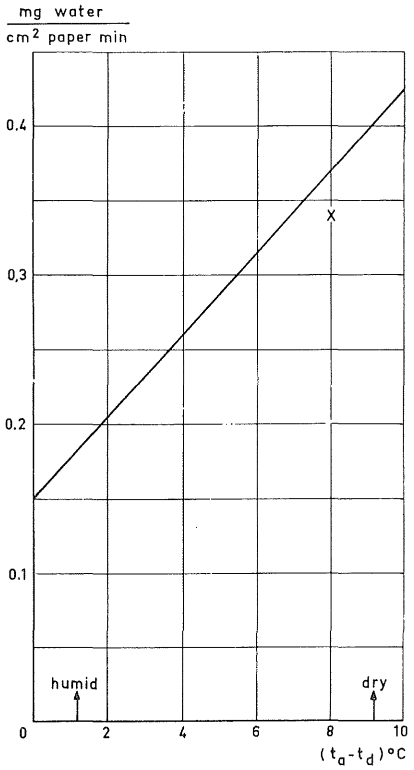

FIG. 3.
The relation between the evaporation rate of a wet black filter paper and the humidity of the air, the latter expressed as the difference between air temperature (t_a) and dew point temperature (t_d). This relation is calculated according to Penman's method; the equations and numerical values for the constants, as used here, are given by DE WIT (8).
Environmental conditions: Radiation from the lamps, infrared included: 9.10^4 ergs cm^{-2} sec^{-1}, air temperature: 19 °C, wind velocity 30 cm sec^{-1}. The net black body radiation is difficult to estimate and supposed to be negligible. Considerable errors, here, do not affect the conclusions.
The $\times$ concerns the measured evaporation rate of a wet black filter paper in a balance exposed to about the same conditions as the leaves of the plants.

The transpiration rates per unit leaf weight for the three species at both humidities are plotted against these calculated evaporation rates in figure 4. For each of the species, the transpiration rate was more or less proportional to the evaporation rate.

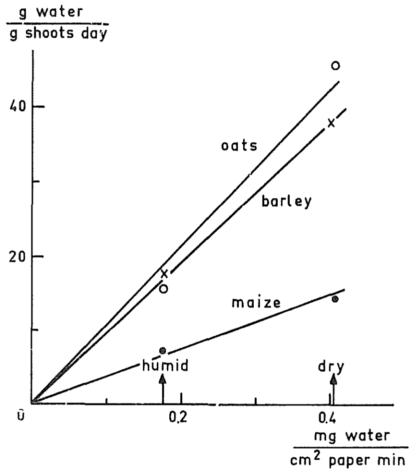

FIG. 4.
The relation between the transpiration rate per unit shoot weight during the last day and the calculated evaporation rate of a wet black filter paper.

Hence, the effect of humidity on transpiration is mainly due to differences in evaporation and not to differences in the diffusion resistance of the leaves at low and high humidity.

The difference between maize and the two small grain species is of course due to a higher resistance against diffusion of water vapour of the leaves of the former species. Estimates of these resistances for the three species are given in the next section.

TRANSPIRATION RATE OF DETACHED LEAVES

In order to measure the rate of transpiration of detached leaves of the three species, an analytical balance was provided with a perspex cover and placed in the dry room in such a position that, with the balance windows open, the conditions for the plants in the room were roughly the same as in the balance.

Instead of the balance pan a frame with nylon threads was mounted, in which a leaf or a filter paper could be kept in a horizontal position. The transpiration rate of detached leaves was measured during five minutes at intervals of one minute. All data concern the average of weighings of 7 leaves. The measured evaporation rate of a black wet filter paper in this balance, did not differ much from the evaporation rate calculated for a similar paper in the position of the plants and is represented by a cross in figure 3. Since the balance did not work properly at high humidities, leaves detached from plants grown at high and low humidities were both placed in the balance at low humidity only.

The water loss of the leaves grown at the high humidity and that of the filter paper are given in figure 5a. This loss was in all four cases constant with time, so that the availability of the water was not limiting and the stomatal apertures did not change markedly during these five minutes.

The diffusion resistance of the leaves against water loss consists of a resistance in the „still air boundary" around the leaves and a resistance in the stomata. The former is equal to a similar resistance of filter paper and amounts to about 0.3 cm at a wind

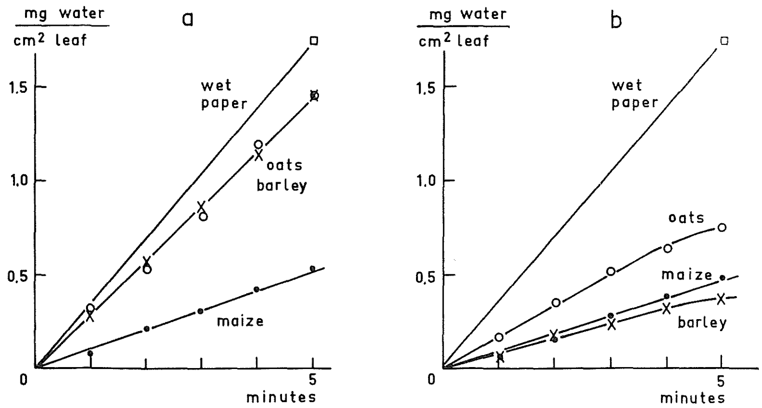

FIG. 5. The water loss of detached leaves grown in humid (a) and dry (b) air, as measured in a balance placed in the growth room with dry air.

velocity of 30 cm sec^{-1} (7). The stomatal resistances can be calculated (9) from the ratio between the transpiration of the leaf and the evaporation of the filter paper. These resistances appear to be roughly 2.1 cm for maize and 0.25 cm for barley and oats.

This high diffusion resistance against water for maize raises the crucial question how this plant succeeds in keeping the diffusion resistance against carbon dioxide at such a level that normal assimilation rates can be maintained.

The transpiration rate of leaves grown under dry conditions is given in figure 5b. For maize the transpiration rate was the same as under humid conditions.

This is in agreement with the conclusion of the preceding section that the diffusion resistance of the non-detached leaves is not affected by the humidity of the air. However, the transpiration rates of oats and barley leaves grown under dry conditions were, respectively, 0.75 and 0.3 times smaller than those of leaves grown under humid conditions. Since, also for these crops, the diffusion resistance of the non-detached leaves is practically independent of the humidity the conclusion lies at hand that the transpiration rate of these detached leaves was reduced due to clipping. Since transpiration was constant during the first few minutes it is apparent that this effect took place during the 30–60 seconds between detachment and the first weighing.

CONCLUDING REMARKS

The plants in both growth rooms were growing on nutrient solutions with a low osmotic value and even in the room with dry air the evaporation rate was small compared with the rates in the open where, due to the high radiation intensity and wind velocity, the evaporation rate may be easily four times higher than that in the growth rooms.

Nevertheless, the experiments give some information on the behaviour of the species, when cultivated under dry conditions.

The transpiration coefficient of maize appears to be considerably lower than that of the other grains, an observation which confirms the results of experiments in the open (8). Such a low transpiration coefficient is of a definite advantage for cultivation under conditions of a limited supply of water, because it enables one to obtain with maize more dry matter than with the small grains. The transpiration coefficient for barley is the same as that for oats.

However, the yield of barley at low humidity tends to be lower than at high humidity, whereas the reverse is the case for oats. A negative correlation between growth and water stress in the leaves is a definite advantage under dry conditions, because it forces the plants to remain small and to save water for the period of seed formation.

It seems worth-while to investigate whether this kind of difference is the explanation for practically experienced fact that barley is more suitable for cultivation under conditions of water shortage than oats, rather than a difference in ability between the two crops to withstand periods of evere drought.

It has been supposed that the transpiration rate of detached leaves is not much different from this rate of non-detached leaves under otherwise the same conditions (6). This opinion is not confirmed by the present experiments.

Summary

Maize, barley and oats were cultivated in growth chambers at two different humidities. The differences in fresh and dry weight under both conditions are given in table 1. Maize appears to have a better growth at high humidity, whereas the reverse is the case for oats. With barley there are no distinct differences, except in leaf area.

The transpiration coefficient is considerably lower for maize than for the small grains. This is not caused by a difference in assimilation, but in the transpiration per unit leaf area. This could be confirmed by an estimation of the transpiration rate of detatched leaves.

The significance of these differences in regard to cultivation under conditions of a limited supply of water is discussed.

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