THESIS

THE DEPENDENCE OF GROWTH UPON TRANSPIRATION UNDER DIFFERENT CONDITIONS OF HUMIDITY

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The phenomenon of growth is one of great complexity it being the resultant of several processes which are carried on within the plant, the several factors concerned with it being in turn influenced to a greater or less degree by external conditions.

The relation of one of these processes, transpiration, to growth has given rise to much discussion among plant physiologists and is still an unsettled question.

Among those who look upon transpiration as primarily a vital process there are three general views held regarding its role : (1) To enable the plant to take up a sufficient supply of mineral salts ; (2) To prevent high temperatures in the plant ; (3) That it is a necessary evil, necessary in that moist membranes must be exposed for the exchange of gases and at the same time an evil since such large quantities of water are required.

Strasburger, Noll, Schenk and Schimper (12) hold that the plants would be unable to obtain a sufficient supply of nutrient salts if they took up only as much water as they could retain and make use of.

They also consider transpiration necessary to secure a proper concentration of those salts.

Pfeffer (9) regards transpiration essential for the distribution of mineral salts in the plant and even maintains that growth varies with the transpiration. He also thinks it probable that transpiration influences the exchange of gases. If it were not for transpitation, the intercellular spaces would become filled with water which would prevent aeration of the tissues thus retarding metabolism and growth. On the other hand, in the presence of a limited supply of water in the plant, the diminution of transpiration must of necessity interfere with the free exchange of gases thus inhibiting the assimilation of CO_2.

Sachs (10) in commenting upon the fact that assimilation may be carried on in land plants which are surrounded by a saturated atmosphere, points out that the assimilation in this case is extremely feeble and furthermore that even under these conditions transpiration may occur to a slight degree and a feeble flow of water maintained.

Edmond Gain (2) concludes from the works of Hellriegel Haberlandt, Wollny and others that a certain relation

exists between the amount of dry matter elaborated and the weight of water transpired by the plants during vegetation. This view is also held by Lawes and Gilbert (7).

Green (4), in addition to the view that transpiration is necessary in order that the leaves may be supplied with inorganic salts, maintains that it is imperative in order to prevent a rise of temperature to a point which would be fatal to the plant. He states that the amount of radiant energy taken up by the leaves has been computed to be nearly 50 times the amount which can be utilized in the process of photosynthesis ; if the heat were allowed to accumulate in the leaf unchecked it has been calculated that its temperature would rise during bright sunshine more than 12° C. per minute. Pfeffer (9) and Tschaplowitz (13) also recognize the probability of a regulatory influence of transpiration upon the temperature of the plant.

Kreusler (6, See Woods, 15), does not regard the checking of transpiration by a complete saturation of the atmosphere as unfavorable to assimilation but, on the other hand, holds that assimilation may be reduced by a dry atmosphere, which is conducive to excessive transpiration, long before the turgescence of the leaf is visibly diminished.

Barnes (1) advances the theory that the amount of salts absorbed is dependent upon the living cortex of the rootlets and the mesophyll of the leaves. He states, "if the cortex be freely permeable equilibrium in the distribution of any given salt will occur, assuming for a time no evaporation from the aerial parts. If then evaporation concentrates the solution the higher diffusion tension of that salt will tend to drive it to those regions where the diffusion tension is lower. This tendency, therefore, would operate against the further supply of that material in the leaves. If the cortical layers be not freely permeable, the amount absorbed is regulated wholly by protoplasmic activity and cannot be affected directly by outside supply. The phenomena of selective absorption show that transpiration does not determine in those cases the amount of salts absorbed."

The experiments conducted by certain investigators serve to indicate that an increase or decrease in transpiration, as influenced by the humidity of the atmosphere, does not necessarily produce a corresponding increase or decrease in growth.

Godlewski (8) found that a sudden in increase or decrease in humidity produced a corresponding change in growth which, however, was only transitory. At the end of one-half hour it returned to its former rate. This led him to the conclusion that the action of humidity was not to change growth but to produce a change of turgescence and consequently turger-distension.

Schlösing (11), working with tobacco plants, found that transpiration was greatly decreased by a moist atmosphere while the gain in dry substance was increased, the plants in the moist atmosphere gaining 5.2 grams per liter of water evaporated as against 1.2 grams in the dry atmosphere. The composition of dry matter was also found to vary under the different conditions of humidity, the percentage of ash being 13 in the moist atmosphere and 21.8 in the dry. In commenting upon this fact, Schlösing states that all tobacco plants of any source, species or degree of development, examined by him, have given in the vicinity of 20% of ash, hence the plants grown under humid conditions were abnormal in this respect.

Wollny (14) found that the dry weight and total amount

find that the quantity of water transpired by some of our common field crops during their period of growth is not a measure of the amount of dry matter formed. That the ratio between these quantities is not constant is shown by the following table which gives the amount of water transpired per unit of dry matter, as determined by different investigators.

TABLE 1.

	Lawes and Gilbert	Hellriegel	Wollny	King
Wheat	225	359	-	-
Barley	262	310	393	774
Oats	-	402	557	665
Red Clover	249	330	453	-
Peas	235	292	477	447

In commenting on these results, Hall (5) says, "The divergencies in these results are intelligible if we consider that the transpiration process by which the water is lost and the assimilation process by which the plant gets heavier have no necessary connection, tho both become active under the same stimuli of light and warmth."

The numerous modifications of desert plants for the purpose of reducing transpiration have been considered by some as evidence that this process is not essential to the growth of plants. It must be borne in mind, however, that under these conditions transpiration is still carried on to some extent, furthermore, the conditions are so favorable for excessive transpiration, that were it not for these special adaptations the plants would soon be deprived of their limited supply of water.

The experiments described on the following pages were undertaken with a view toward determining what relation, if any, exists between transpiration and growth under different conditions of humidity.

Five species of plants were employed for this purpose, viz., corn (State Flint), sunflowers, peas, wheat (Dawson's Golden Chaff) and buckwheat.

The plants were grown in wire baskets 3 inches in diameter and 3 inches deep. The manner of preparation was as follows : The tops of the baskets were first dipped in melted paraffin to the depth of about one inch. This formed a collar around the top which prevented the paraffin

from flowing over the surface of the soil while the remainder of the basket was being coated after filling. It also prevented the water which was added from time to time during the experiment from flowing off at the sides of the basket. The baskets were filled within three-fourths of an inch of the top with soil which had been thoroly mixed, pulverized, and screened to remove the lumps and stones. They were then dipped in paraffin until coated sufficiently to prevent loss of water. The paraffin also served to cement the soil particles on the outer portion of the soil column to the sides of the basket, thus preventing the formation of an air space between the soil and basket.

The seeds were soaked in water before planting until germination had commenced. This method of treatment hastened germination and also enabled a selection to be made of seeds which were of nearly uniform vigor, thus eliminating to some extent extremes of individual variation. A few more seeds were planted than the number of plants required. This permitted another selection to be made after the plants had begun to grow. When the plants were 2 to 2 1/2 inches in height, they were thinned to the required

number and the tops of the baskets sealed to prevent evaporation from the surface of the soil. This was done as follows : A circular piece of paper having a diameter a little less than that of the basket was dipped in paraffin and a slit of sufficient length and width to admit the young plants was cut into it. Previous to sealing a layer of fine sand, about one-fourth inch in thickness, was added to each of the baskets to aid in preventing evaporation from the surface of the soil. The paper was then adjusted and fastened in place by running melted paraffin around the edge, thus cementing it to the sides of the basket.

The amount of paraffin added was determined by weighing the baskets before and after sealing. The difference added to the weight at planting gave the final optimum, i.e., the weight of the paraffin and basket plus that of the soil in which the moisture content had, by the addition of water, been brot up to the amount considered to be most favorable for the growth of plants.

The loss of water by transpiration was determined by weighing the baskets at intervals of three or four days.

Water was added at this time until the weight of the basket was a few grams above the optimum, the excess depending upon the rate of loss.

The plants were divided into three lots and each subjected to one of the three conditions, which were designated as dry, check and moist. The three lots were placed side by side in the greenhouse, the dry and moist being under bell-jars while the check was unenclosed.

The average relative humidity of the dry was 78°, of the check 88° and of the moist 98°. The excess of moisture was removed from the atmosphere of the dry, by placing calcium chloride in open dishes under the bell-jars. The calcium chloride was changed as soon as it had become saturated with moisture, usually morning and night. The high degree of humidity of the moist bell-jars was maintained by placing pieces of wet filter paper under them.

The bell-jars were aerated each morning in the following manner : With those subjected to the dry conditions this was accomplished by forcing air, from which the moisture had been removed by passing thru a column of calcium chloride and pumice stone, into the bell-jars. In the case of those in which the moist conditions obtained, the

air was changed by removing the bell-jars for a few minutes. This was done at a time when the humidity of the atmosphere in the greenhouse was relatively high.

The temperature of the three conditions was the same as that in the open greenhouse, viz., about 65°F. during the day and 60°F. at night, except that on bright, clear days the rays of sunlight caused a rise in temperature of several degrees in the bell-jars above that in the open greenhouse. This change of temperature was the same in both the dry and moist. The temperature factor must be taken into consideration when comparing the check with the other two conditions.

The following table gives the number of baskets used, the number of plants in each and the date of the beginning and end of the period during which transpiration records were taken.

Table II.

Kind of plant	No. of baskets	No. of plants in each.	Beginning of trans. period	End of trans. period.
Corn	12	2	Feb. 2	Feb. 22
Sunflowers	9	2	Feb. 2	Mar. 2
Peas	9	2 in 6 3 in 3	Feb. 17	Mar. 7
Wheat	9	6	Mar. 5	Mar. 23
Buckwheat	15	4	Mar. 19	Apr. 5.

At the close of each part of the experiment, which was on the date indicated in the last column of Table II, the plants were cut at the surface of the soil, measured, the green weight, dry weight and ash determined, also the ratio between the water transpired and the dry matter produced. The results are given in the following table :

Table III.

	Av. ht. cm.	Green weight gms.	Dry matter gms.	% d.m.	Ash gms.	% ash in d.m.	Trans. gms.	Water transp. per gm. d.m. gms.
Corn -								
Dry	42.2	25.0	1.9630	7.85	.3405	17.35	380.0	193.6
Check	39.2	25.4	1.8177	7.15	.3227	17.75	180.9	99.5
Moist	39.9	27.0	1.8352	6.80	.3374	18.38	123.9	67.5
Sunflower								
Dry	29.9	19.6560	1.6140	8.21	.3878	24.02	615.0	381.66
Check	24.5	16.7638	1.2115	7.23	.2910	24.02	348.4	287.58
Moist	25.6	15.0080	.8565	5.71	.2295	26.80	110.2	128.66
Peas-								
Dry	40.2	9.2365	.7992	8.65	.1178	14.74	227.3	284.41
Check	37.0	9.0737	.7406	8.16	.1071	14.46	154.9	209.10
Moist	42.9	9.7130x	.9145	9.42z	.1144	12.51	46.4	50.74
Wheat -								
Dry	32.2	6.1905	.8548	13.81	.1300	15.21	302.6	354.00
Check	23.4	4.3537	.6897	15.84	.0794	11.51	155.9	226.04
Moist	33.0	7.6445	.9665	12.64	.1335	13.81	95.4	98.71
Buckwheat -								
Dry	17.8	10.5875	.9720	9.18	.1682	17.30	299.8	308.44
Check	14.1	6.6035	.6345	9.61	.1110	17.50	159.3	251.07
Moist	23.6	10.6190	.9315	8.77	.1625	17.44	122.4	131.40

x. Figures too low. The plants wilted very rapidly as soon as removed from the moist atmosphere thus reducing the weight.

z. Figures too high. Same reason as above. Should be less than figures for "dry".

An inspection of this table shows that height, total weight and composition are influenced to a greater or less degree by the amount of water transpired, the direction and extent of this influence varying with the species.

It will be noted that in the first two series the results for the checks are, in general, intermediate between those of the dry and moist, while in the case of peas, wheat and buckwheat the results are lower than those obtained under either of the other two conditions. This is attributed to the fact that the three last series named were run later in the season (see table II) when the number of hours of sunshine per day was greater, as was also the number of bright, clear days. The effect of this was to cause a rise of temperature in the bell-jars above that of the air surrounding the check plants. Since we have another factor entering into the problem which exerts a considerable influence on growth, the results obtained from the checks are not comparable with those obtained under the other conditions, hence they will be omitted from the present discussion.

With the exception of the sunflowers the plants appeared to suffer no ill effects from either the dry or

moist atmospheres. In the instances referred to the plants growing in the atmosphere saturated with moisture were more or less distorted, the stems being somewhat knotted or twisted. It is probable that the excessive strain due to the increase in turgor, as a result of the checking of transpiration, caused the tissues to assume somewhat abnormal shapes.

There was a preceptible difference in the height of the plants grown under the two conditions as is shown by the figures in table III. Corn and sunflowers reached their greatest height in the dry atmosphere, while peas, wheat and buckwheat were taller where moist conditions prevailed. The increase in height was in every instance coincident with an increase in total dry matter except in the case of buckwheat. With the exception of corn this same relation exists between the height and green weight.

It will be seen that the amount of water transpired exerted a marked influence on the composition of the plants. In every instance the percentage of water was greater in the plants grown in the moist atmosphere. We would expect this to be the case as the turgidity of the

cells, and consequently the amount of water contained in the tissues, would be much greater where there was but little loss by transpiration. The percentage of ash in dry matter also varied in the plants grown under the different conditions.

It is significant to note that in every instance, comparing the plants grown under dry and moist conditions, the higher percentage of ash in dry matter is coincident with a lower yield of total dry matter, tho the total amounts of ash constituents are practically the same under both conditions. This appears to indicate that the conditions which are unfavorable for growth inhibit the elaboration of organic food substances to a greater degree than the absoprtion of mineral salts.

It will be observed that transpiration was not entirely checked in the moist atmosphere. This is in accordance with the view generally held by plant physiologists that, in the presence of sunlight, the temperature of the plant usually rises above that of the surrounding air and that under these conditions transpiration may be carried on to a slight degree even in an atmosphere saturated with moisture.

In the case of corn and wheat, more particularly the latter, part of the water recorded under the head of transpiration was removed from the plants by guttation. During their early period of growth drops of water were often seen, in the morning, on the ends of the leaves of those plants which were in the moist atmosphere. Toward the latter part of the experiment this was not noticed.

The results show very conclusively that transpiration varies directly with the humidity of the atmosphere surrounding the plants, but growth, however, does not appear to show a similar relationship to either of these factors, in fact the largest total yield of dry matter in three cases out of five was where the least quantity of water was transpired.

If growth were directly dependent upon transpiration, as many of the leading plant physiologists assert, then we would expect to find, for each species, a constant ratio between the increase in substance and the water transpired but such is not the case, as is shown in the last column of Table III and by the results of experiments conducted along this line by certain investigators.

Conclusions.

The results show that in certain of the species of plants under investigation maximum growth may be carried on when transpiration is reduced to a minimum, at least during the early period of vegetative growth.

Where there is a decrease in growth coincident with a checking of transpiration the decrease appears to be due to the inhibition of the elaboration of organic matter rather than by limiting the quantity of mineral salts absorbed.

In general the checking of transpiration does not appear to decrease the total amount of mineral salts absorbed by the plant, at least for the period of growth during which the plants were under observation.

The composition of the plant is materially affected by variations in the rate of transpiration, especially the percentages of moisture in the fresh plant and of ash in the dry matter.

There appears to be no constant ratio between the quantity of dry matter produced and the amount of water transpired, the relation varying according to the envir-

onment of the plant.

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