

## 4 Maize

Uit : Crop photosynthesis : methods  
and compilation of data obtained  
with a mobile field equipment.

H.H. van Laar, D. Kremer and C.T. de Wit

Th. Alberda et al.

Assimilation and transpiration of maize in the field are being measured and compared with simulated results under the same conditions. Another publication (de Wit & Penning de Vries, 1977) will treat this evaluation in detail, while this paper presents some typical examples.

A short description of the Basic Crop Simulator (BACROS) is given first.

A crop in the vegetative phase of growth, well supplied with water and nutrients, is considered. Growth of this crop is defined as increase in dry weight of the structural plant material, so that those organic substances that may be classified as reserves are excluded. The model is based on physical, chemical and physiological processes, and may be applied under any condition.

The  $\text{CO}_2$  assimilation is calculated by adding the assimilation rates of the variously exposed leaves in successive leaf layers. These rates are dependent on the light intensity, the  $\text{CO}_2$  concentration in the ambient air and the resistance to  $\text{CO}_2$  diffusion from the atmosphere towards the active sites. Transpiration and  $\text{CO}_2$  assimilation interact closely, not only because a relatively large transpiration may lead to a low plant water status and subsequent closure of stomata, but also because a low assimilation rate may lead to closure of stomata and low transpiration, through regulation of the  $\text{CO}_2$  concentration in the stomatal cavity.

One of the main problems is the introduction of the assimilatory properties of the leaves, which depend on past exposure to light and temperature and on age. As yet this subject has been insufficiently investigated. Assimilation of energy through the reduction of  $\text{CO}_2$ , as well as that through the reduction of  $\text{NO}_3^-$  in the leaves in the light are considered.

The respiration is the sum of maintenance respiration and growth respiration. The growth respiration is caused by the conversion of reserves into structural material and is therefore proportional to the growth rate and dependent on the chemical composition of the plant. Apart from the dependence of the rate of growth on temperature, growth respiration is independent of

temperature.  $\text{CO}_2$  evolution resulting from active loading and unloading of the phloem with organic substances is usually included in the growth respiration term. The rate of maintenance respiration depends on the turnover rates of proteins and the maintenance of ionic gradients between cells and between cells and their surrounding. This respiration process is largely proportional to the amount of proteins in the biomass and sensitive to the temperature of the tissues.

The level of reserves is increased by the assimilation rate and decreased by growth and respiration. No distinction is made between different pools of reserves in different organs, but some discrimination is made with regard to their availability for growth of various parts of the plant.

The growth rate of the organs is dependent on the amount of reserves and temperature. Under water stress, the growth of the shoots is retarded so that accumulation of reserves is favoured and thus, the roots grow. By this mechanism a functional balance is obtained between root and shoot growth.

The maintenance of the functional balance between root and shoot growth is a first attempt to simulate some aspects of the development of form and function of the plant. Up to now, no satisfactory solution has been found for the simulation of the growth of leaf surface in relation to the growth of leaf or shoot weight, so that these aspects are mimicked rather than simulated, that is, described on the basis of information obtained from field experiments and not derived from knowledge of the underlying processes.

The plant water status is determined by the balance between transpiration and water uptake from the soil. The transpiration rate of the crop is found by adding the transpiration rates of the variously exposed leaves in successive leaf layers of the crop.

These rates are calculated from the absorbed radiation, the resistance of the laminar layer, the humidity and temperature of the ambient air and the stomatal resistance. The calculation also provides leaf temperatures, which are used in the photosynthesis section and also averaged to give the crop temperature that affects growth and respiration. The water uptake is determined by the conductivity of the root system and the plant and soil water status. The latter is assumed to be optimal ('field capacity'), so that the transport of water within the soil does not play an important part. The conductivity of the root system is proportional to the amount of roots and dependent on their degree of suberization and the temperature. The growth of the roots is governed by the soil temperature and the amount of reserves.

The micro-weather is calculated from the weather measured at screen

height, taking into account the extinction of radiant energy from sun and sky within the crop. The thermal radiation from the canopy is also computed. A calculation of the distribution of radiation over the leaves is necessary for computation of assimilation and transpiration. The extinction of turbulence in the canopy is also considered so that transfer of heat, vapour and  $\text{CO}_2$  can be computed. The ratio of latent and sensible heat exchange governs to a large extent the micro-weather, and this ratio is governed largely by stomatal behaviour. Basically, temperatures of leaf and soil surface are simulated. For the latter, transfer of heat within the soil has also to be taken into account so that the temperature profile in the soil is also computed.

The output of this model is evaluated by comparison of simulated daily courses of  $\text{CO}_2$  assimilation and transpiration with measured courses within enclosures. The influence of the enclosure on the radiation climate, and that of the ventilation speed on the turbulence within the crop is taken into account and time lags introduced by the measuring method are simulated.

The measurements were in general carried out in a maize field with rows spaced at 80 cm and the plants in the rows spaced at 10-12 cm. The surface of the enclosure is  $0.64 \text{ m}^2$  and it contains about 7 plants of one row. Even if there is no lodging in the experimental fields, some disturbance of leaf position is unavoidable because the leaves of plants of adjacent rows overlap. The height of the perspex enclosure may be adjusted to plant height between 120 cm and 300 cm. Even within the highest enclosure the turbulence is large enough to ensure a uniform distribution of temperature, humidity and  $\text{CO}_2$ . The evaporation of the soil is suppressed by a gravel layer of a few centimeters.

Considerable attention was paid to the measurement of leaf temperatures within the enclosure, but the overall accuracy of the Heimann's radiation meter used for this purpose was too small to allow evaluation of computed leaf temperatures for various reasonable assumptions with respect to stomatal behaviour. A daily course of air and leaf temperature is given in Fig. 9a. The measured leaf temperature at night was found to be higher than the air temperature but this is probably due to inaccuracies in the method.

Daily courses of net assimilation are given in Fig. 8a and 9a. The negative  $\text{CO}_2$  assimilation during daytime is achieved by complete shading and is in general larger than the respiration during the night. This difference is attributed to the larger growth rate, one of the assumptions that is evaluated by simulation. The relation between  $\text{CO}_2$  assimilation and light intensity measured throughout the day are given in Fig. 8b and 9b. Fig. 8b concerns a

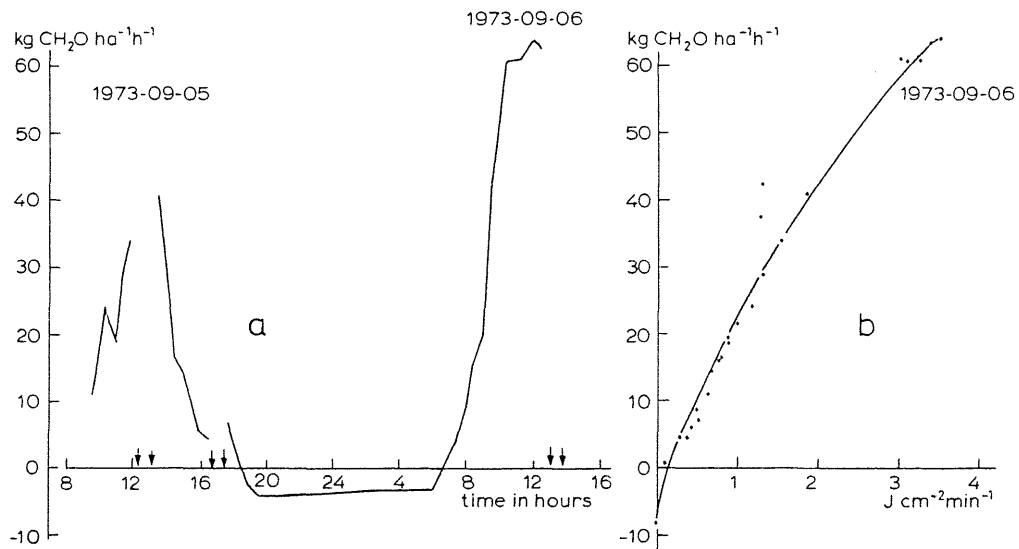


Fig. 8.  $\text{CO}_2$  assimilation expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{h}^{-1}$  as a function of time (a) and as a function of light (b) of a maize crop.

Species: *Zea mays* cv. Caldera 535; density: 10 plants  $\text{m}^{-2}$ ; measuring date: 1973-09-06; sowing date: 1973-08-06; location: Born-Zuid, Wageningen; leaf area index: about 10  $\text{m}^2 \text{m}^{-2}$ ; dry weight shoot: about 3600  $\text{kg ha}^{-1}$ ; stage: 0.5 - 1.0 (Hanway, 1966); height: 50 cm.

Between arrows: dark respiration during the day.

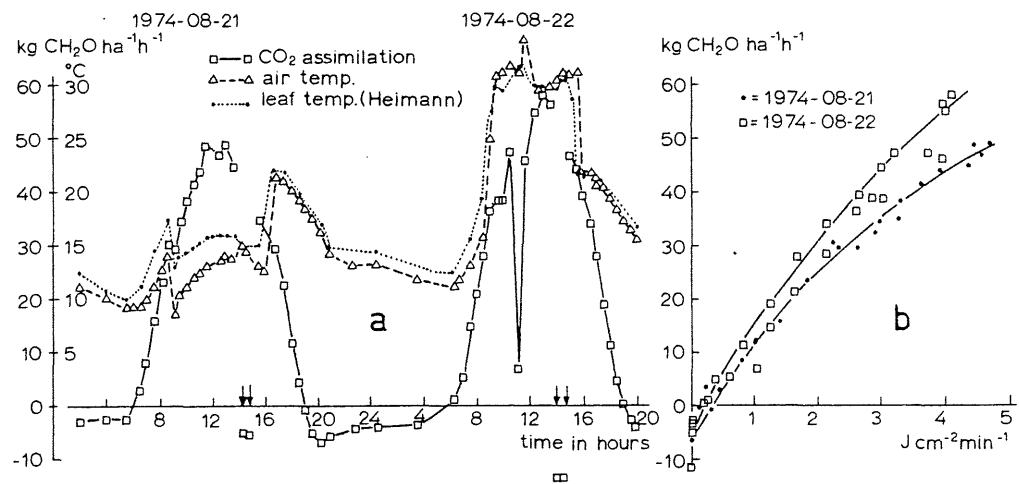


Fig. 9.  $\text{CO}_2$  assimilation expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{h}^{-1}$  as a function of time (a) and as a function of light (b) of a maize crop. Also leaf and air temperature as a function of time (a).

Species: *Zea mays* cv. Caldera 535; density: 10 plants  $\text{m}^{-2}$ ; measuring date: 1974-08-21; sowing date: 1974-04-25; location: Oost-Flevoland, Lelystad; leaf area index: 5.14  $\text{m}^2 \text{m}^{-2}$ ; dry weight shoot: 10 678  $\text{kg ha}^{-1}$ ; stage: 4.5 (Hanway, 1966); height: 280 cm.

Between arrows: dark respiration during the day.

young crop in the stage 0.5-1 (after Hanway, 1966), and its  $\text{CO}_2$  assimilation at a radiation of  $3 \text{ J cm}^{-2} \text{ min}^{-1}$  is about 30 % higher than that of the older crop in Fig. 9 which is in the grain filling stage. The increase in assimilation of the crop surface in successive days in the enclosure is not fully understood.

The  $\text{CO}_2$  assimilation of a closed crop surface of maize in the period of 31 July to 18 September is given in Fig. 10a and 10b for two replicates. The assimilation drops considerably with age. One of the objectives of the simulation was to analyse to what extent such a decrease may be attributed to a

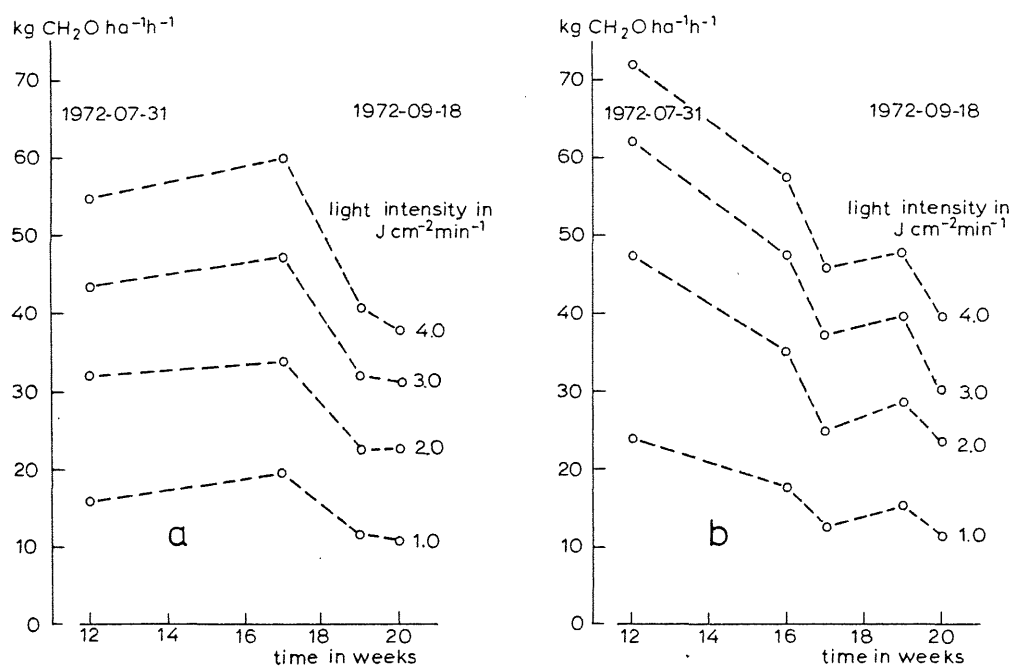


Fig. 10.  $\text{CO}_2$  assimilation expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{ h}^{-1}$  at the light intensities 1.0, 2.0, 3.0 and  $4.0 \text{ J cm}^{-2} \text{ min}^{-1}$  as a function of time of a maize crop (2 replicates).

Species: *Zea mays* cv. Caldera 535; density:  $10 \text{ plants m}^{-2}$ ; sowing date: 1972-04-28; location: Droevendaal, Wageningen.

Measuring date	LAI (3a) ( $\text{m}^2 \text{ m}^{-2}$ )	LAI (3b) ( $\text{m}^2 \text{ m}^{-2}$ )	Dry wt. (3a) shoot (kg $\text{ha}^{-1}$ )	Dry wt. (3b) shoot (kg $\text{ha}^{-1}$ )	Stage (Hanway)
1972-07-31	3.01	3.83	4373	5650	2.5 (12 weeks)
1972-08-21	3.62	3.76	10009	10208	4.0 (16 weeks)
1972-08-30	4.08	3.60	11156	11220	4.5 (17 weeks)
1972-09-11	3.15	3.53	11766	13461	5.0 (19 weeks)
1972-09-18	3.06	3.13	11937	11461	5.5 (20 weeks)

decrease in photosynthetic capacity of the leaves, decrease in leaf area index (LAI), interception of light by non-photosynthesizing tissue, temperature, lack of sink capacity, and so on. In so far as the problem of linking laboratory and field data through simulation is concerned, the difficulty remains that fully grown maize plants can hardly be obtained and analysed under controlled conditions. Experiments on the influence of temperature on assimilation were done with young and old crop surfaces. Closed crop surfaces with young plants in stage 1 (after Hanway, 1966) were obtained by a 6 to 10 times higher planting density than normal.

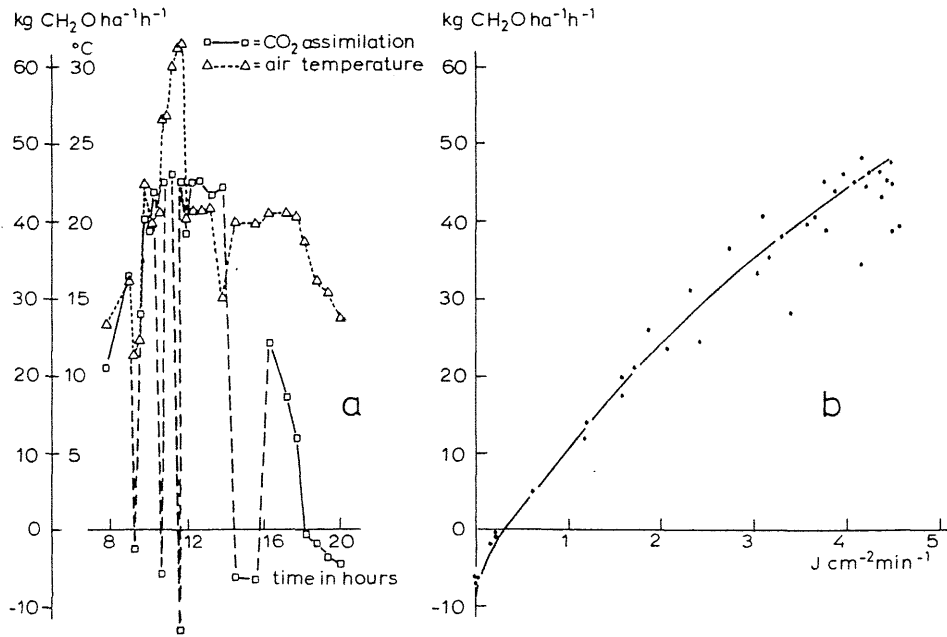
The temperature was varied throughout the day in a range dictated by ambient temperatures, by the capacity of the cooling system and of the additional heating system. Daily courses of temperature and assimilation are given in Fig. 11a and 11c. The dark periods were included to evaluate the effect of the temperature changes on respiration. The light response curves, based on these data are given in Fig. 11b and 11d.

The scattering of the observations for the crop surface of old plants is much smaller than for the crop surface of young plants and further analyses of these and other data show indeed that the influence of temperature on assimilation is small for plants in their later stages of growth and higher for plants in younger stages. The largest measured effects of the temperature are given in Fig. 12a and 12b for young plants.

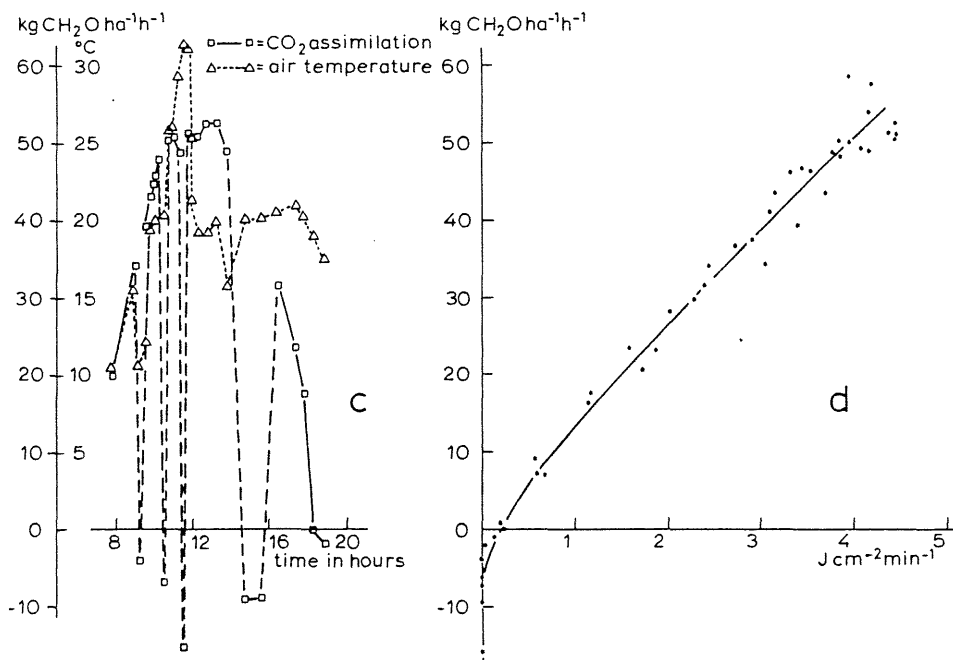
However, even with young plants the temperature influence on assimilation is considerably smaller than that simulated from laboratory data for the temperature response. The physiological causes for this difference between plants grown under field and laboratory conditions are further analysed. Practical experience in the Netherlands has already indicated that weight increases at the end of September are unexpectedly high for this 'heat loving' plant.

The influence of the  $\text{CO}_2$  concentration in the enclosure is presented in Fig. 13. The assimilation is independent of  $\text{CO}_2$  concentrations above  $200 \text{ cm}^3/\text{m}^3$  and this confirms the observations in the laboratory that in this range the stomata close with increasing  $\text{CO}_2$  concentration to such an extent that the internal  $\text{CO}_2$  concentration is maintained at about  $100 \text{ cm}^3/\text{m}^3$ . This closure of the stomata is also reflected in a reduced transpiration rate. Since it is difficult to change the water content of the soil, experiments on the relation between water status, assimilation and transpiration are being done by cutting the plants in the enclosure at the base but keeping them otherwise in the same position. The transpiration rate is measured at low resolution

YOUNG CROP 1973-08-22



OLD CROP 1973-08-22



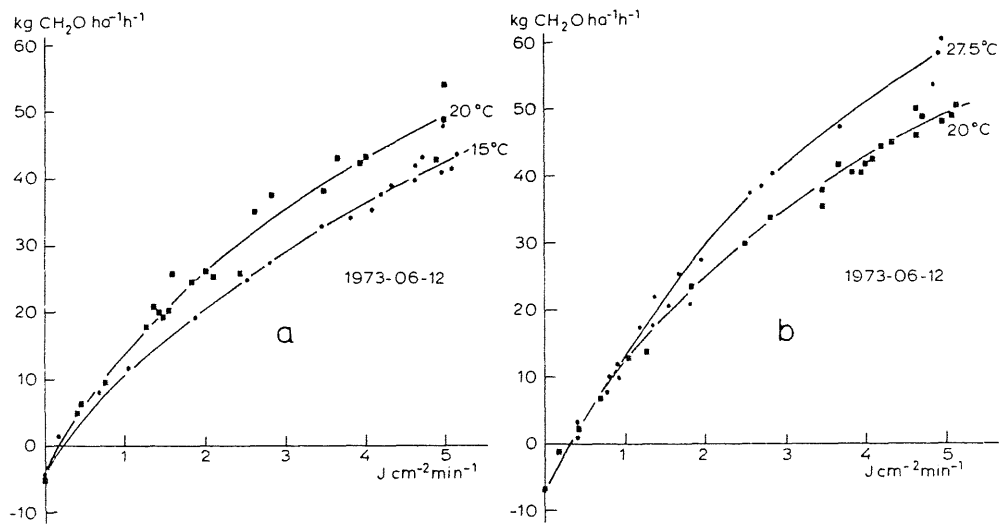


Fig. 12.  $\text{CO}_2$  assimilation expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{h}^{-1}$  at 15, 20 and 27.5 °C as a function of light.

Species: *Zea mays* cv. Caldera 535; density: 3 x 3 cm (a), 4 x 4 cm (b); measuring date: 1973-06-12; sowing date: 1973-05-01; location: Droevendaal, Wageningen; leaf area index: 17.5  $\text{m}^2 \text{m}^{-2}$  (a), 14.7  $\text{m}^2 \text{m}^{-2}$  (b); dry weight shoot: 3708  $\text{kg ha}^{-1}$  (a), 3297  $\text{kg ha}^{-1}$  (b); stage: about 1.0 (Hanway, 1966); height: about 30 cm.

Fig. 11.  $\text{CO}_2$  assimilation expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{h}^{-1}$  as a function of time (a, c) and as a function of light (b, d) of a young and an old maize crop. Also air temperature as a function of time (a, c).

Species: *Zea mays* cv. Caldera 535; density: 10 plants  $\text{m}^{-2}$ ; measuring date: 1973-08-22; location: Droevendaal, Wageningen.

Young crop: sowing date: 1973-07-11; leaf area index: 15.5  $\text{m}^2 \text{m}^{-2}$ ; dry weight shoot: 5010  $\text{kg ha}^{-1}$ ; stage: 0.5 - 1.0 (Hanway, 1966); height: 75 cm.

Old crop: sowing date: 1973-05-01; leaf area index: 5.7  $\text{m}^2 \text{m}^{-2}$ ; dry weight shoot: 16 300  $\text{kg ha}^{-1}$ ; stage: 4.5 (Hanway, 1966); height: 280 cm.

Broken line: dark respiration during the day (a, c).



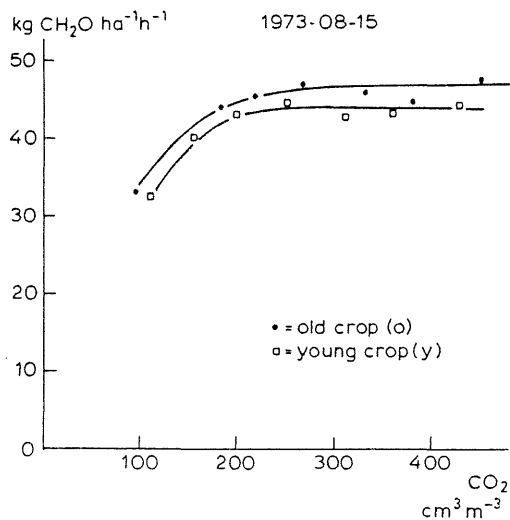


Fig. 13. CO<sub>2</sub> assimilation expressed in kg CH<sub>2</sub>O ha<sup>-1</sup> h<sup>-1</sup> as a function of CO<sub>2</sub> concentration of a young (y) and an old (o) maize crop.

Species: *Zea mays* cv. Caldera 535; density: 10 plants m<sup>-2</sup>; measuring date: 1973-08-15; sowing date: 1973-05-01 (o), 1973-07-11 (y); location: Droevendaal, Wageningen; leaf area index: 10.7 (y), 5.3 (o) m<sup>2</sup> m<sup>-2</sup>; dry weight shoot: 3403 (y), 12645 (o) kg ha<sup>-1</sup>; stage: 0.5 - 1.0 (y), 4.5 (o) (Hanway, 1966); height: 50 (y), 280 (o) cm.

via the rate of condensation of water on the cooler, corrected for the humidity of the ingoing and outgoing air. The outcome of one experiment is given in Fig. 14a and 14b.

Fig. 14a gives the assimilation rate and the transpiration rate dependent on time. The loss of water from the shoot and with this the drop in fresh weight may be found by integrating the transpiration rate, so that the results may also be presented with shoot fresh weight along the horizontal axis, as done in Fig. 14b.

It is observed that assimilation drops more rapidly than transpiration and this observation is contradictory to what is expected from the laboratory measurements where the decrease in water supply is affected by gradually drying of the soil.

From harvests it has been known for a long time that the potential crop growth rate of maize in the cool climate of the Netherlands is at least as high as that of other species, even late in the season, so that the adverse effect of temperature on the assimilation of maize, as found in the laboratory, does not manifest itself so strongly in the field. A comparison of the light response curves of maize with those of other species in this paper con-

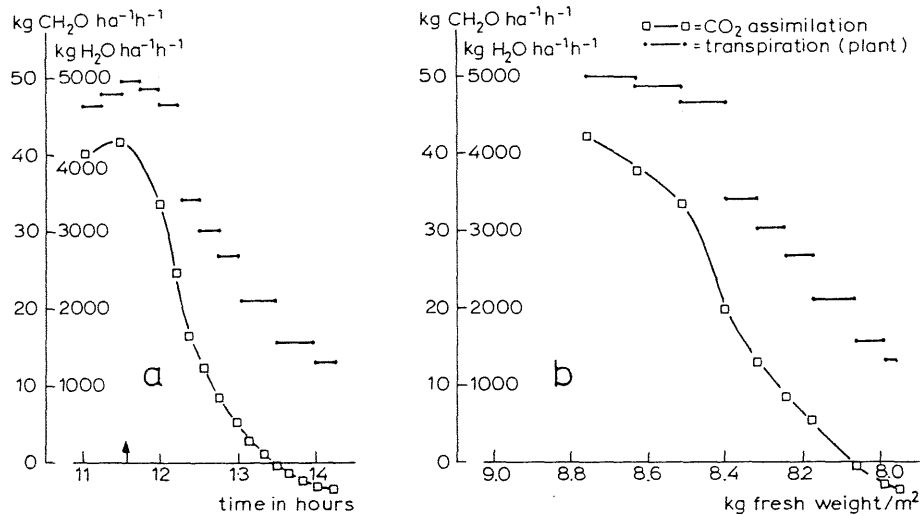


Fig. 14. CO<sub>2</sub> assimilation and transpiration expressed in kg CH<sub>2</sub>O ha<sup>-1</sup> h<sup>-1</sup> and kg H<sub>2</sub>O ha<sup>-1</sup> h<sup>-1</sup>, respectively as a function of time (a) and as a function of fresh weight (b).

Species: *Zea mays* cv. Caldera 535; density: 10 plants m<sup>-2</sup>; measuring date: 1973-08-16; sowing date: 1973-05-01; location: Droevendaal, Wageningen; leaf area index: 5.3 m<sup>2</sup> m<sup>-2</sup>; dry weight shoot: 12 645 kg ha<sup>-1</sup>; stage: 4.5 (Hanway, 1966); height: 280 cm.

firms that maize also grows very well in cool climates. Further physiological research may be centered around a more thorough analysis of the influence of temperature on assimilation in association with its effect on germination and early growth.

Detailed comparisons between simulated and experimental results for maize and other crops also show that the effect of different environmental conditions on the simulated results is in general larger than on the experimental results. Hence adaption mechanisms to changing environmental conditions are not very well presented in the simulation program. Relatively little attention has been paid to these adaptation phenomena in laboratory studies up to now, both for adaptation with time constants of the order of a day that are reflected in the biochemical properties of the plants and for adaptations with longer time constants that are reflected in morphological properties.