

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 72-33 (1972)

INFLUENCE OF WATER STRESS
ON PHOTOSYNTHESIS,
RESPIRATION AND LEAF GROWTH
OF *ZEA MAÏS* L.

J. C. WESSELIUS AND R. BROUWER (1)

*Laboratory of Plant Physiological Research,
Agricultural University, Wageningen, The Netherlands*

(331th Communication)
(106th Comm. on Photosynthesis)

(Received 17-IX-1972)

INTRODUCTION

A disturbance in normal plant growth, as occurs in the case of water stress, inhibits leaf growth, photosynthesis and respiration. When the 'timing' of the inhibitory action on these processes is not the same and the sensitivity towards drought is different, shifts in the energy distribution within the plant may be induced. GROBBELAAR (1963), used young maize plants in which the roots were cooled. Growth was inhibited and the content of soluble carbohydrates increased during a period of ten days to levels, depending on the cooling temperature. A rise in soluble carbohydrates and a shift in top/root ratio was found by BROUWER (1968) in maize when the osmotic value of the culture solution was increased. In some cases the increased level of soluble carbohydrates may adapt the plant to the deteriorated water conditions and partially restore the leaf water content. KLEINENDORST and BROUWER (1970) described an adaptation of ageing maize plants to low root temperatures. Leaf elongation was strongly reduced immediately after cooling but increased after a few days probably due to osmotic adaptation of the plants.

It is questionable whether the increased soluble carbohydrate level in maize which occurs after a period of water stress only helps the plant to resume water uptake, or that it also induces an increased respiration rate. Reduced rates of photosynthesis in loblolly pine and tomato which are due to water stress were attributed to an increase in stomatal resistance when normal air was used (cf.

¹ Botanical Laboratory, Lange Nieuwstraat 106, Utrecht

BRIX, 1962). Another possibility might be that a change in hydrature (cf. WALTER, 1955) affects the photosynthetic process more directly.

This article deals with influences of drought on photosynthesis, respiration and leaf elongation of intact maize plants which were measured continuously and at the same time.

Methods:

Maize, variety *Caldeira C 351*, was germinated in river sand at 20°C. After 10 to 14 days, the seedlings were transferred to plastic pots, diameter 17 cm, filled with river sand. Plants were grown in the phytotron at 20°C, a relative humidity of $70 \pm 10\%$ and a light period of 12 hours. Light was given from above and aside by means of series of PHILIPS TL:33-40 Watt fluorescent tubes. Light intensity ranged from 80,000 to 120,000 ergs.cm⁻².sec⁻¹.

The rates of photosynthesis and respiration were measured in an open system. The assimilation chamber consisted of a glass tube with a length of 47 cm and a volume of 0.8 l. Air was drawn over the leaf by a 'Reciprotor' pump with a flow of 100 to 200 l.hour⁻¹ yielding a rate of the air stream over the leaf of 2 to 4 cm.sec⁻¹; the air was dried over CaCl₂, and passed to a WÖSTHOFF Ultragas-3 CO₂ analyser. Air from the phytotron room was taken as a reference.

In some experiments, the CO₂-content of the air was measured in a partially modified open assimilation chamber with a diaferometer as described by PIETERS (1970) or with a far-red CO₂ gas analyser (HILGER and WATTS). When the CO₂ concentration of the air was to be enhanced, air enriched with 0.5% CO₂ was pressed through the assimilation chamber with a flow rate of 60-100 l.hour⁻¹. A sample taken from the middle of the assimilation chamber was dried over CaCl₂, analysed with the diaferometer, and recorded with a KIPP micrograph BD1.

Leaf elongation was measured at intervals or continuously. The tip of a leaf was attached to a wire running over two pulleys and stretched by a load. The movement of the load could be read directly on a cm scale, or was continuously recorded. In the latter case the wire ran over a wheel connected to a potentiometer. Leaf growth then caused changes in resistance, which could be recorded on a PHILIPS mV meter.

Water content in the leaf was estimated by weighing leaf samples. Samples taken from a leaf at the start of the light period were placed at 2°C in a Petri dish; floating on water in the dark till the next day on which they were weighed. This value was considered to represent a fully turgescient leaf. Relative water contents in % of a fully turgescient leaf were estimated from leaf samples taken at intervals after a change to low root temperature.

Osmotic pressure of the leaf was estimated with the freezing point depression method. Small droplets of leaf juice were brought on a thermocouple which was placed in the middle of a test tube. By cooling the test tube and recording the potential derived from the thermocouple the freezing point could be determined.

Drought conditions were given to the plant by drying of the soil, or by percolating the soil several times with NaCl, or by cooling the pot in a water bath.

Results:

a) *Rate of photosynthesis, dark respiration and leaf elongation during drying of the soil.*

In order to follow the course of respiration during water stress a maize plant was not watered to reduce the moisture content of the soil. During the treatment, the plant gradually wilted. The respiration rate of an adult leaf decreased during wilting, but could be restored after rewatering (cf. fig. 1). Combined measurements of photosynthesis, respiration and leaf growth are presented in fig. 2. Leaf elongation rate was rather slow. The first days photosynthesis started at a rather high level, but as a prelude of water stress it decreased during the course of the day at 26/1 and 27/1, and ultimately became zero at 28/1. Water addition partly restored photosynthetic activity. Respiratory activity was fairly constant during the periods with decreasing photosynthesis overday, but it decreased when excessive water deficits existed which also reduced photosynthetic activity to zero level. Rate of respiration tended to decrease somewhat further after watering, although the rate of photosynthesis recovered considerably. Simultaneous measurements of leaf elongation and photosynthesis thus show that an effect of water shortage appears somewhat earlier on leaf elongation than on photosynthesis, suggesting that leaf elongation is more sensitive towards water deficit than photosynthesis. This conclusion is supported by the measurements of the recovery phenomena after drought (fig. 3). After rewatering photosynthesis in a wilted plant rose more quickly than leaf growth.

Since photosynthesis in a wilted plant was inhibited, it is questionable whether the decrease is due to an increased stomatal resistance or to an inhibition of

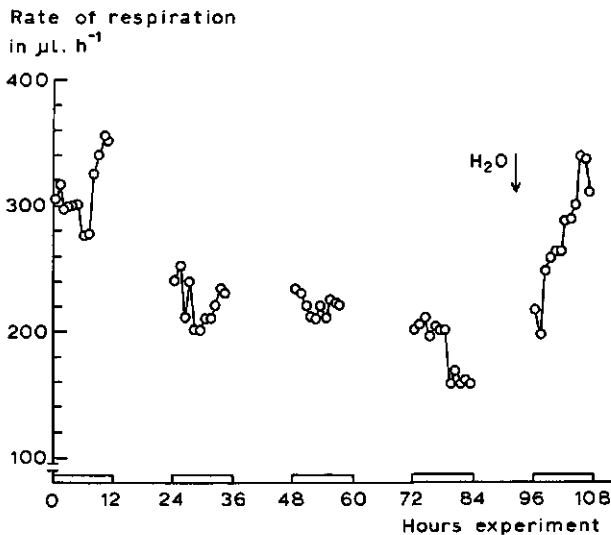


FIG. 1. Rate of respiration of a maize leaf; plant in drying soil. WÖSTHOFF measurements; 0.03% CO₂; light intensity 80,000 ergs.cm⁻².sec⁻¹; temperature 20°C; □ dark period.

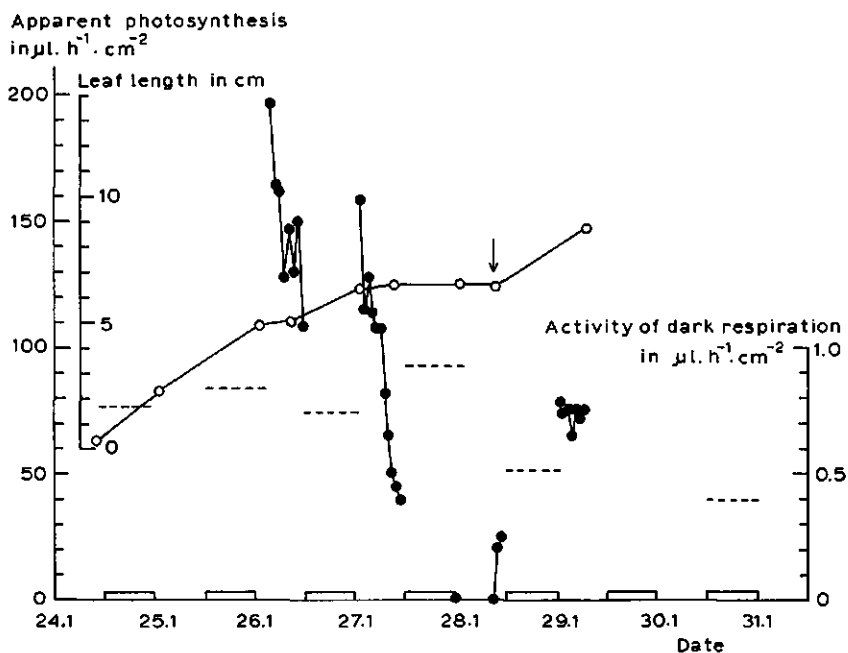


FIG. 2. Photosynthetic activity, respiratory activity and leaf growth of maize plants in drying soil. WÖSTHOFF measurements; 0.03% CO_2 ; light intensity $80,000 \text{ ergs.cm}^{-2} \text{sec}^{-1}$ temperature 20°C . ●—● photosynthetic activity 9th leaf, ○—○ leaf growth 10th leaf, - - - respiratory activity 9th leaf. ↓ H_2O addition, □ dark period.

biochemical activity. Therefore, photosynthetic activity in 0.03% and 0.5% CO_2 was measured on a plant in dry soil just before wilting. A dialometer as described by PIETERS (1970) was used. Next day the leaves wilted and photosynthesis was measured at 4 light intensities, as is shown in fig. 4. Photosynthetic activity in a wilted and non-wilted plant was independent of the CO_2 -concentration in the range of 0.03% to 0.5% at the highest light intensity. Continuous water stress decreased photosynthetic activity as is shown by the measurements at $5.5 \times 10^4 \text{ ergs.cm}^{-2} \text{sec}^{-1}$. Apparently, reduction in photosynthetic activity is not due to closing of the stomata, but to a reduced biochemical activity.

b) *Influence of osmotic solutions on the rates of photosynthesis and of respiration, and on leaf growth.*

Rates of photosynthesis, dark respiration and growth were measured on leaves of maize plants which were exposed to various NaCl concentrations in the

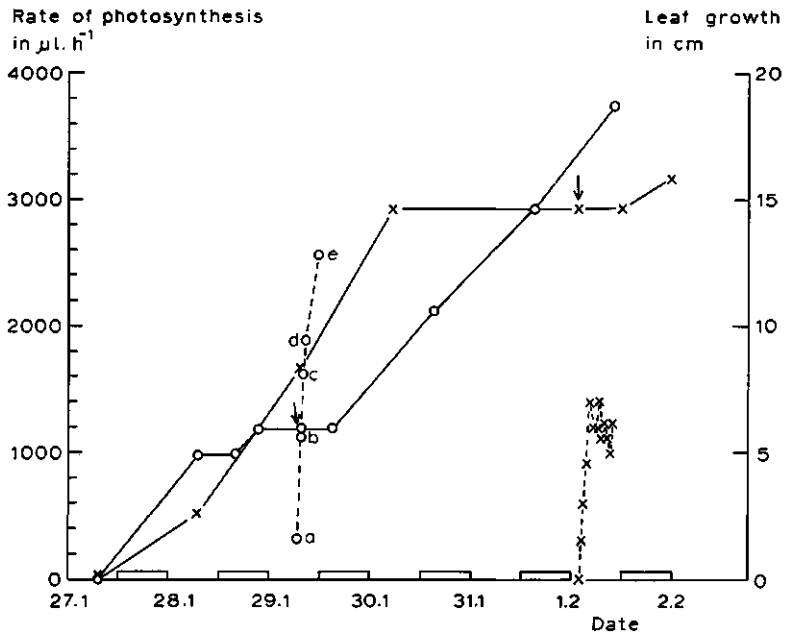


FIG. 3. Leaf growth and rate of photosynthesis of 2 maize plants in drying soil. Watering indicated by arrows. I.R.A. measurements, temperature 24.5°C; light intensity 100,000 ergs.cm⁻².sec⁻¹; 0.03% CO₂; ○—○ plant 1 leaf growth; ○ - - - ○ plant 1 photosynthesis after water addition (a→e); ×—× plant 2 leaf growth; × - - - × plant 2 photosynthesis after water addition; □ dark period.

root medium. Leaf growth was inhibited (fig. 5). Respiration and photosynthesis were also reduced to fractions of the original rates (Tables 1 and 2). High osmotic concentrations reduced photosynthesis and respiration. An adaptation occurred in the 16 atm. series 4 to 8 hours after NaCl addition. Next day however, photosynthesis decreased further on. Since the inhibition of photosynthesis was irreversible in the 16 atm. series, we assume that the same occurred at 20 atm. The irreversible change observed with 16 atm. NaCl was probably due to salt damage. No reduction in rate of photosynthesis occurred with 5 atm. NaCl in most cases (cf. Table 2). The rate of respiration after NaCl addition was higher than in the control. This may be due to the soluble carbohydrate content in the NaCl plants. The rate of respiration is only 1.6% of the rate of photosynthesis. One may expect therefore, that the effect of this increased leaf respiration on photosynthesis is negligible.

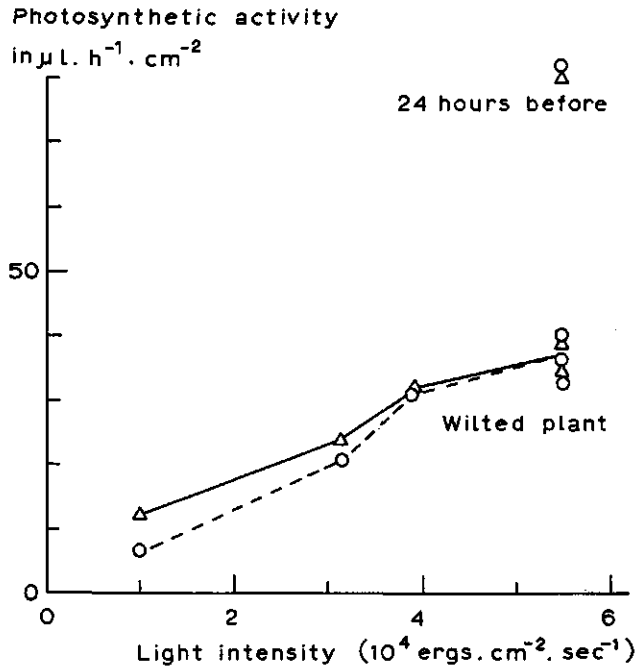


FIG. 4. Photosynthetic activity of one maize leaf during two subsequent days, respectively non-wilted and wilted. Diaferometer measurements at 20°C, 0.03% CO₂ (○ --- ○); and 0.5% CO₂ (△—△); light intensity ranged from 1×10^4 to 5.5×10^4 ergs.cm⁻².sec⁻¹.

TABLE 1. Relative rates of photosynthesis and respiration for maize plants treated with 20, 16 and 5 atm. NaCl. Measurements with WÖSTHOFF in 0.03% CO₂ at a temperature of 20°C. Light intensity 80,000 ergs.cm⁻².sec⁻¹.

Expt.	Osmotic value atm. NaCl	Photosynthesis in % of original value	Respiration in % of original value	Time after application (hours)
71-5	20	16	—	4
		41	—	8
		41**	—	20
71-4	16	40	—	3
		—	33	4-16
		33*	—	16*
71-13	5	—	50	10-22
		—	120	58-70
		—	—	—

** after 8 hours during the next day (23 hours after NaCl addition) photosynthesis was completely inhibited; inhibition was irreversible.

* after dark period.

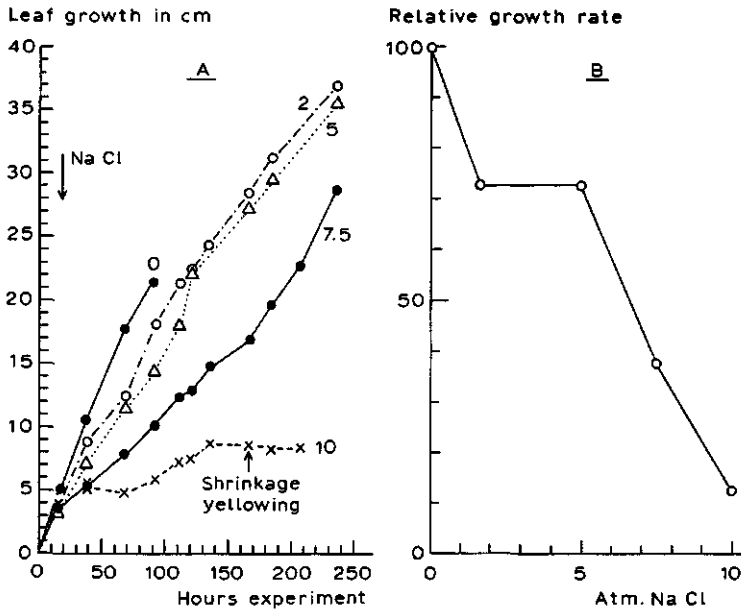


FIG. 5. Leaf growth of maize leaves at 0, 2, 5, 7½ and 10 atm. NaCl (part A). Relative growth rates of maize leaves, expressed in percentages of the growth rate before NaCl addition (part B). Air temperature 20°C, light intensity 80,000 ergs.cm⁻².sec⁻¹.

TABLE 2. Rate of photosynthesis and respiration in a maize leaf before and after 5 atm. NaCl addition. Figures are averages of 12-13 measurements. Analyses with WÖSTHOFF in 0.03% CO₂, 20°C and light intensity of 80,000 ergs.cm⁻².sec⁻¹. NaCl addition at zero hour experimental time.

Hours before or after NaCl addition	Rate of photosynthesis (μl.hour ⁻¹)	% of original rate	Rate of respiration (μl.hour ⁻¹)	% of original rate
-21- -9 (dark)	-	-	140.3	100.0
-9 -0 (light)	8480*	100	-	-
0-3 (light)	8992**	106	-	-
3-15 (dark)	-	-	178.7	127.5
15-27 (light)	9088	107	-	-
27-39 (dark)	-	-	165.3	118.0
39-51 (light)	9567	113	-	-
51-63 (dark)	-	-	175.4	125.0
63-75 (light)	8928	105	-	-

* average from 9 measurements
 ** average from 3 measurements.

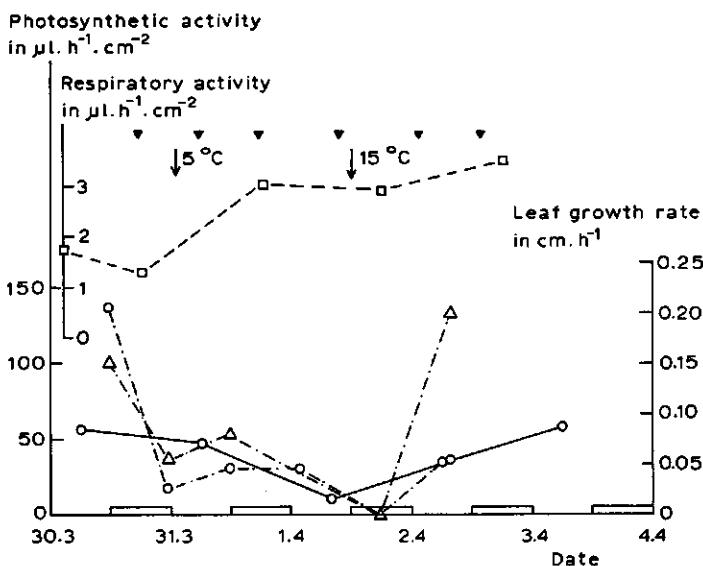


FIG. 6. Photosynthetic activity, respiratory activity and leaf growth of maize plants transferred from 20°C to 5°C root temperature. WÖSTHOFF measurements; 0.03% CO₂; light intensity 80,000 ergs.cm⁻².sec⁻¹; air temperature 20°C; □ - - - □ respiratory activity (7th leaf); ○—○ photosynthetic activity (7th leaf); ○ - . - . ○ growth rate 8th leaf; △ - . - . △ growth rate 9th leaf. Leaf growth rates determined over periods denoted with ▼ ▼ at top of the figure.

c) *The effect of cooling of the roots on leaf growth, photosynthesis and dark respiration.*

A synthesis of the events occurring after cooling is given in fig. 6, which is an extension of BROUWER and KLEINENDORST's experiments about leaf growth as affected by cooling. Leaf growth was directly inhibited to 20% of the rate before cold stress. Photosynthetic activity decreased more slowly to 34.3% of the activity before cooling, whereas respiratory activity increased from 1.7 μl.cm⁻².h⁻¹ to 2.9 μl.cm⁻².h⁻¹, which is a relative increase to 170%. Cooling of the roots of maize increased soluble carbohydrate content as was shown by GROBELAAR (1963) and KLEINENDORST and BROUWER (1970), which may be a reason for the increased respiratory activity in our experiment. Leaf growth and photosynthetic activity increased after increasing root temperature from 5° to 15°C whereas respiratory activity was a little higher the first night after transfer to 15°C. KLEINENDORST and BROUWER (1970) found that a reduced leaf growth rate after cooling was combined with an increased soluble carbohydrate content. As was shown in fig. 6, photosynthetic activity decreased less than leaf growth and only after some time. It coincided with an increased respiratory activity.

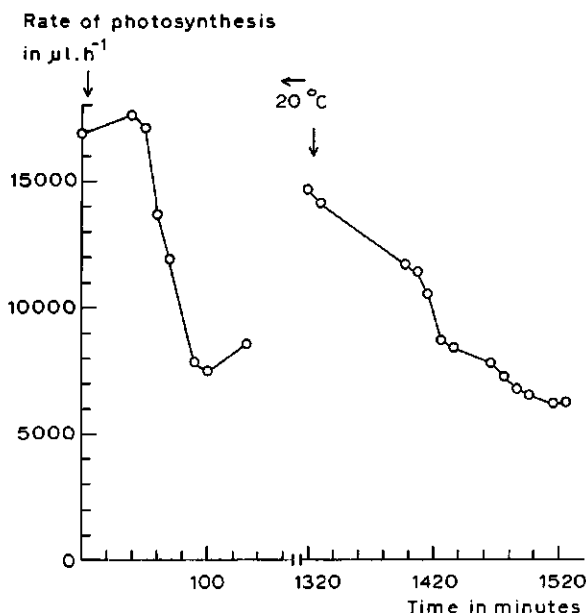


FIG. 7. Rates of photosynthesis on two subsequent days as affected by cooling the roots to 1°C. Plants were transferred to 20°C root temperature over night; ↓ 1°C root temperature; I.R.A. measurements; light intensity 55,000 ergs.cm⁻².sec⁻¹; air temperature 20°C; 0.03% CO₂.

The decrease in rate of photosynthesis followed the same course when root temperature was decreased to 1°C during two subsequent days intercalated by a night period at 20°C root temperature (cf. fig. 7). Photosynthesis recovered to 80% of the rate before cooling after transfer from 1°C to 20°C root temperature, which means that the inhibition of photosynthesis by cold is partly reversible. Considering the results in fig. 6 and 7 we are inclined to describe these phenomena in terms of water balance. Since air with 0.03% CO₂ was used the question arises whether the reduced rates of photosynthesis are due to an increased stomatal resistance or to a decrease in hydrature directly. Photosynthetic activity, which was inhibited after cooling, could not be restored with a higher CO₂ content of the air as is shown in fig. 8. This suggests that the decrease in photosynthetic activity after cooling is not only caused by an increased stomatal resistance but by an inhibition of the biochemical activity. The water balance of the leaf may in some way influence biochemical activity; in that case a correlation between water content and photosynthetic activity might be expected.

The relation between photosynthetic activity and relative leaf water content is given in fig. 9. Photosynthetic activity gradually decreased with a relative

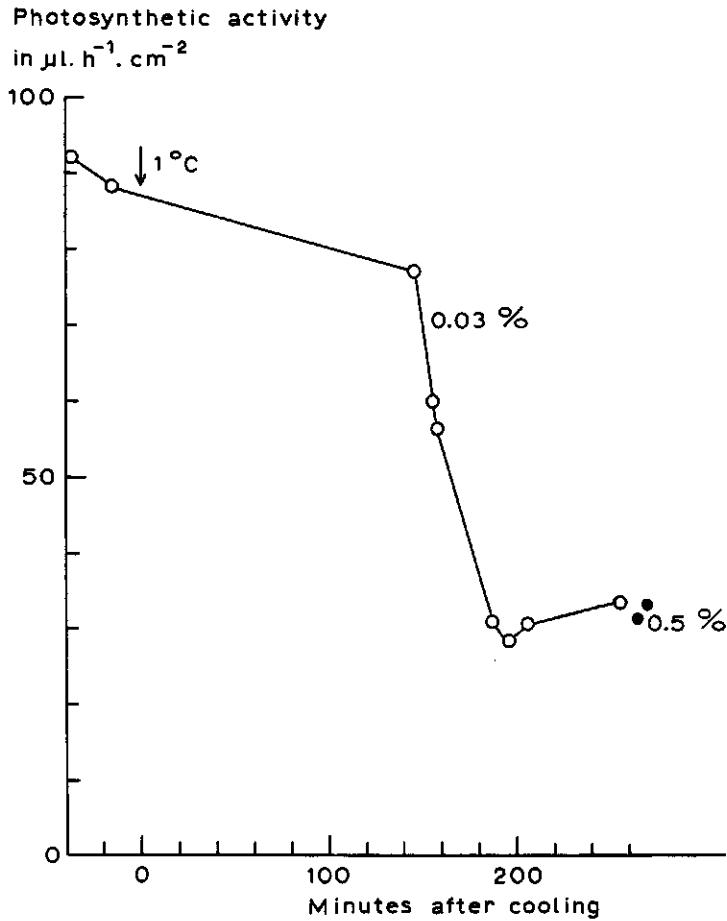


FIG. 8. Photosynthetic activity of a maize leaf after cooling of the roots to 1°C. Diaferometer measurements in 0.03% CO₂ (○—○) and 0.5% CO₂ (●—●); air temperature 20°C; light intensity 55,000 ergs.cm⁻².sec⁻¹.

water content from 100% till about 80 - 85%. The average relative leaf water content did not decrease to values lower than 75 to 80%, whereas photosynthetic activity still decreased.

Corresponding osmotic pressures were not measured in this experiment, but in a separate one with *Caldeira* C535, since the hybrid *Caldeira* C351 previously in use was no longer obtainable. Photosynthesis was measured with the WÖSTHOFF and osmotic pressures were determined from samples taken from the same leaf. Osmotic pressures were determined with the freezing point depression as measured with a thermocouple. Physiological drought was attained by

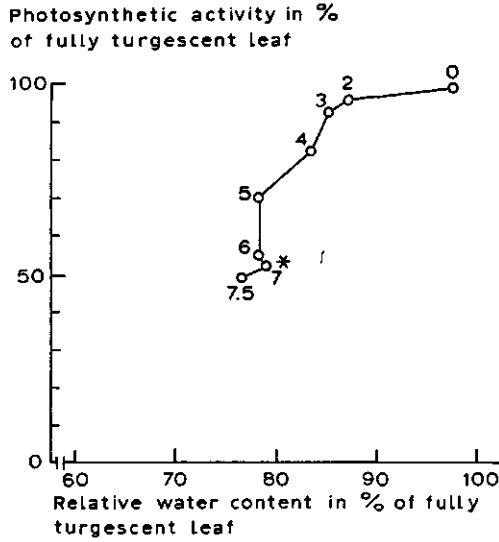


FIG. 9. Relation between photosynthetic activity and relative water content, both expressed in percentages of these parameters measured on a fully turgescient leaf. Averages from 5 leaves were taken (* 3 parallels); WÖSTHOFF measurements; air temperature 20°C; light intensity 70,000 ergs.cm⁻².sec⁻¹; root temperature 1°C.

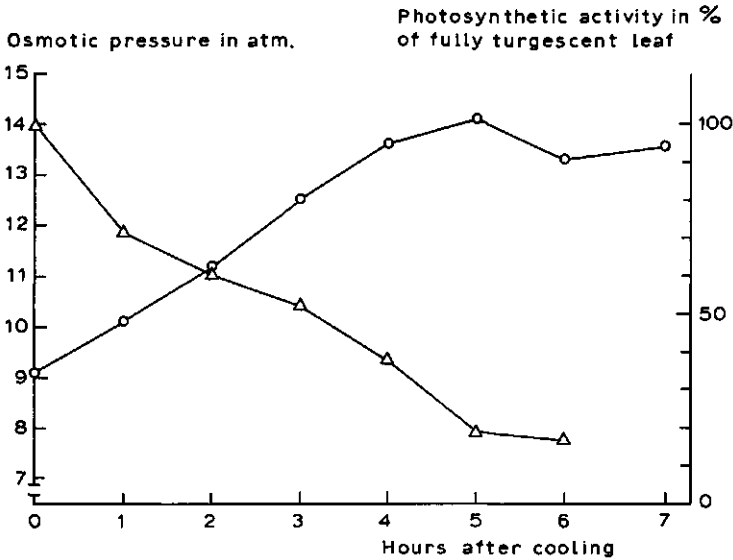


FIG. 10. Photosynthetic activity in % of a fully turgescient leaf (Δ — Δ) and osmotic pressure of the leaf sap (\circ — \circ) after cooling of the roots to 1°C. Temperature air 20°C., light intensity 70,000 ergs.cm⁻².sec⁻¹, WÖSTHOFF measurements in 0.03% CO₂. Osmotic pressures averages from 6 leaves. Photosynthetic activity averages from 4 leaves. Maize *Caldeira C 535*.

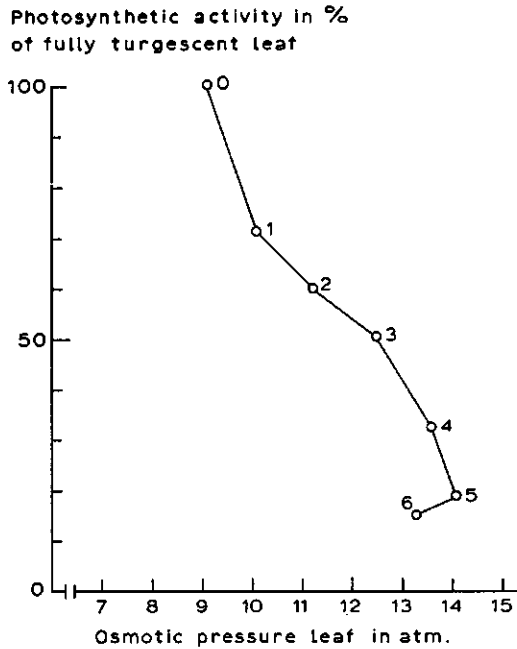


FIG. 11. The relation between photosynthetic activity (expressed in percentage of the activity of a fully turgescient leaf) and osmotic pressure of the leaf for maize *Caldeira C 535*. Average from the 8th leaves of 4 plants were used. WÖSTHOFF measurement in 0.03% CO₂; temperature air 20°C, roots 1°C. Light intensity 70,000 ergs.cm⁻².sec⁻¹. Figures in the graph denote the number of hours after cooling.

putting the roots in ice. As is shown in fig. 10 the average osmotic pressure of the leaf juice gradually increased to a level of 13 to 14 atm. In fig. 11 the relation between photosynthetic activity and osmotic pressure of the leaf juice is given. Photosynthetic activity linearly decreased till osmotic pressures of 13 to 15 atm. were attained. These values were not surpassed and osmotic adaptations sometimes appeared. Nevertheless, photosynthetic activity decreased further on. This can be seen from the determinations at 6 hours after cooling. It was assumed that as a consequence of osmotically induced water uptake the osmotic pressure of the leaf juice decreased whereas photosynthetic activity still decreased.

When fig. 9 and 11 are compared it can be observed that the inhibition of photosynthetic activity by a cold stimulus was more sluggish in fig. 9 than in fig. 11. The reason for this may be that *Caldeira C 535* was cultivated under more humid conditions as compared with *Caldeira C 351*, viz.: pots were put with their feet in a box with a small layer of water whereas *Caldeira C351* was watered once a day. Therefore, we assumed that the differences in behaviour towards cold are due to drought resistances cultivated into the plants.

DISCUSSION

Physiological drought caused a severe reduction in leaf growth rate which was rather abrupt and could be restored by water addition or an increase of root temperature.

KUIPER (1963) found that transpiration rates, and therefore also water uptake was temperature dependent in a range of low root temperatures. Therefore, changed permeabilities for water in the roots may have been the cause of the stress effect of cooling. Irreversible inhibition of leaf growth was observed with 16 atm. NaCl, which is probably due to chloride poisoning. BERNSTEIN (1961) pointed out that roots are to a certain extent adaptable to increased osmotic concentrations in the root medium, which may have occurred in the 5 atm. NaCl treatments described in Table 2. Contrary to KLEINENDORST and BROUWER (1970) no adaptation of leaf growth to cold was observed although plants in the 10th leaf stage were used. It may be that the time of measurement was too short or that our culture in river sand caused a water availability worse than that in the water cultures of KLEINENDORST and BROUWER.

Photosynthesis was also affected by drought but the inhibition depended on the strength of the drought stimulus. For instance a severe cooling of the roots to 1 °C (cf. fig. 7) or high osmotic concentrations of NaCl caused a reduction in the rate of photosynthesis which could be observed within a period of 5 to 8 hours, whereas cooling to 5 °C (cf. fig. 6) showed a decreasing photosynthetic activity during 2 to 3 days, and 5 atm. NaCl had no influence on photosynthesis at all (Table 2).

Leaf growth reacted earlier to soil water conditions and root temperatures than photosynthesis, which suggests a greater sensitivity towards water stress (cf. fig. 2, 6). Respiratory activity was the least sensitive to water stress. A reduction in respiratory activity was found when the soil dried out (cf. fig. 1) but an increase was observed with root cooling (cf. fig. 6) or with low osmotic concentrations (cf. Table 2).

Reduction in rate of photosynthesis and respiration caused by drought was described by BRIX (1962) for tomato and pine. Rates of transpiration and photosynthesis declined concomitantly after drought, and photosynthesis in wilted plants could be enhanced by increasing the CO₂ concentration of the ambient air. This indicates that the reduced rates of photosynthesis are due to an increased stomatal resistance, which is in contradiction with our results suggesting a reduction in photosynthetic activity due to a decreased biochemical activity of the photosynthetic apparatus.

SLATYER (1970) measured in an elegant way the internal resistance for CO₂. In two *Atriplex* species and in millet the reduction in photosynthetic activity after drought could be attributed to increased stomatal resistance. In maize and cotton, however, internal resistance for CO₂ increased at leaf water potentials below the wilting point.

Our results suggest that photosynthetic activity sharply decreased below a relative water content of 80%. After a cold stimulus the increase in osmotic

pressure in the leaf is a gradual one. At osmotic pressures of about 13 to 15 atm photosynthetic activity still decreased whereas the osmotic pressure in the leaf diminished, probably due to osmotically induced water uptake. The results in fig. 4 and 8 indicated that a reduced photosynthetic activity was independent of the CO_2 -concentration with dry soil or cooled roots respectively. The relation between osmotic pressure of the leaf and photosynthetic activity as given in fig. 11 suggests a linear or a slightly S-shaped curve. The conclusion would be that a strong water deficit increases $R_{\text{carbox.}}$ and the osmotic pressure of the leaf. A linear relationship between $R_{\text{carb.}}$ and osmotic pressure of the leaf can be expected.

BOYER (1970), using maize, found that a drought induced reduction of photosynthesis could mainly be attributed to an increase in $R_a + R_s$. If the different results in our experiments are not due to the difference in maize varieties, it can be observed that the light intensities which were applied were different. In our experiments light limited conditions existed for normal plants whereas BOYER used saturating or nearly saturating light intensities. When water deficits in maize induce lower rates of photosynthesis by increasing $R_s + R_{\text{carb.}}$ it is feasible that the choice of the experimental situation, i.e. the light intensity, determines whether the stomata or the biochemical activity are limiting the rate of photosynthesis. Our results show that the inhibition of the biochemical activity is partially reversible.

The different sensitivities towards water deficits for leaf growth, photosynthesis and respiration suggest that the hydrature of the plant (WALTER, 1955) is of extreme importance for some processes but less for others. Further knowledge of the water conditions necessary for isolated processes seems, therefore, of utmost importance. The significance of these items, however, can only be fully understood from the standpoint of the whole plant.

SUMMARY

Maize exposed to drought showed a reduced leaf elongation rate and a reduced rate of photosynthesis. Rate of respiration was increased when the roots were exposed to 5°C during a couple of days. Sensitivity towards drought was highest for leaf elongation rate, less for photosynthesis and lowest for the rate of respiration. The reduced rates of photosynthesis which were due to water shortage could not be enhanced by increasing the partial pressure of CO_2 in the ambient air from 0.03% to 0.5%. It was concluded that a reduced biochemical activity was the limiting factor under this set of experimental conditions.

Rates of photosynthesis decreased from a relative water content of 100% to 85%. Relative water content of the leaf decreased to about 75–80% on the average, whereas the rate of photosynthesis still decreased. The osmotic pressure of the leaf showed an increase and the rate of photosynthesis a decrease during water stress. A nearly linear relationship existed between osmotic pressure of the leaf and rate of photosynthesis during a period of 5 hours after cooling of the roots.

LITERATURE

- BRIX, H., The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings; *Physiol. Plant.* **15** (1962): 10-21.
- BROUWER, R., Morphological and physiological adaptations to external conditions; *Acta Bot. Neerl.* **17** (1968): 78-80.
- BERNSTEIN, L., Osmotic adjustments of plants to saline media. I Steady state; *Am. J. of Botany* **48** (1961): 909-918.
- BERNSTEIN, L., Osmotic adjustments of plants to saline media. II Dynamic phase. *Am. J. of Botany* **50** (1963): 360-370.
- BOYER, J. S., Leaf enlargement and metabolic rates in corn soybean and sunflower at various leaf water potentials. *Plant Physiol.* **46** (1970): 233-236.
- BOYER, J. S., Different sensitivity of photosynthesis to low leaf water potentials in corn and soybean; *Plant Physiol.* **46** (1970): 236-240.
- GROBBELAAR, W. P., Responses of young maize plants to root temperatures; *Meded. van de Landbouwhogeschool Wageningen* **63(5)**, (1963): 1-71.
- KLEINENDORST, A. and BROUWER, R., The effect of temperature of the root medium and the growing point of the shoot on growth, water content and sugar content of maize leaves. *Neth. Journ. of Agric. Sc.* **18** (1970): 140-148.
- KUIPER, P. J. C., Water uptake of higher plants as affected by root temperature. *Meded. van de Landbouwhogeschool Wageningen* **64(4)**, (1964): 1-13.
- PIETERS, G. A., Katharometric (diaferometric) determination of CO₂, O₂ and water vapour. In: *Manual of Methods of plant photosynthetic production*; J. JANÁČ, ČATSKÝ, J., PURVIS, P. G., et al.; Dr. W. Junk, Publishers, The Hague, (1971): 177-197.
- SLATYER, R. O., Effects of short periods of water stress on leaf photosynthesis; *Unesco Symp. of Plant Response to Climatic Factors*. Uppsala, Sweden (1970): SC/Conf 44/36.
- WALTER, H., The water economy and the hydrature of plants; *Ann. Rev. of Pl. Physiol.* **6** (1955): 239-252.
- WIT, C. T. DE, BROUWER, R., PENNING DE VRIES, F. W. T., The simulation of photosynthetic systems. *Proceed. IBP/PP Techn. Meeting, Třeboň, (1969) PUDOC, Wageningen (1970): 47-71.*