

ADAPTATION OF MAIZE TO DROUGHT

H.G. McPherson and J.S. Boyer

Plant Physiology Division DSIR
Private Bag, Palmerston North
and
Botany Department, University of Illinois,
Urbana, Illinois

ABSTRACT

The grain yields of maize plants subjected to drought under controlled environment conditions were substantially influenced by the evaporative demand that had been placed on them during their previous development.

This adaptive protection against subsequent drought was largely due to a change in the plant's ability to regulate water loss rather than a change in the response of photosynthesis to desiccation.

INTRODUCTION

It is well known that plants adapt to their environment and that this adaption can influence their subsequent survival and growth. Nurserymen, for example, "harden off" plants gradually rather than transferring them abruptly from favourable to unfavourable conditions. Despite the recognised importance of such adaptation in some fields and its undoubted, but unrecognised importance in others, little is known about the physiology of the phenomenon or its implications for plant production.

Information on the adaptation of plants to drought is particularly sparse. Jordan and Ritchie (1971) found that field-grown cotton exhibited less closure of stomata during drought than did similar plants growing in controlled environment facilities. They attributed this to differences in the water deficits previously experienced by the plants and this was confirmed subsequently by controlled environment studies where the response of previously droughted and undroughted leaves was compared (Brown *et al.*, 1973). Denmead and Shaw (1960) observed from their study of moisture stress on development and growth in corn that there was a tendency for recurring periods of stress to have a less and less detrimental effect on assimilation and yield. However, the evidence was tenuous.

We believe that further information is needed on plant adaptation both because of its possible agronomic significance and the effect it could have in the interpretation of physiological studies using plant material from diverse environments.

The objective of the work reported here was to determine whether the effects of drought on maize yield are reduced in plants that have had previous exposure to moderate desiccation.

The long term control of plant water status by controlling the supply of soil moisture to the plant is difficult. Plant water status is also influenced by the atmospheric demand for water and it is possible to use the alternative approach of manipulating evaporative demand to induce plant desiccation. These experiments were conducted from sowing to grain maturity in controlled environment rooms in the Climate Laboratory at Palmerston North, where reliable control of humidity can be achieved over a wide range. The plants were grown during the vegetative phase in well watered soil under either high or low evaporative demands * "pretreatment". Subsequently, low evaporative

demands were imposed on both groups. After anthesis and fertilisation had occurred, a more severe desiccation was imposed by withholding water from the soil ("treatment". The effect of the pretreatments and treatments on final dry matter yield was measured. Associated measurements of net photosynthesis rates, water use rates, and water status were made to assist interpretation of the observed yield responses.

*(High evaporative demand = low air humidity = low air vapour pressure VP) Conditions are normally referred to here as being high or low VP.

MATERIALS AND METHODS

Maize plants [*Zea mays* L. var. De Kalb XL45] were grown from seed in 23 1 pots containing modified soil in a controlled environment in the Climate Laboratory, Palmerston North. Except for the evaporative demand, conditions were identical throughout. Air temperature at the top of the plant canopy = 27.5/18.0 deg C (\pm 0.3) day/night. The rate of temperature and humidity change between day and night conditions was 2 hours. The night to day change over was completed immediately before the lights came on and the day to night change was initiated as soon as the lights went off. The radiant flux density of photosynthetically active radiation (as measured by an Eppley pyranometer and Schott RG8 filter system, 0.4 - 0.7 μ m waveband) was 170 W/Bqm. The photosynthetic light duration was 12 hours with abrupt day-night change. The modified soil mixture consisted of Opiki peat loam: peat: sand in the ratio of 70 : 15 : 15 : parts by volume.

During the first weeks from planting sufficient water was applied to keep the top of the profile moist. Subsequently, standard Hoagland's nutrient solution was applied every few days in quantities sufficient to bring the soil to field capacity and produce some drainage from the pot.

The evaporative demand pretreatment was imposed until tassel emergence occurred. Half the plants were grown in a controlled environment room with high vapour pressure (VP) (relative humidity = 86/90% (\pm 3%) day/night) and the other half in a second room with low VP (relative humidity = 29/76% (\pm 3%) day/night). At tassel emergence the low VP room was changed to the high VP conditions. The plants were kept well watered during the critical flowering period and the drought treatment was commenced after sufficient time had elapsed for fertilization to be complete.

Of the 36 plants receiving each pretreatment, 12 were harvested for dry matter analysis immediately prior to the start of the drought. Of the remaining plants, approximately half were retained as well-watered controls and the other half were subjected to drought by withholding water from the soil. Thereafter, the desiccated plants received small amounts of water which maintained leaf water potentials at approximately -20 bars for the remainder of the grain filling period.

Leaf water potentials were measured either with a pressure chamber or with a thermocouple psychrometer as described previously (Boyer and Knipling, 1965; Boyer, 1969). Plant height was measured as the maximum height to which any part of the plant (usually a leaf) would reach above the soil. Net photosynthesis rates were measured using a leaf chamber which enclosed the major portion of a single, attached leaf. The measurement system used was similar to that described by McPherson and Slatyer (1973). All measurements of photosynthesis were made on the 4th leaf from the top of the plant. This leaf was regarded as being representative of those contributing to grain filling by virtue of its position on the plant (Eastin, 1969) and its area. The water use rates of sample plants were measured using a counterbalanced arm to offset the major portion of the 15 kg pot weight and adjusting to a null position detected by a top-loading balance.

RESULTS AND DISCUSSION

Vapour pressure pretreatment effects on plant height were evident from a very early stage and the height differential increased progressively throughout the vegetative stage of growth (Fig. 1). However, the final leaf area and total number of leaves was comparable by the end of the pre-treatment period (high vp leaf area = 6,430 sq cm/plant, 16.0 leaves/plant; low VP leaf area = 6,250 sq cm/plant, 15.4 leaves/plant).

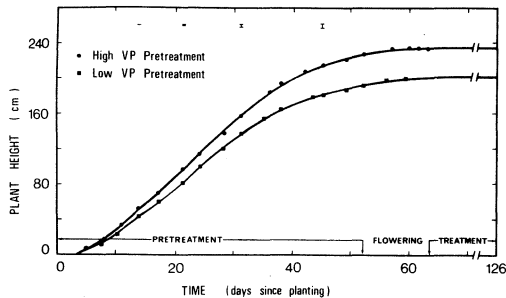


FIGURE 1: The effect of the air vapour pressure (v.p.) pretreatment on plant height. Vertical bars indicate the least significant difference ($p = 0.01$).

Plants harvested immediately prior to the start of the soil desiccation treatment showed that the vegetative dry matter yields were essentially unaffected by the pretreatment, differing by only 1%. The reproductive component (grain + cob) was higher in the low vp pretreated plants, but this was probably due to the harvest for the group being delayed by 3 days (Fig. 2).

The final dry matter harvest of the remaining plants was taken when grain maturity had been reached in the well-watered control plants (Fig. 2). No vp pretreatment effect occurred in the total dry matter of the control plants, although the balance of reproductive and vegetative dry matter production was slightly different.

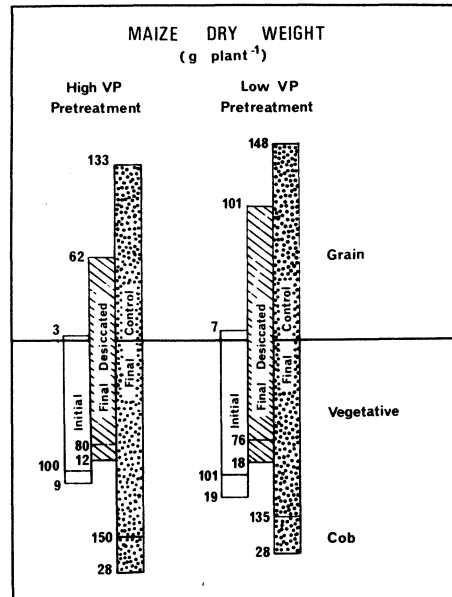


FIGURE 2: The effect of air vapour pressure (v.p.) pretreatment on dry matter yield. Mean weights (g plant^{-1}) are indicated for each component of yield.

The drought treatment on the other hand, showed a substantial effect of the VP treatment. The low VP pretreatment plants yielded 27% more total dry matter under desiccation than those given the high VP pretreatment. Most of this effect was due to differences in grain yield, the low VP treatment plants yielding 63% more grain than the high VP plants ($P < 0.01$). The vegetative and cob yield difference was in the same direction but small ($P < 0.05$).

In the drought treatment, desiccation became sufficiently severe that net photosynthesis had dropped sharply to 10% of the control rate after 7 days of desiccation in the high VP pretreatment and 11 days in the low VP pretreatment. The mean rate of grain accumulation in the control plants was 2.2 g/day. If the same initial rate applied in the drought treatment only 18 g and 31 g of grain would have accumulated by the time this rapid deduction in photosynthesis occurred. This represents only 29% and 30% respectively, of the final grain yield actually harvested. Clearly a significant portion of the grain laid down must have been derived from photosynthate fixed and stored before this period or from continuing low levels of net photosynthesis. Results indicate that both factors were contributing.

Figure 2 shows that the final vegetative yield of the desiccated treatment was substantially lower than the dry matter present at the start of the drought. The reduction was 20% in the high VP treatment and 25% in the low VP pretreatment. Most of the loss and vegetative dry matter was from the stem.

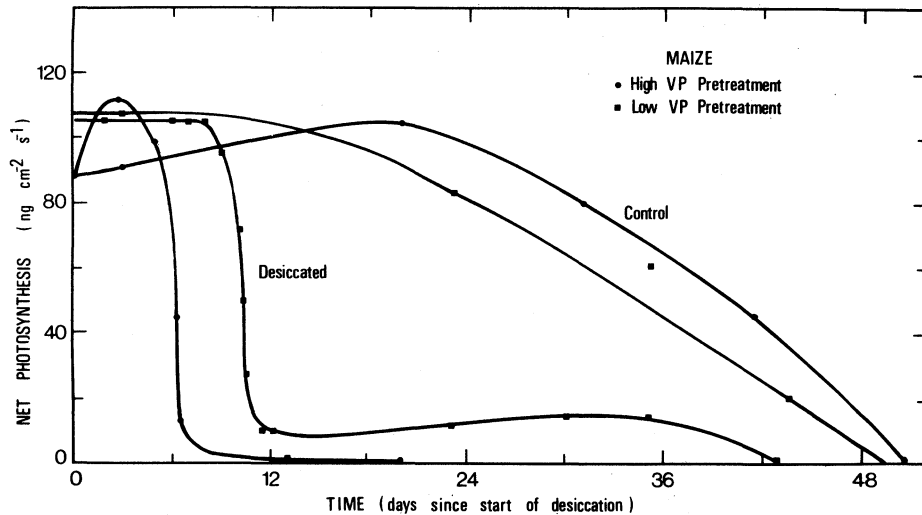


FIGURE 3: The time course of net photosynthesis rates in the well-watered control and droughted plants. Both groups had been grown previously under high or low air vapour pressure (v.p.) pretreatment conditions.

Measurements of net photosynthesis during the drought period show that the plants which had previously been exposed to the low VP pretreatment maintained significant net photosynthesis for approximately 28 days longer than the high VP plants (Fig. 3). This applied even though the desiccated plants experienced the same evaporative demand and received the same maintenance rations of water.

It can be seen from the above that although an important contribution to grain production came from stem reserves, the amount was similar for both pretreatments. Most of the pretreatment differences were due to difference in the plants' ability to maintain photosynthesis. Such differences could either be due to a difference in the activity of the photosynthetic tissue under desiccating conditions, or a difference in the plant water use rates which affect the degree of desiccation that occurred.

The first of these alternatives was examined by following the decline in photosynthetic rate that accompanied the desiccation of sample plants during the drought treatment. Figure 4 shows that the relationship between net photosynthesis and leaf water potential was unaffected by the pretreatment.

The second possible explanation for the pretreatment effect on grain yield was examined by measuring the daily weight loss during the drought treatment of sample plants from each of the VP pretreatments. Although the plants' leaf areas were similar and the evaporative demand was the same, the water use rates differed quite significantly (Fig. 5). Initially, when the soil was at field capacity, the plants which had experienced the low VP pretreatment used only 67% as much water per unit leaf area as the high VP pretreated plant.

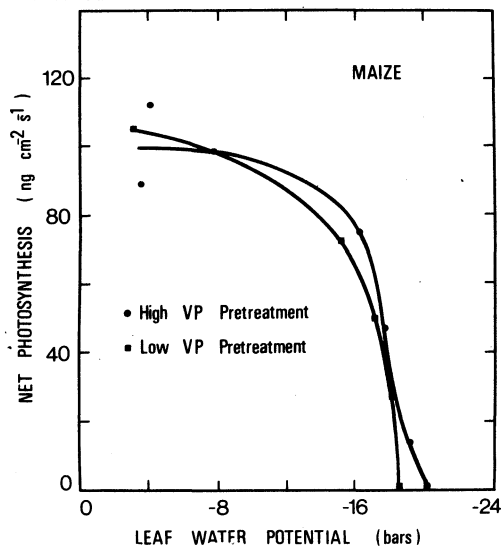


FIGURE 4: The response of net photosynthesis to leaf water status in plants previously grown under high or low air vapour pressure (v.p.) conditions.

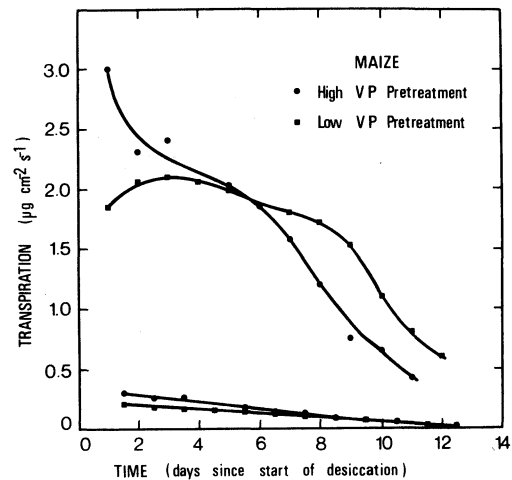


FIGURE 5: The time course for water use rates during the drought treatment under low vapour pressure (v.p.) conditions. The plants had been grown previously under high or low v.p. pretreatment conditions. Both daytime and nighttime values are shown.

It is apparent then, that the early conservation of water accounts for the extended period during which normal rates of photosynthesis continued in the low VP pretreated plants and that this had a major contribution to pretreatment effects on grain yield. The continuation of photosynthesis at low rates in the low VP pretreated plants would also have been important in contributing to grain yield differences. In this case, however, it was difficult to establish whether the pretreatment effects were due to small differences in water status in the range where photosynthesis is so sensitive to water potential, or whether some gradual change occurred in the plants' ability to photosynthesize under desiccating conditions.

CONCLUSIONS

These experiments have shown the following.

1. Maize can adapt sufficiently in response to relatively mild desiccation that its ability to withstand subsequent drought is significantly enhanced.
2. The adaptation was largely in the plants' ability to regulate water loss rather than in their ability to photosynthesize under a reduced plant water status.
3. Stem reserves can contribute substantially to yield under stress conditions. It should be noted that the translocation process could apparently still operate in quite severely desiccated plants.
4. In desiccated tissue small differences in water potential can have quite large effects on photosynthesis rates.

ACKNOWLEDGEMENTS

This study was conducted while J.S. Boyer was holding a DSIR, Climate Laboratory Fellowship at Plant Physiology Division. We wish to thank G. Holden for his able assistance with the experimental work and the Climate Laboratory staff for setting and maintaining the controlled environment conditions.

REFERENCES

- Boyer, J.S. 1969. Measurement of the water status of plants. *Annual Review of Plant Physiology*. **20**: 351-364.
- Boyer, J.S. and Knipling, E.B. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. *Proceedings of the National Academy of Science* **54**: 1044-1051.
- Brown, K.W., Jordan, W.R. and Thomas, J.C. 1973. The preconditioning influence of soil moisture stress on stomatal response of cotton. *Agronomy Abstracts*, 1973 Meetings, American Society of Agronomy, p. 30.
- Denmead, O.T. and Shaw, R.H. 1960. The effects of soil moisture stress at different stages of growth on the development and yield of corn. *Agronomy Journal* **52**: 272-274.
- Eastin, J.A. 1969. Carbon-14 labeled photosynthate distribution in corn in relation to leaf position and leaf function. *Proceedings 24th Annual Corn and Sorghum Research Conference*, American Seed Trade Association Publication No. 24, p. 81-89.
- Jordan, W.R. and Ritchie, J.T. 1971. Influence of soil water stress on evaporation, root absorption and internal water status of cotton. *Plant Physiology* **48**: 783-788.