

Some observations on the relation between transpiration and soil moisture

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SOME OBSERVATIONS ON THE RELATION BETWEEN TRANSPIRATION AND SOIL MOISTURE ¹⁾

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SUMMARY

Pot experiments on transpiration with kidney beans (*Phaseolus vulgaris*) were carried under controlled conditions of light intensity and temperature. Transpiration was measured by loss of weight. Measurements were taken at different moisture contents from the field capacity down to the wilting point. From the regularly recorded data on loss of weight the moisture content at each interval was calculated. The transpiration rate is greater at higher light intensities. It increases with the increase in the available moisture content from the wilting point and then becomes nearly constant at higher levels of moisture availability. At the highest light intensity it shows a maximum beyond which it slightly decreases. This may be explained by the deficiency of oxygen at higher moisture contents.

INTRODUCTION

Evidence regarding the availability of soil moisture between *field capacity* (maximum moisture content in equilibrium with the force of gravity) and *wilting point* is rather conflicting. In light and medium soils moisture appears to be equally available throughout this range (9). Other observations, however, indicate that deep rooted species on heavy soils may show a marked plant response to moisture deficit before the wilting point, as in stomatal behaviour, photosynthesis, respiration, transpiration, and starch accumulation. Growth is markedly influenced, particularly in plants grown in pots or containers (12). It has been assumed that water movement and root growth are more rapid in light and medium soils, and that this results in a fairly uniform depletion of soil moisture up to the wilting point. On the other hand, in heavy clay soils the upper zone together with the bulk of the roots may be depleted up to or below this percentage long before the lower zone, the average calculated availability still being high. It may be expected that plant species with sparse rootsystems will be more sensitive and respond earlier to drought than species with an intensive rootsystem.

The question as to whether or not soil moisture is equally available between field capacity and wilting point also depends upon the overall shape of the pF-curve, as has been shown by RICHARDS and WADLEIGH (8). It is evident from their figures that Olympic clay holds nearly 50 per cent of available water with a tension of one atmosphere and 25 per cent with a tension of three atmospheres, whereas Yolo clay loam holds 25 and 15 per cent respectively at these tensions. Many investigators have made experiments with plants in Yolo clay loam or similar soils in which the margin between the wilting point and the point at which soil moisture begins to be available is so narrow that it cannot be detected in field experiments.

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The difficulty of maintaining a constant moisture tension during an experiment is well-known. The use of drying cycles in which growth occurs at low tensions during relative long periods but still for short times at higher tensions tends to minimize plant response. HALKIAS *et al.* (3) observed a regular decrease in soil moisture down to the wilting point using various crops. They concluded that water is equally available throughout the whole range. It seems that this conclusion is not right since the exhaustion of water from the soil is controlled by the evaporative power of the atmosphere [MAKKINK and VAN HEEMST (5)] and also to the increase in leaf area.

Further evidence on factors affecting the relation between soil moisture and plant growth has been summarized by VEHMEYER and HENDRICKSON (10), RICHARDS and WADLEIGH (8) and HAGAN (2). It is obvious that the contradictory data of transpiration obtained by different authors can be attributed to differences in experimental conditions. Experiments described in this paper were carried under controlled conditions of temperature and light intensity.

MATERIAL AND METHODS

Kidney beans (*Phaseolus vulgaris*) were cultivated in small white tins containing 1 kg of a light clay soil. This soil holds about half of its available water at a tension of one atmosphere (fig. 1), which, as mentioned above, is important for this kind of investigation. After sowing, the tins were placed in a growth cabinet at $20 \pm 2^\circ$ C and illuminated for 12 hours a day by fluorescent daylight tubes at a light intensity of 2×10^4 ergs/sq.cm sec. The

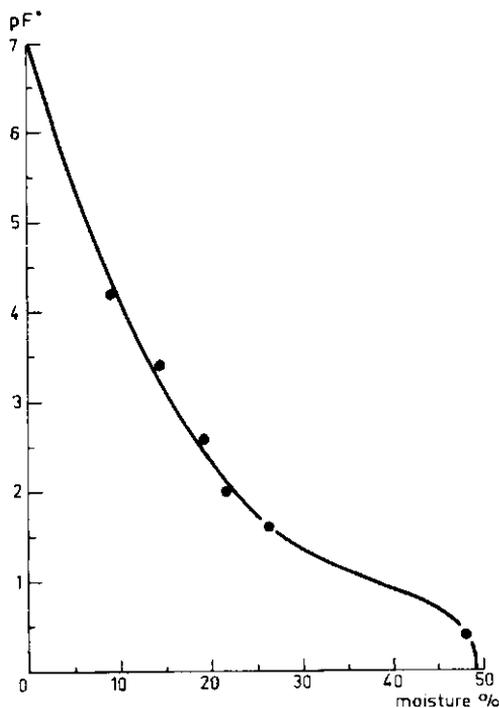


FIG. 1 THE MOISTURE CONTENT (WEIGHT PERCENT) VERSUS THE MOISTURE TENSION (pF) OF A LIGHT CLAY SOIL.

soil was kept at field capacity by sprinkling the tins every day if possible. This way ensures a rapid growth. After a period of three weeks when the leaf area was 100–130 sq.cm, the soil surface was covered with vaseline to prevent evaporation. Then, the tins were placed in thermostats for measuring transpiration under controlled conditions.

The four thermostats at 15°, 20°, 25° and 30° C can be kept at constant temperatures with an accuracy of 0.5° C by means of a thermorelay. The upper side of the thermostat was covered by a glasspanel above which fluorescent daylight tubes were placed. Various light intensities were obtained by placing different white paper screens on the glasspanel. The light intensities were measured with a photocell which had been calibrated against a large surface thermopile. The relative humidity was measured by means of an ASSMAN-psi-chrometer and recorded by a hygrograph. In this way transpiration was measured at four temperatures and four to five light intensities ranging from $0-4.5 \times 10^4$ ergs/sq.cm sec.

The tins were weighed on a balance every hour with an accuracy of 10 mg. The measurements were taken during the daytime until the moisture content of the soil reached the wilting point. This period ranges between 4 to 10 days depending on the intensity of transpiration. Then, soil samples were taken and dried at 105° C in order to determine the moisture content. From this percentage and the regularly obtained data of loss in weight the moisture content at each interval could be calculated. Leaf area was measured by squares on a natural size image.

EXPERIMENTS

The plants from the growth cabinet were selected according to equal leaf area and placed into the thermostats the night before the experiments started in order to establish an equilibrium between air and soil temperature.

Figure 2 shows the transpiration in gms/100 sq.cm hr versus the moisture percentage of the soil at various light intensities at 20° C and 40 per cent relative air humidity. The results obtained by VEIHMAYER and HENDRICKSON (11) using beans have also been plotted in the figure. It is evident that much higher transpiration rates were observed in our experiments. Obviously the curves represented tend to meet at the wilting point (moisture content $\pm 9\%$) where the transpiration rate is 0.3 gms/100 sq.cm hr. In another experiment carried by the author under lower evaporation conditions the transpiration rate was 0.15 which is nearly equal to that obtained by VEIHMAYER and HENDRICKSON. The latter authors concluded that soil moisture is equally available over the entire range studied due to the maintenance of the transpiration rate at a constant level. Examination of the results obtained in this paper shows that the transpiration rate is influenced by the change in the availability of moisture. At the highest light intensity of the order of 4.5×10^4 ergs/sq.cm sec the transpiration rate was 0.3 gms/100 sq.cm hr near the wilting point, then it increases gradually with the increase of the available moisture content until it attains a maximum of 1.2 gms/100 sq.cm hr at a moisture content of 16%. At a moisture content above 16% the transpiration rate exhibits a slight fall. The decrease in transpiration at low moisture tensions may be due to lack of oxygen, which strongly affects water absorption [Mc DERMOTT (5)]. At lower light intensities the curves show nearly the same trend but tend to flatten.

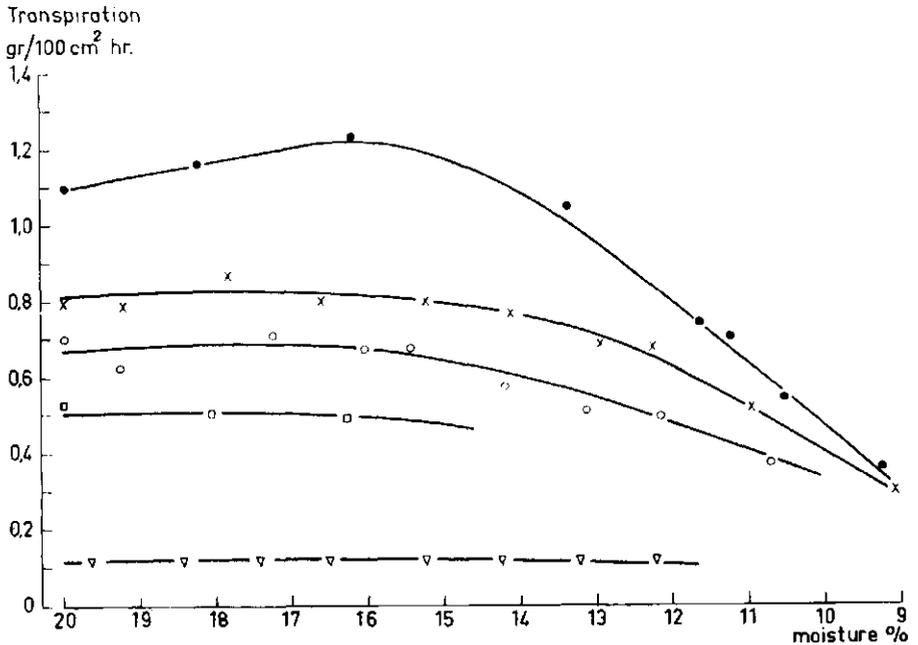


FIG. 2 THE TRANSPIRATION OF BEANS IN GMS/100 SQ.CM HR VERSUS THE MOISTURE PERCENTAGE OF THE SOIL, AT VARIOUS LIGHT INTENSITIES AT A TEMPERATURE OF 20° C AND A RELATIVE HUMIDITY OF 40%.

- light intensity 4.5×10^4 ergs/sq.cm sec
- × light intensity 2.4×10^4 ergs/sq.cm sec
- light intensity 1.4×10^4 ergs/sq.cm sec
- light intensity 0.66×10^4 ergs/sq.cm sec
- ▽ results from VEIHMAYER and HENDRICKSON (11).

Therefore it is evident that the transpiration rate shows a remarkable change with the variation in the soil moisture availability. The amplitude of this change becomes less pronounced at the lower light intensities. Comparable results were obtained at 15°, 25° and 30° C and other relative humidities. The effects of light intensity, temperature and saturation deficit on transpiration, however, will be dealt with in a subsequent paper.

MAKKINK and VAN HEEMST (5) draw a similar conclusion. They demonstrated that a decrease of the actual evapo-transpiration of grass with increasing moisture tensions only occurs at high evaporation conditions. At low evaporation conditions no such decrease was observed. The lack of the relation between transpiration rate and availability of soil moisture in VEIHMAYER and HENDRICKSON'S results may be due to the fact that they carried their experiments under a limiting potential evapo-transpiration. Moreover since transpiration rates of 1–3 gms/100 sq.cm hr and under extreme conditions up to 6 gms/100 sq.cm ha have been recorded on many occasions and this is at least ten times the rate observed by these authors.

DISCUSSION

Various soil factors, for example shape of the moisture tension curve and root growth affect the results obtained in experiments on moisture availability, as has already been explained in the introduction. VAN DEN HONERT (4) treated water uptake, water movement through the plant and transpiration as a series

of linked processes in which the overall rate is determined by the slowest process. This implies that investigations concerning the availability of moisture should be made under optimal atmospherical conditions. It has been shown (fig. 2) that the experiments with beans conducted by VEIHMAYER and HENDRICKSON (11) cannot serve as a general proof that soil moisture is equally available from field capacity to wilting point, since transpiration was only one tenth of that normally occurring in the field. On the other hand, the same authors arrived at a similar conclusion with sunflowers in a glasshouse. In this case atmospherical conditions were not limiting and a transpiration rate of roughly 40 gms/100 sq.cm day, or 4 mm/day was found. Examination of the figure obtained by the mentioned authors shows that the points indicating the transpiration rate at different moisture content are scattered. Moreover the total leaf area in the several containers varied from 450–1300 sq.cm. Transpiration was measured by using large plants in the wet region and small plants in the dry region. In representing transpiration per unit leaf area one assumes a linear relation between leaf surface and transpiration. However, BIALOGLOWSKI (1) and PARKER (7) showed that this relationship does not always exist and depends on other factors among which may be shading of the leaves and change in the top-root ratio. This ratio may be higher in small containers since root extension is limited by the walls whereas the transpiring leaves can occupy a larger surface especially when grown in the wet region as compared with a field vegetation. It is possible, therefore, that in VEIHMAYER and HENDRICKSON'S (11) experiments with sunflowers the computed transpiration values per unit leaf area for the large plants in the wet region for this reason are relatively too low as compared with those for the considerably smaller plants in the dry region.

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THE EFFECT OF SOME ENVIRONMENTAL FACTORS ON THE TRANSPIRATION OF PLANTS UNDER CONTROLLED CONDITIONS

by

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INTRODUCTION

An extensive review of literature on the effect of climatic and soil factors on the transpiration of plants has been given already by BURGERSTEIN (5), and recently by STÄLFELT (7). It is obvious that factors like temperature, relative humidity and wind velocity affect leaf transpiration mainly through the physical process of evaporation.

Other factors as *e.g.* light intensity and water supply, affect leaf transpiration also by a physiological process in the plant changing the stomatal movement and stomatal diffusion resistance.

According to STÄLFELT (7), the stomatal mechanism is activated by light; this light sensitive reaction appears to be related with photosynthesis (8). On the contrary, with a large water deficit of the plant an osmotic system is the main regulator of the stomatal aperture. Though various methods were developed to determine the aperture of the stomata, it is rather difficult to measure the width of the slit at values below 2μ , whereas changes in this range have a large effect on the rate of transpiration (1, 7). Moreover, it is difficult to estimate the joint effect of all the stomata of a leaf. It is therefore more convenient to compute stomatal diffusion resistance from quantitative measurements of transpiration.

Theoretical considerations on transpiration based on FICK'S diffusion law were set up by BROWN and ESCOMBE (3) and by BANGE (1). The latter author determined the relation between the stomatal aperture and the stomatal resistance to the transport of water vapour from inside the leaf to the surrounding air. Simplifications were made by taking the total diffusion resistance in the heterogeneous system as an algebraic sum of the respective resistances of the component parts while only the concentrations of water vapour at the beginning and at the end of the diffusion path are needed for calculation of the vapour gradient.

Our aim was to study quantitatively the effect of some environmental factors on the transpiration of plants, keeping in mind the above considerations which had FICK'S diffusion law as a basis.

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MATERIAL AND METHODS

The transpiration experiments were performed with beans, rye, and tomato under controlled conditions of temperature and light intensity. The plants were cultivated in small containers with about 1 kg of a light clay soil of which the pF-curve was determined. The beans (one plant per pot) were placed in a growth cabinet at a temperature of 20°C, and a light intensity of 2.0×10^4 erg.sec.⁻¹ cm⁻² σ sphere (for explanation see below) and sprinkled every day. In this way a rapid growth occurred. After 10 to 12 days, when the first pair of leaves was completely developed, the transpiration measurements were started. The soil surface of some pots was covered with paraffine to prevent soil evaporation. Rye was cultivated in a cold glass house. A week before the investigation, when the plants had a height of about 10 cm, the pots were placed in the growth cabinet. Tomato plants for potometer experiments were also grown in this cabinet.

For the study of transpiration under controlled conditions movable light boxes and thermostats were used.

In the range between 5° and 15°C the movable light boxes were placed in low temperature rooms. Between 15° and 35°C, thermostats were used which could be controlled with an accuracy of 0.5°C by means of a thermorelay. Each thermostat was divided in two compartments by means of a horizontal floor, perforated with holes of a diameter of 7 mm. The lower compartment contained the electric heating elements, small fans for mixing the air, a fan introducing cool air from outside the laboratory, and petri dishes with water, to maintain, as far as possible, a constant vapour pressure of the air. In the higher compartment the experimental plants were placed in quiet air. The air temperature proved to be the same in the whole thermostat. The relative humidity was constant during short-time experiments up to one day, and varied within a range of 7 % in long-time experiments (several days, up to 1½ week). The relative humidity was measured with a psychrometer before and after each experiment, whereas a thermo-hygrograph recorded temperature and relative humidity during the whole experimental period.

The upper side of the thermostat was covered by a glasspanel above which fluorescent tubes TL 55 "daylight" were placed. Various light intensities were obtained by placing different white paper screens on the glass-panel and by placing white gauze inside the thermostat. In the movable boxes different light intensities were obtained by varying the distance between the plants and the fluorescent tubes. In this way, the light intensity could be varied between 0 and 6.0×10^4 erg. sec.⁻¹ cm⁻² σ sphere measured with the spherical radiation meter (9). The latter responds to direct as well as to reflected light.

The transpiration was measured with plants in soil, or with cut leaves in potometers. For the potometer experiments the leaves were cut, submerged under water, in order to prevent the formation of air bubbles in the xylem vessels. Hereafter, they were placed in the potometer with a small piece of wet cotton wool. An air-tight enclosure of petiole and potometer was obtained with cacao butter. It was proved that under the most extreme climatic conditions of the experiments, the water uptake of the petiole, measured with the potometer, was equal to the transpiration of the leaf, measured as loss of weight on an analytical balance. The transpiration of plants in soil was measured by weighing the pots every hour with an accuracy of 10 mg. These weighings were continued until

the moisture content of the soil had dropped to the wilting point. Dependent on the transpiration rate the experiment lasted 4–10 days. Afterwards, soil samples were taken in order to determine the moisture content. From this value, and the obtained data on loss of weight, the moisture content of the soil could be calculated at any moment during the course of the experiment.

EXPERIMENTAL RESULTS

Experiments with potometers

The transpiration rate was measured with cut leaves of bean and tomato in potometers. The choice of suitable tomato leaves was somewhat difficult, due to differences in age, exposure to light, etc. The effect of age was studied *e.g.* in a young tomato plant with 9 leaves, and one cluster of flowers. The water loss of each leaf was measured by weighing within 3 minutes after cutting. It appears that the transpiration rate per unit area decreases with an increase in leaf age, as is shown in Table 1, while it also is higher at the tip of the leaf than at its base. The main cause of these differences is a higher number of stomata per unit area in younger leaves than in older ones. In the former the cells were smaller, since cell enlargement was not yet complete. The stomatal index, *i.e.* the ratio of epidermis cells per stoma, proved to be the same for all the leaves and was about 12 for the tomato. In the potometer experiments with tomato, described hereafter, only leaves of nearly identical age and development (4th–6th leaf from the tip of the plant) were chosen.

TABLE 1. The effect of age on the transpiration rate of the different tomato leaves as an example out of 5 experiments.
t = leaf tip b = leaf base

Leaf no.	Transpiration rate in mg.h. ⁻¹ 100 cm ⁻²
1	415
2	348
3b	312
3t	480
4b	150
4t	196
5b	175
5t	225
6b	196
6t	245
7	96
8 (eldest leaf)	155

In figure 1, the effect of light on transpiration of tomato is represented, as an example out of many experiments.

This figure contains several lines distinguished by different temperatures and different values of the relative humidity of the air.

At each air temperature and relative humidity the transpiration rate shows a linear increase with the light intensity.

Two main reasons for this relation are obvious:

1. the increase in leaf temperature due to the irradiation,
2. the increase in the aperture of the stomata with increasing light intensity.

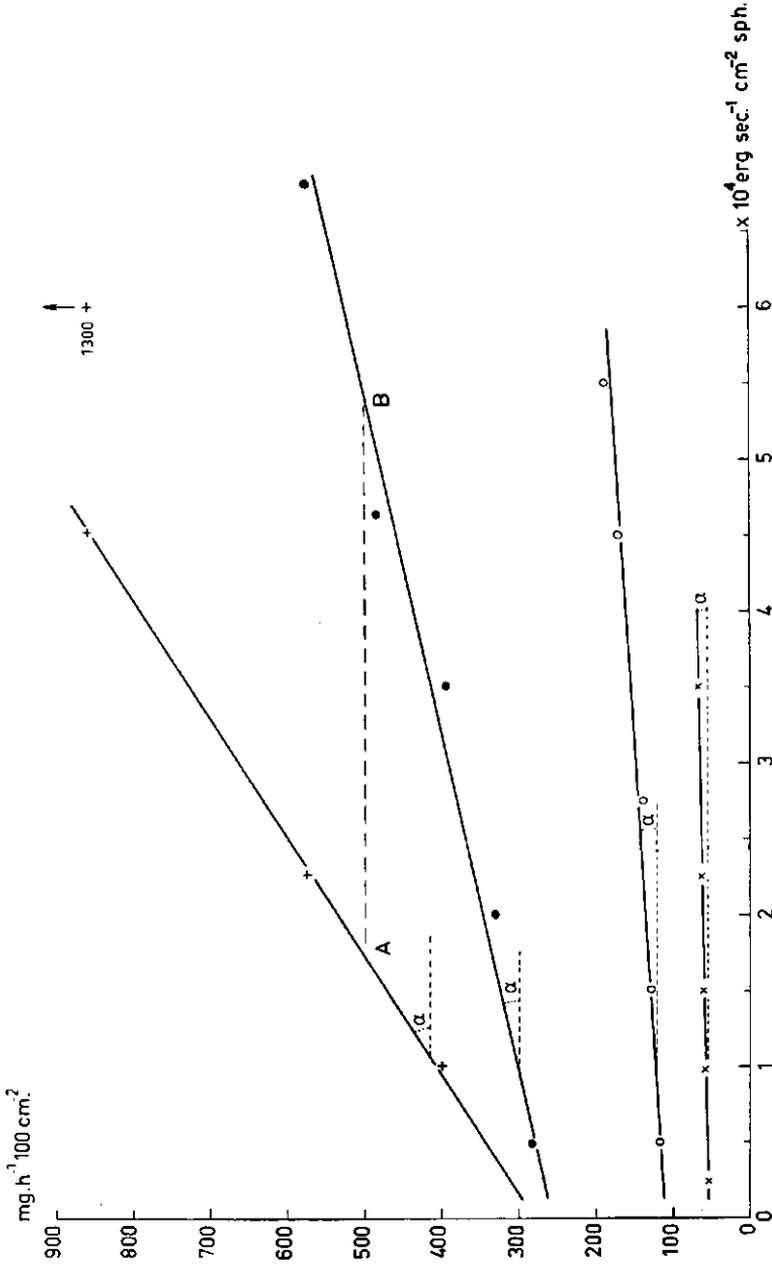


FIG. 1. The effect of light ($\text{erg. cm.}^{-2} \text{ sec}^{-1}$) on the transpiration rate ($\text{mg. h}^{-1} \cdot 100 \text{ cm.}^{-2}$) of tomato at various temperatures, with cut leaves in potometers.
 (+) at 32.5°C, 25% r.h., (•) at 18.1°C, 51% r.h., (o) at 11.5°C, 61% r.h., (x) at 4.5°C, 69% r.h.).

It appears that the slope α of the various curves in fig. 1 depends on the water vapour pressure deficit of the air which is determined by leaf and air temperatures and the relative humidity of the air (see below).

For an explanation of these observations it is useful to consider FICK's diffusion law in relation to the transpiration of leaves. For this purpose, we will, therefore, formulate this law as follows:

$$T = k \frac{c - c^1}{R}$$

T = transpiration rate in mg.h^{-1} . 100 cm^{-2} leaf surface

k = diffusion coefficient for water vapour.

c = maximal vapour pressure of water at leaf temperature (mm Hg).

c^1 = actual vapour pressure of the surrounding air (mm Hg).

R = diffusion resistance for the transport of water vapour from the leaf to the surrounding air.

In this formula $c - c^1$ represents the vapour pressure deficit, abbreviated further as V.P.D.

The actual vapour pressure of the air, c^1 , is derived from the measurements of air temperature and relative humidity. The stomatal aperture affects the diffusion resistance R .

In figure 1, the points A and B represent the same transpiration rate, at 32.5 and 18°C air temperature respectively, while the vapour pressure c^1 (in mm Hg) was practically identical in both cases. One may ask whether the leaf temperature, and thus also the maximal vapour pressure c are identical in both cases. This seems improbable since it would imply very large differences between leaf and air temperature. In the following lines we may attempt to estimate the amount of energy that has to be dissipated in B in excess of that in A and the differences between leaf and air temperature that would have to be expected for this reason.

The light intensity increases from A to B with $3.5 \times 10^4 \text{ erg.sec}^{-1} \text{ cm}^{-2}$ \varnothing sphere, which corresponds in our equipment with $2.6 \times 10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$, measured with a flat light meter in the position of the leaf. The absorption of the leaf as measured in an ULBRICHT sphere was 75%. Since transpiration is the same, the larger amount of energy absorbed by the leaf ($1.95 \times 10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$) will mainly have to be transformed into thermal emission. The values for the thermal emissivity coefficient of bean leaves in literature (4, 6) vary from 0.012 to 0.036 $\text{cal. cm}^{-2} \text{ min}^{-1}$ or 1.6×10^4 to $4.8 \times 10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$ for 1°C difference in leaf and air temperature respectively. These values are of the same order of magnitude of those quoted above for the energy absorbed by the leaf in the range of light intensities applied in our experiments. It is, therefore obvious that only small differences in leaf and air temperature, of the order of 1°C, may be expected, so that along each single curve of figure 1 only relatively small differences in the vapour pressure deficit at constant air temperature and constant vapour pressure exist.

Some preliminary measurements of the leaf temperature with thermocouples confirmed that in all experiments only small deviations of leaf and air temperature, not exceeding 1.5°C, occurred.

Assuming a maximal difference of 2.5°C between the leaf temperature in dark (which leaves may be slightly "cooled") and that at $6.0 \times 10^4 \text{ erg. sec}^{-1} \text{ cm}^{-2}$ \varnothing sphere, it can be computed that the increase in V.P.D. along each single curve of fig. 1 does not exceed 14 % owing to this temperature increase. Since transpiration is — according to FICK's law — proportional to $c - c^1$, or V.P.D., this implies that the linear increase in the rate of transpiration owing to the rise in leaf temperature is, in the range of light intensities applied, at most 14 % of the dark value.

The remainder of the observed rise — expressed by the slope α — must be due to the second aspect mentioned above, the effect of light on the opening of the stomata.

The effect of light on stomatal aperture has been incidentally confirmed by microscopic observation. The linear increase in transpiration with an increase in light intensity would correspond to a linear decrease in the diffusion resistance of the water vapour transport to the surrounding air. It may be possible that this linear decrease in the stomatal diffusion resistance depends on the rate of photosynthesis, since also a linear relationship between light intensity and photosynthesis is generally observed. It seems probable that transpiration is related with photosynthesis, because light affects the stomatal aperture and the stomatal diffusion resistance via the process of photosynthesis.

We may assume that the increase in transpiration with increasing light intensity (fig. 1: $\text{tg } \alpha = \Delta T / \Delta I$) is mainly due to a linear decrease in the stomatal diffusion resistance R , so that $\Delta T / \Delta I$ may be replaced by $\Delta T \Delta R$.

It is clear from figure 1 that the slopes α of the different curves must depend on the V.P.D.-values prevailing in the different cases. Turning back to FICK'S diffusion law, we may expect that $\Delta T \Delta R = k(c-c^1)$ so that the relation between $\text{tg } \alpha$ and V.P.D. will be a linear one in cases in which this law holds. This relationship is plotted in figure 2, and indeed appears to be linear under the conditions of our (potometer) experiments.

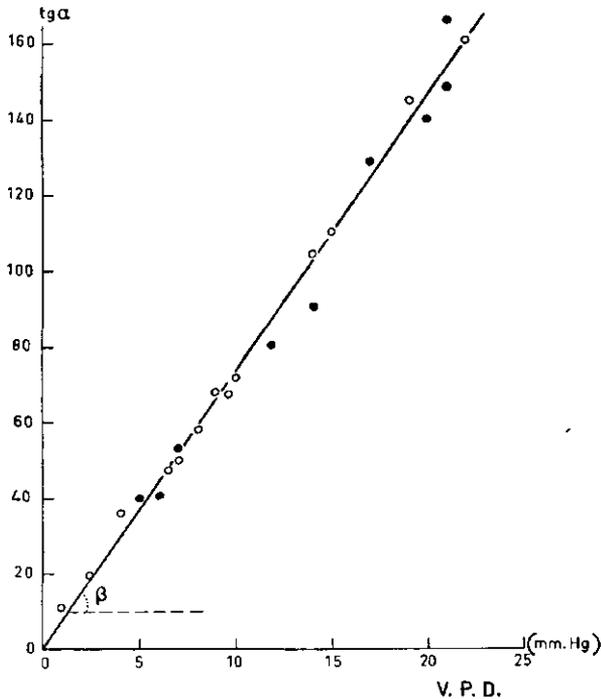


FIG. 2. The effect of the vapour pressure deficit ($c-c^1$, in mm Hg) on the increase in transpiration per unit increase of light intensity with beans (●—●) and with tomato (○—○). The unit on the ordinate is $\text{mg. h.}^{-1} 100 \text{ cm}^{-2}$. $(10,000 \text{ erg. cm}^{-2} \text{ sec}^{-1})^{-1}$, and represents $\text{tg } \alpha$ from fig. 1.

In figure 2, $tg \beta$ represents the amount of water transpired per unit light energy ($tg \alpha$ of fig. 1), the numerical values indicating $mg \text{ water} \cdot h^{-1} \cdot 100 \text{ cm}^{-2}$. ($10^4 \text{ erg} \cdot \text{sec}^{-1} \text{ cm}^{-2} \text{ sphere}^{-1}$) in relation to V.P.D. (expressed in mm Hg.). The magnitude of β is a numerical answer to the question how much water is transpired more, at a given V.P.D., on increasing the light intensity with the unit defined above. This increase in transpiration must be due to a decrease in the transpiration resistance under the influence of light.

It is well known that a major effect of light in this respect is the wider opening of the stomata. It should be emphasized that the transpiration resistance of a leaf consists not only of a light-dependent stomatal diffusion resistance but to non-light dependent resistances as well. However, under the conditions of our experiments, with ample water supply, it may be assumed that the light dependent stomatal diffusion resistance plays by far the major role.

We may thus assume that the magnitude of β also is a quantitative expression of the reaction of the stomata to increase in light intensity (see also 1). It appears, moreover, that $tg \beta$ is about the same for tomato and for beans (7.3 and 7.5 respectively, according to the units in figure 2). This indicates that the leaves of both species have about equal numbers of stomata per unit leaf area and the same stage of leaf development. This has been confirmed by microscopical observation.

In the dark, the stomata are closed or nearly closed, and transpiration takes place mainly through the cuticula. It may be expected that FICK'S law of diffusion applies also for the dark transpiration. The latter can be calculated from fig. 1, through extrapolation of the curves to the ordinate. In figure 3, the transpiration of beans and tomato in dark at various temperatures and relative humidities has been plotted versus V.P.D. Also in this case a linear relation between these two factors is evident, the curve passing again through the origin. Also here no

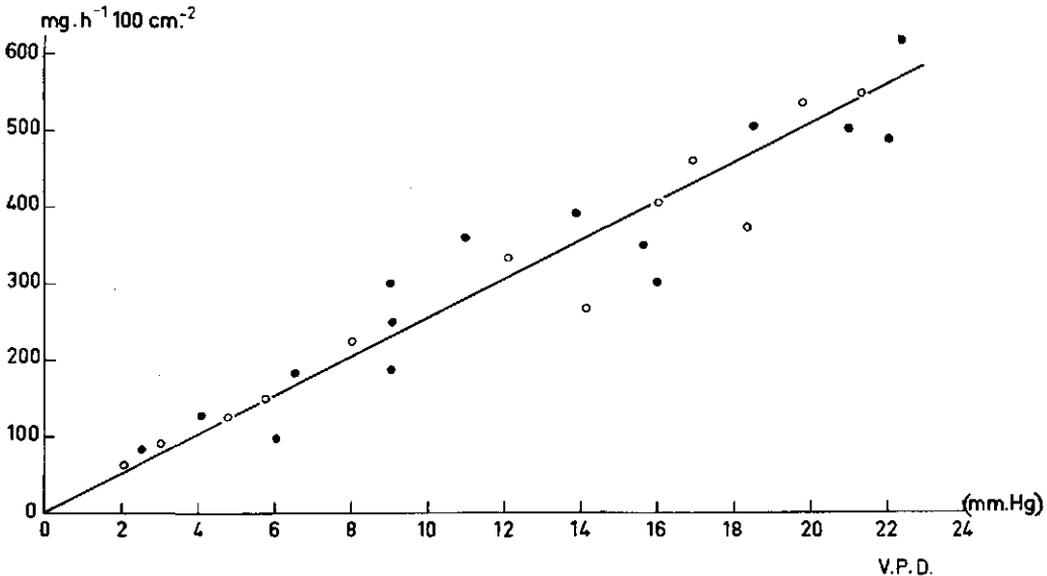


FIG. 3. The effect of the vapour pressure deficit ($e-c^1$, in mm Hg) on dark transpiration ($mg. h^{-1} 100 \text{ cm}^{-2}$) of bean (● — ●) and tomato (○ — ○).

significant differences were observed between beans and tomato. We may accept that the scattering of the points is partly due to differences in the diffusion resistance of the cuticle and to small differences in the stomatal aperture, which affect the transpiration rate strongly at the small apertures prevailing in dark.

According to the data presented in figures 2 and 3, we may conclude that for leaves under the conditions of our potometer experiments which include experiments at various light intensities, temperatures, and relative humidities, transpiration can be described by the following relation:

$$T = p \times \text{V.P.D.} + q \times \text{V.P.D.} \times I$$

If we express T in mg water. h.⁻¹ 100 cm⁻² leaf surface, V.P.D. in mm Hg and I in erg. sec.⁻¹ cm⁻² \emptyset sphere $\times 10^4$, in our experiments we found:

$$p = 25.8, q = 7.4.$$

Experiments with plants, grown in soil

The aim of these experiments was to investigate the effect of soil moisture on the transpiration rate in the range between field capacity and wilting point. Tins with rye were placed in the thermostats and the transpiration was measured every hour by weighing. The plants were illuminated during 12 hours a day. The experiment lasted 3–10 days depending on the transpiration rate. During the experimental period, the growth and the increase in dry matter production were very slight, and negligible. With respect to the amount of transpired water the transpiration rate was expressed as mg water. h.⁻¹ (g dry weight)⁻¹.

Some experiments with models were carried out to measure the soil evaporation under a cover of rye. For this purpose narrow strips of green paraffined paper (length 15 cm, width 3 mm) were placed right up into the soil, in order to imitate a non-transpiring rye crop. The models were prepared with 0, 25, 30, 40, 50, and 60 strips of paper in the soil, on a surface of 80 cm².

Some results are shown in Table 2.

TABLE 2. The evaporation rate of a soil in mg. h.⁻¹ 80 cm⁻² pot surface, with various numbers of strips, at 20 mm V.P.D.

Strips	Soil evaporation rate
0	850
25	650
30	570
40	560
50	570
60	555

It is evident from this Table that the evaporation decreases with an increase in number of strips up to about 30. With more strips no further decrease was observed.

The evaporation of the soil with a cover of strips was hardly affected by light nor by soil moisture. It depends, however, on V.P.D., as is shown in figure 4 for a bare soil, and a model with 30 strips. The evaporation increases linearly with V.P.D. according to $y = 38.2x$ for a bare soil and $y = 26.6x$ for a soil with 30 strips taking the units used in figure 4. In the experiments with rye, the total loss of weight of the pot at each time interval was corrected for by the loss due to soil evaporation with 30 strips at the corresponding V.P.D.

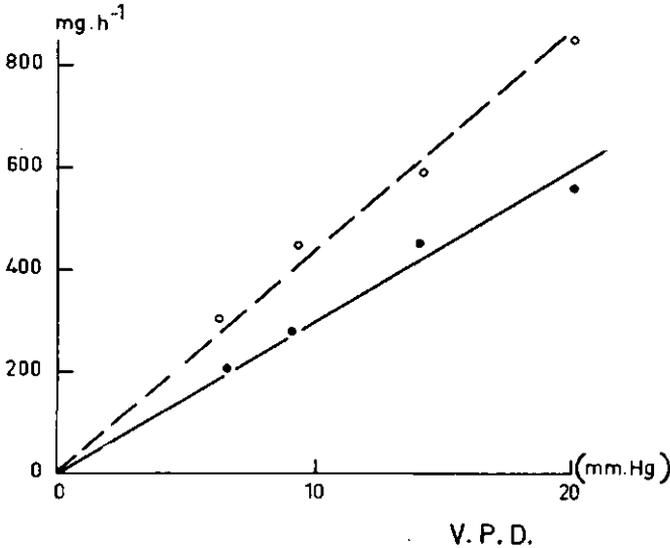


FIG. 4. The effect of the vapour pressure deficit on the evaporation of a bare soil (o—o) and a model with 30 strips (●—●).

In figure 5, the transpiration of rye at various light intensities, temperatures and relative humidities is plotted against soil moisture content, as an example out of many experiments. It is obvious that the effect of soil moisture content on transpiration is large under high transpiration conditions such as high light intensity, high temperature and low relative humidity.

Under low transpiration conditions the effect of soil moisture on transpiration is negligible which is easily understood since water supply obviously is not the limiting factor. An optimum was observed at pF 2.7 with a decrease above and below this value. In the latter case the decrease in transpiration is probably due to unfavourable conditions for the living root cells, *e.g.* lack of oxygen.

From the data of fig. 5 and its analogues at other temperatures, transpiration can be plotted versus light intensity for each pF value in the same way as in fig. 1. It was found that in the range of light intensities studied all curves were linear. From such figures, the tangents α of these curves have been plotted versus V.P.D. at some pF values in the same way as in fig. 2, and represented in figure 6. A linear relation with V.P.D. is found at each pF value, the angle depending on pF. This shows that the water supply from the soil to the shoot affects transpiration independent of light intensity. This may be achieved either by drying of the cells surrounding the intercellular holes and decreasing the relative humidity in the latter (incipient drying), or by decrease of the stomatal aperture which increases the diffusion resistance. In the latter case a change in water content of the leaf and in osmotic value of the cell sap in the vacuoles of the guard cells can be supposed to change the stomatal aperture independent of the light sensitive reaction. Consequently, a change in leaf temperature may occur, affecting the actual V.P.D. In extreme cases, *e.g.* at pF 4.2, this fact has been observed, and the curve does not pass through the origin (see fig. 6) since no correction in V.P.D. has been applied in this case.

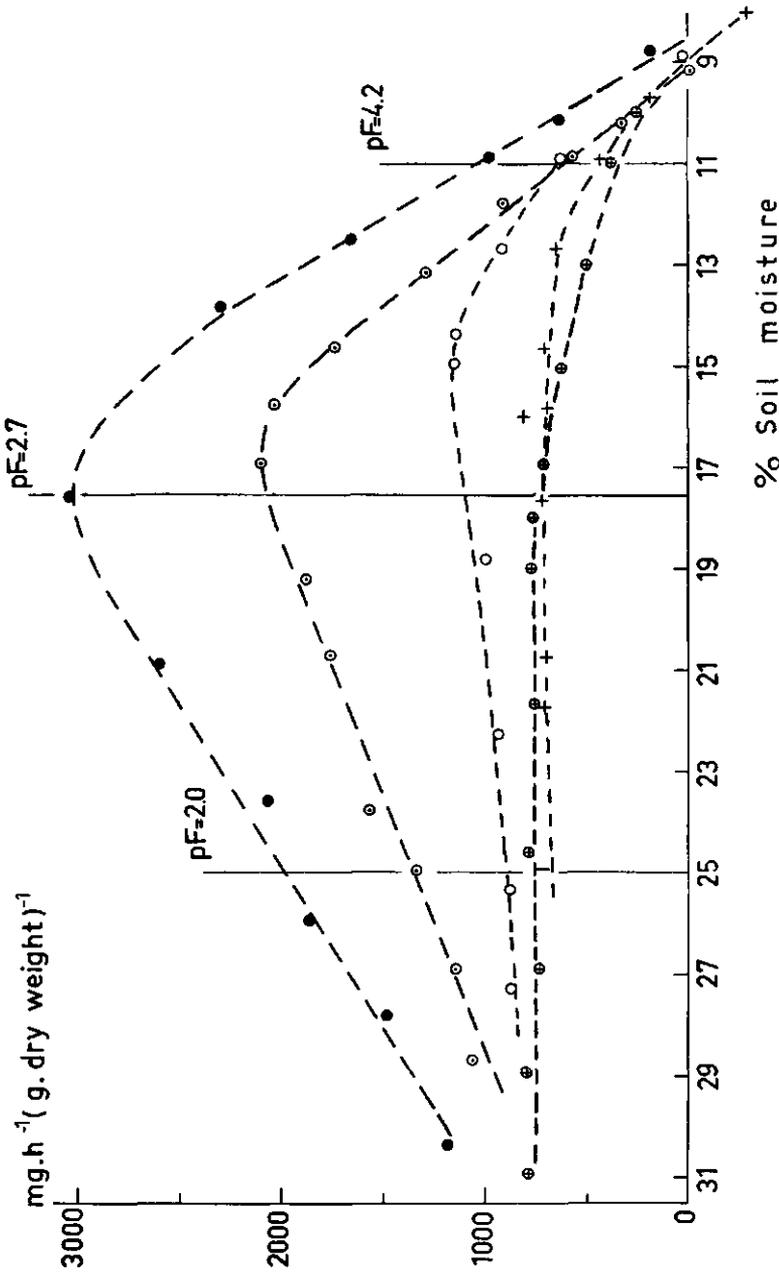


FIG. 5. The effect of the soil moisture content (in %) on the transpiration rate of rye at various light intensities and temperatures.

- ---● at 30.5°C , 32% r.h. and $6.5 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere,
- ---○ at 30.5°C , 32% r.h. and $3.5 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere,
- ---○ at 30.5°C , 32% r.h. and $1.5 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere,
- + ---+ at 30.5°C , 32% r.h. and $0.5 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere,
- ⊕ ---⊕ at 16.5°C , 53% r.h. and $6.5 \times 10^4 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere.

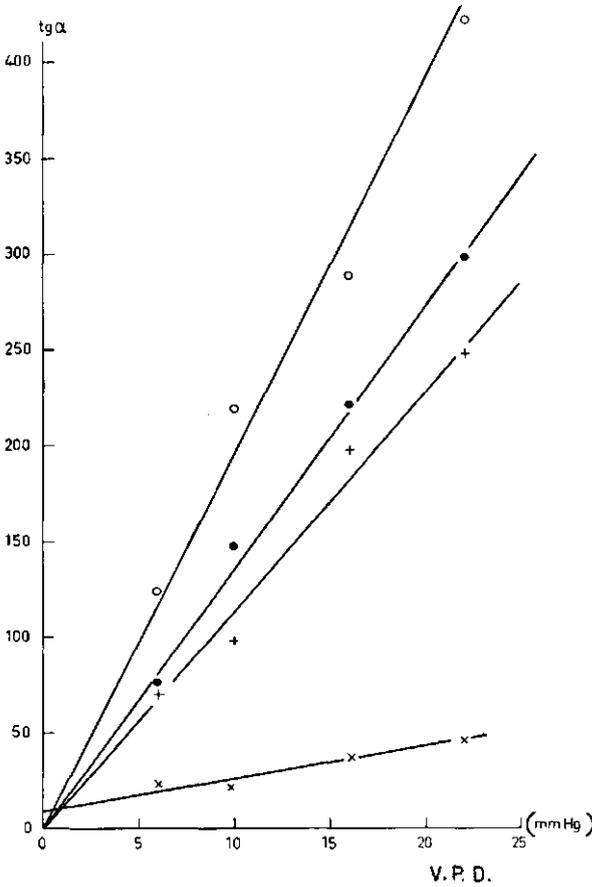


FIG. 6. The effect of the vapour pressure deficit on the increase in transpiration per unit increase of light intensity with rye at various pF values. The ordinate is calculated in the same way as in figs. 1 and 2.
 (o — o at pF 2.7, ● — ● at pF 2.0, + — + at pF 3.5, × — × at pF 4.2).

It is obvious from figure 5 that the transpiration at low light intensities (*e.g.* at $5000 \text{ erg. sec.}^{-1} \text{ cm}^{-2}$ sphere, + ---- +), is constant for nearly the whole range of soil moisture values and only decreases when not more than 10 % of the total soil moisture content is available ($\text{pF} > 3.8$). It is evident that this observation also holds for the dark transpiration. This indicates that the cuticular diffusion resistance and also the "incipient drying" resistance of the mesophyll cellwalls affect transpiration markedly but only at very limited water supply to the shoot. For this reason, the data on dark transpiration may be plotted against V.P.D. within nearly the whole range of soil moisture contents, so that a curve similar to that in fig. 3 is obtained.

It is clear from fig. 5 that transpiration at high light intensities (● --- ● and ○ --- ○) which is mainly stomatal transpiration, is affected by soil moisture up to 17 %, whereas transpiration at low light intensities, which is mainly cuticular transpiration is affected by soil moisture only below 13 %.

Experiments with beans were performed in the same way as with rye. The correction for water loss through soil evaporation was made by covering the soil in some pots with paraffine wax. The rate of evaporation was calculated by subtracting from total water loss measured (transpiration + evaporation) the corresponding value with paraffine (transpiration). The effect of soil moisture on transpiration of beans was almost identical with that in rye; some of these results which are similar to those of fig. 5 have been represented earlier (2).

We have again estimated $\text{tg } \alpha$ and $\text{tg } \beta$ in the same way as in the case of rye (not represented in graphs).

In order to compare the transpiration of beans with that of rye in relation to pF of the soil, the maximum value of $\text{tg } \beta$ in both cases was taken as 1.00. Transpiration of beans was calculated per unit leaf area. In the case of rye, it was more convenient to relate transpiration to unit dry weight which seems allowed, since leaf thickness varied very little while, moreover, the total weight of the different samples was nearly equal. The various $\text{tg } \beta$ values, thus obtained, are represented in figure 7. It is evident from this figure that the effect of soil moisture on rye and on beans is nearly identical. This implies that both species as grown under the conditions of our experiments show the same physiological reaction to decreasing soil moisture with regard to water uptake, transpiration and stomatal reaction.

Since the transpiration of bean plants in soil was measured per unit leaf area, the results obtained can be compared with those in the potometers. It is evident from fig. 7 that $\text{tg } \beta$ with beans in a soil at pF 2.7 is higher than $\text{tg } \beta$ as obtained with the potometers. In the latter case cutting of the leaf probably may have lead

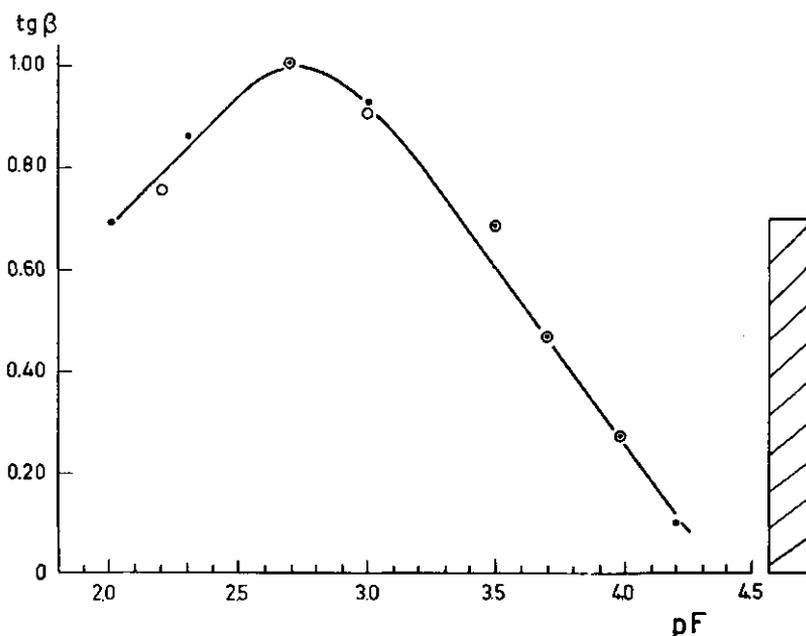


FIG. 7. The effect of soil moisture tension (pF) on $\text{tg } \beta$ of rye (● — ●) and bean (○ — ○). The values on the ordinate are expressed as a ratio of maximal $\text{tg } \beta$ at pF 2.7. The height of the column represents $\text{tg } \beta$ obtained with bean and tomato in the potometers (fig. 2).

to less favourable conditions for the plant, influencing e.g. the stomatal aperture.

Similar to the procedure developed (p. 8) for potometer data, we can represent transpiration in soil by:

$$T = \text{transpiration in dark} + \text{transpiration in light.}$$

$$T = p \times \text{V.P.D.} + q \times \text{V.P.D.} \times I \times f(\text{pF})$$

We express T in mg water h.⁻¹ 100 cm⁻² leaf surface, V.P.D. in mm Hg, I in erg. sec.⁻¹ cm⁻² \emptyset sphere $\times 10^4$, $f(\text{pF})$ in numerical value of tg β in relation to pF, as can be read from fig. 7.

Then we find, according to the data presented in fig. 3, 6, and 7 for the bean plants under our experimental conditions: $p = 25.8$, $q = 10.0$.

For transpiration of rye, a similar relation as mentioned for beans can be derived from the obtained data:

$$T = \text{transpiration in dark} + \text{transpiration in light}$$

$$+ \text{soil evaporation under a cover of rye.}$$

$$T = p \times \text{V.P.D.} + q \times \text{V.P.D.} + r \times \text{V.P.D.} \times I \times f(\text{pF})$$

If we express T in mg water h.⁻¹ (1 g dry weight)⁻¹ + mg water h.⁻¹ 80 cm.⁻² soil surface, V.P.D. in mm Hg, I in erg. sec.⁻¹ cm⁻² \emptyset sphere $\times 10^4$, $f(\text{pF})$ in numerical value of tg β as related to pF which can be read in fig. 7, in our experiment we found: $p = 23.2$, $q = 20$, $r = 26.6$.

DISCUSSION

The experiments described in this paper show that the application of FICK'S diffusion law is valid also for transpiration of leaves.

In the potometer experiments the leaf temperature hardly deviates from the air temperature under all conditions applied. Therefore, the vapour pressure deficit remains nearly constant within the range of light intensities used at each temperature and at each relative humidity. A linear relationship between transpiration rate and light intensity was observed. This is due to a linear decrease in the stomatal diffusion resistance with increasing light intensity. This stomatal reaction to light is related with the process of photosynthesis (8). Also in some field experiments dry matter production and transpiration are linearly related (10).

YAMAOKA (11), measuring the transpiration of *Myrica rubra* in potometer experiments, also observed a linear increase in transpiration with increasing light intensity. In his experiments much higher light intensities were applied with incandescent lamps as a light source. Some of his results have been represented in fig. 8, including measured leaf temperatures which increase strongly at high light intensities. This results in a large increase in vapour pressure deficit.

In order to investigate the effect of light on the stomatal diffusion resistance, YAMAOKA'S data on transpiration were corrected on an equal V.P.D. of 5.25 mm corresponding to an air temperature of 20°C and 70 % relative humidity, which are YAMAOKA'S experimental conditions. It is evident that no decrease in stomatal diffusion resistance (or increase in stomatal conductivity) occurs at light intensities above 17.5×10^4 erg. cm.⁻² sec⁻¹. A comparison of YAMAOKA'S

data with ours suggests, that the maximal aperture is reached in the range between 6.5 and $17.5 \times 10^4 \text{ erg. cm.}^{-2} \text{ sec.}^{-1}$.

From YAMAOKA's data an approximate calculation of the thermal emission can be made. Assuming a stationary situation, a light absorption factor of 0.75 , and neglecting the energy consumed or dissipated by photosynthesis and respiration, some values have been calculated for the thermal emissivity coefficient of the leaf, and represented in Table 3 (columns 1, 3, and 6 represent YAMAOKA's experimental data).

The thermal emission takes place on both sides of the leaf, whereas light absorption and transpiration mainly occur at one side of the leaf.

Obviously, the thermal emissivity coefficient is nearly the same at the various light intensities. These data on thermal emission confirm those obtained by other authors (4, 6).

We may expect that in the winter season at a relatively low light intensity the linear relationship between transpiration and light intensity depends mainly on the stomatal diffusion resistance, in accordance with the results of our experiments. In summer, with bright sunshine, this linear relationship is caused mainly by the increase in leaf temperature, since the stomata reach their maximal aperture far below the maximum light intensity, as in YAMAOKA's experiments.

In the experiments with plants in soil, the soil moisture content (pF) affects the total diffusion resistance of the leaves independent of the light intensity. The effect of soil moisture on the diffusion resistance may be partly due to a decrease in the relative humidity of the intercellular spaces in the leaf, through drying of the cell walls surrounding the intercellular spaces (incipient drying), and

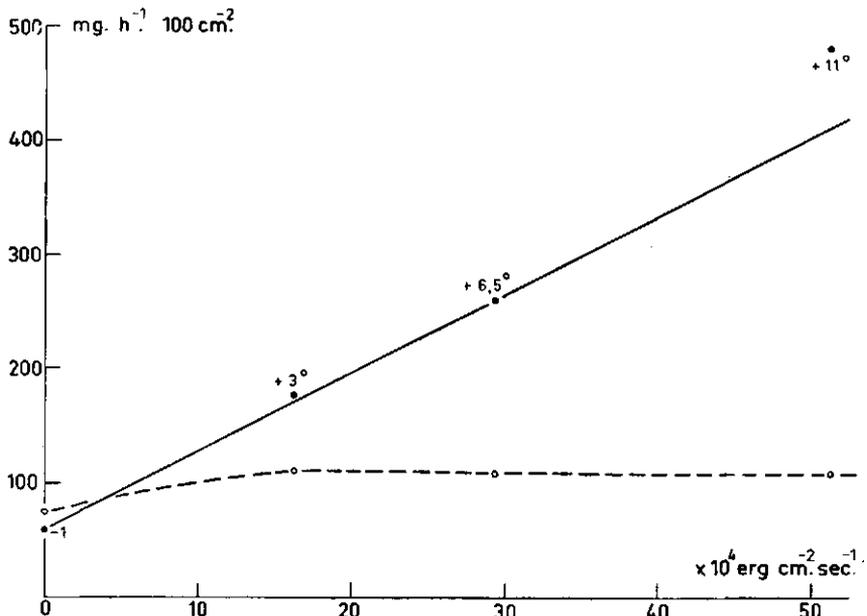


FIG. 8. The effect of light on the transpiration of *Myrica rubra* with cut shoots in potometers (● — ●). Data from YAMAOKA, and as obtained after correction to equal vapour pressure deficit (○ - - - ○). Wind velocity 0.

TABLE 3. Thermal emissivity of a leaf of *Myrica rubra* as calculated from YAMAOKA's data.

1	2	3	4
Light intensity erg. cm ⁻² . sec ⁻¹	Absorbed light in erg. cm ⁻² . sec ⁻¹	Transpiration in mg. h ⁻¹ . 100 cm ⁻² leaf surface	Energy dissipated by transpiration erg. cm ⁻² sec ⁻¹ .
15 × 10 ⁴	11.2 × 10 ⁴	0.18	1.2 × 10 ⁴
30 × 10 ⁴	22.5 × 10 ⁴	0.26	1.8 × 10 ⁴
50 × 10 ⁴	37.6 × 10 ⁴	0.48	3.3 × 10 ⁴
5	6	7	
Thermal emission (difference column 2 and 4) erg. 2 cm ⁻² . sec ⁻¹	Difference between leaf and air temperature in °C	Thermal emissivity coefficient in erg. cm ⁻² . sec ⁻¹ /1°C differ- ence in leaf and air temperature	
10 × 10 ⁴	+ 3	1.7 × 10 ⁴	
20.7 × 10 ⁴	+ 6.5	1.6 × 10 ⁴	
39.3 × 10 ⁴	+ 11	1.6 × 10 ⁴	

partly to an osmotic stomatal reaction. In fig. 7 the effect of soil moisture on the stomatal diffusion resistance is represented. An optimum is observed at pF = 2.7. The decrease at higher pF values is due to a decrease in the soil moisture available to the plant; the decrease of tg β at lower pF values may be due to lack of oxygen in the living root cells.

This effect is large under high evaporation conditions and does not exist under low evaporation conditions when water loss is limited by low values of V.P.D.

In this connection it is of interest that we have found in some preliminary greenhouse experiments that an optimum as discussed above was situated at pF = 2.0 for a coarse sand and at pF = 3.2 for a heavy clay soil. It seems probable that the structure of the soil is an important factor in determining the degree of oxygen shortage.

In examining figure 5 one is struck by the fact that the maxima in transpiration in the various curves at the same (high) temperature shift to higher pF-values as the light intensity (and the transpiration maximum) decrease. The lower the transpiration rate is, the longer the experiment lasts. One may wonder whether at pF values up to around 2.7 lack of oxygen exerts a harmful influence on transpiration in the long run, which conditions are more quickly overcome at high transpiration rates.

These relations will be the object of further studies.

SUMMARY

Experiments on transpiration of cut leaves of bean and tomato in potometers were performed under controlled conditions of light, temperature and relative humidity.

It was proven that FICK's diffusion law can be applied to the transpiration of leaves. A linear relationship between transpiration rate and light intensity was observed. Within the range of light intensities of the experiment, obtained with fluorescent tubes, the light intensity affects the transpiration rate mainly by changing the stomatal diffusion resistance to water vapour, less than 14 % being due to an increase in vapour pressure deficit, owing to the increase in leaf temperature under the influence of light.

Experiments on transpiration of bean plants and rye were performed with plants in soil. The effect of soil moisture is large under high transpiration conditions and negligible under low transpiration conditions. It can be assumed that the water supply to the shoot affects transpiration independent of the light intensity by changing the water content of the leaf, and by changing the diffusion resistance of the leaf by an osmotic reaction of the stomata, independent of the light sensitive stomatal mechanism.

It seems probable that in the experiment of YAMAOKA (11), performed under a wider range of light intensities, obtained with incandescent lamps, the linear relationship between transpiration and light intensity depends mainly on the increase in leaf temperature and vapour pressure deficit, and only for a small part on a change in the stomatal diffusion resistance.

The outcome of our experiments is that the transpiration may be expressed by a formula of the following nature:

$$\begin{aligned} & T = \text{dark transpiration} + \text{transpiration in light} \\ \text{or:} & \quad T = p \times \text{V.P.D.} + q \text{ V.P.D. } I.f(\text{pF}). \end{aligned}$$

in which leaf temperature and air temperature and relative humidity determine the value of vapour pressure deficit (V.P.D.), whereas other environmental factors as light intensity (I) and soil moisture (f [pF]) affect the diffusion resistance to water vapour. A quantitative expression of these relations is to be found in figures 2, 6 and 7.

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