Comparison of Zea diploperennis and Zea mays under water stress conditions

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SUMMARY Effects of cessation of watering on leaf water potential ($\psi_l$), leaf diffuse conductance (G) and dry matter were observed in Zea diploperennis (Z.D.) and maize, under controlled conditions. A more rapid decrease of soil water content was observed in containers where Z.D. was grown, indicating a higher transpiration in Z.D. than in maize. Despite that difference, Z.D. was found to maintain constant G during 2 weeks after $\psi_l$ started to decline, whereas in maize G values were not maintained. Moreover recovery to control G values occurred within 2 days in Z.D., but not in maize. Dry matter and leaf area were less reduced by drought in Z.D. than in maize. At equivalent leaf potential value, $CO_2$ exchange rate (CER) and G were less reduced by water stress in Z.D. than in maize.

Additional key words: Water potential, leaf conductance, photosynthesis.

RÉSUMÉ Relations hydriques de Zea diploperennis et Zea mays, soumis à la sécheresse.
Les effets d’un arrêt de l’arrosage furent étudiés chez Zea diploperennis (Z.D.) et chez le maïs en conditions contrôlées. Le contenu en eau du sol des conteneurs où croissait Z.D. baissa plus rapidement, indiquant une transpiration plus élevée chez Z.D. (par rapport au maïs). Malgré cela, la conductance foliaire (G) de Z.D. fut maintenue à sa valeur initiale pendant les deux premières semaines qui suivirent, alors que chez le maïs une chute de G fut observée rapidement. De plus, lors de la reprise des arrosages, les valeurs de G du maïs ne se rétablirent pas rapidement au niveau des témoins comme ce fut le cas chez Z.D. Finalement, la masse sèche et la surface foliaire du maïs furent moins réduites par le stress hydrique que chez le maïs.

Mots clés additionnels : Potentiel hydrique, conductance foliaire, photosynthèse.

I. INTRODUCTION

Zea diploperennis Itlis, Doebly, Guzman is a primitive relative of Zea mays L. discovered recently (ILTIS et al., 1979). The species crosses easily with maize and might therefore be used to bring new germplasm into a maize breeding programme (GALINAT, 1980 ; GAY, 1984). For this reason, an investigation was started on physiological characters of Zea diploperennis (which will be referred to as Z.D.) in comparison with maize.

Since we intend to study in future the behaviour of interspecific hybrids between maize inbred lines and Z.D. we chose as a first step to compare Z.D. with one maize inbred line. In this paper we examine, under controlled conditions, the effect of water stress on photosynthetic capacity ($CO_2$ exchange rate, CER), stomatal opening (leaf conductance, G), and dry matter. Photosynthetic rates per unit leaf area may differ among genotypes, and this character might have some value in maize breeding (CROSBIE et al., 1981 ; MOROT-GAUDRY et al., 1981).

On the other hand, water can be a very important factor limiting productivity (MORIZET et al., 1984 ; ALGANS & DESVIGNES, 1984) and CER of maize can be drastically affected by water stress (MCPHERSON & BOYER, 1977).

II. MATERIALS AND METHODS

A. Plant material, conditions of growth

Seeds of Z.D. (Zea diploperennis) were harvested in 1983 on plants grown in the botanical garden of INIREB (Xalapa, Mexico). Maize seeds were commercial seeds on inbred line F, from I.N.R.A., France.
After germination in Petri dishes at 24 °C, seeds were transplanted in containers. An additional series of seeds was transplanted to pots. Pots and containers were placed in growth chambers (PGV 36, from Controlled Environment).

Containers were 80 x 50 cm by 64 cm depth. There were four containers (two for each species). Each contained a bottom layer of gravel (10 cm thick) and a top layer (40 cm) of a fifty-fifty sand/loam mixture. There was no opening in the containers for drainage. Water was supplied through perforated pipes buried 35 cm below the soil surface. The quantities provided were not recorded. In each container plants were placed in 2 rows 34 cm apart.

In the growth chamber plants were kept under a 1 h h photoperiod and 21° (day), 15° (night) temperatures. Air relative humidity was 60 % (day) and 80 % (night). Photosynthetic photon flux density on plant tops was 250 frmol m-2 s 1.

The pots used for the additional series of plants (16 pots per species) had a 24 cm diameter and contained a mixture of 25 % sand, 25 % peat, 50 % loam. In each pot the number of shoots was limited to three : three plants in the case of maize, or one plant trimmed to its main shoot and two tillers in the case of Z. D. Other tillers were removed as soon as they became visible.

### C. Environmental and physiological measurements

The water content of the soil in the containers was determined gravimetrically on 3 samples. No measurements of water content were made on the soil in pots. Leaf diffusive conductance (G) was measured using a diffusive porometer (Delta T, Cambridge). Total conductance was obtained summing G on adaxial and abaxial surface. In the case of Z.D. measurements were soon limited to the abaxial surface since G on adaxial surface was found to be negligible, as in a previous study (GOLBERG & RENARD, unpublished data). Leaf water potential (ψ) was determined on leaf parts 5 cm long using a membrane press (J-14 Press, Crump, Raleigh). With a hydraulic pump, a pressure is applied on a flexible membrane, pushing the leaf material against the translucid wall of a chamber. The pressure applied when sap flows out of the leaf and change in the leaf coloration occurs is recorded. A close relationship exists between the results obtained with this method and the measurements made with a pressure bomb (RENARD & NDAYISHIME, 1982).

CO₂ exchange rates (CER) were measured using a slightly modified version of a rapid CO₂ pulse method described by SHIMSHI (1969).

Light was provided by 4 mercury vapour lamps of 400 W each. A transparent tank through which water was flowing was placed as a screen between lights and plants. Air containing 385 μl l⁻¹ CO₂ + 14CO₂ with a specific activity of 61 406 dpm/ml was passed through a miniature assimilation chamber (8 mm diameter). Clamping the chamber on the leaf for 20 s released an air flow (speed 3.9 cm s⁻¹) on both sides of the enclosed leaf part. Air temperature was 20 °C, and RH 50 %.

Immediately afterwards the treated leaf part was punched out and subjected to chemical digestion with Soluene before being processed for counting in a Packard Tricarb liquid scintillation counter. We are aware of conflicting results in the literature concerning comparison of CER measured by this method and with the infra red gas analyzer (IRGA) ; see for instance VAN DICK & LEDENT, 1984 ; KEMP & BLACKLOW, 1984.
method is simple and convenient (portable equipment, rapidity) and it seems sufficient when no absolute values of CER are needed.

With a few exceptions, physiological measurements were taken at least daily after cessation of watering. Measurements of the different parameters (table 1) were made successively on the same leaves. G were measured at different hours per day but since the same trend through days was observed only daily averages will be discussed. For measurements of photosynthesis plants in pots were removed from the growth chamber at 9 a.m. and brought to the laboratory. They were placed 30 minutes under a PPFD (photosynthetic photon flux density) of 500 μmol m⁻² s⁻¹ then PPFD was increased to 1 200 μmol m⁻² s⁻¹ and measurements started 30 minutes later. After measurement of photosynthesis, plants in pots were discarded.

Leaf area of all leaf laminae was measured at the end of the experiment with an electronic leaf area meter (AAM-7, from Hayashi Denko). Dry weights of different plant parts (laminae, stems,...) were determined after drying at 80 °C for 48 h.

III. RESULTS

A. Soil water content

Soil water content, θw (percentage on dry weight basis) of controls in containers showed erratic variations between 75 % and 120 % f.c. When water was withheld, θw decreased very regularly in a linear fashion, to reach 50-60 % of f.c. just before watering was resumed. The decrease was faster in the case of Z.D. (fig. 1). A θw value of 5.6 % was reached 8 DCW (Days after Cessation of Watering) in the case of Z.D. whereas in maize it took 12-13 DCW to reach that value. Thus transpiration by Z.D. was higher than for maize. This result may be explained by the higher leaf area of Z.D. (see below) and/or a higher transpiration rate per unit leaf area. No measurements of soil water content were made on plants growing in pots.

B. Leaf water potential

In containers, ψl of controls remained around -0.2 MPa at all times. Cessation of watering had no effect on ψl, ψp or ψs (pressure potential) (data not presented) during an initial period (IP) of 6 DCW. The following days a drop of ψl was observed and values of 1.2 and -1.4 MPa (Z.D. and maize respectively) were finally reached. Plots of ψl versus θw are presented in figure 2. The association of ψl with θw was looser in the case of Z.D. (r = 0.89** for maize and r = 0.65 N.S., p ≤ 0.05 for Z.D.; corresponding slopes were 0.15 N.S. and 0.25**). Fitting the equations ln(ψl) = a + bθw gave values of b = -0.54 and -0.26, a = 3.30 and 0.93, r = -0.95** and 0.61 N.S., for maize and Z.D. respectively. In plants grown in pots stressed maize showed significantly lower ψl than Z.D. starting 3 days after cessation of watering.

C. Leaf diffusive conductance

In containers, leaf diffusive conductance (G, fig. 3) of plants deprived of water remained relatively constant during the initial period (IP) of 6 DCW for both species. Differences between maize and Z.D. appeared afterwards: after a small decrease at day 6 (DCW) G of Z.D. remained remarkably constant (around 0.12 cm s⁻¹) whereas in maize a continuous decrease to 0.05 cm s⁻¹ was recorded. Only on day 13, a decrease of G (to values of 0.05 cm s⁻¹) was observed for Z.D., i.e. one week later than for maize. Thus, despite lower soil water contents, Z.D. maintained higher G than maize.

Only a sample of control values for G are presented in figure 3 to improve readability. G values started from similar values and showed the same trend with time in

![Figure 1](image1.png)

Soil water content, θw (% on a dry weight basis) in containers with Zea diploperennis (Z.D.) ■, or maize ▲, with time (in days after cessation of watering DCW).

Teneur en eau du sol, θw (% p.100 sur la base du poids sec) dans les récipients contenant Zea diploperennis (Z.D.) ■, ou le maïs ▲, en fonction du temps (en jours après l'arrêt des arrosages, DCW).

Les lignes verticales correspondent à θw de chaque milieu. L'arase indique la reprise de l'arrosage.

![Figure 2](image2.png)

Leaf water potential ψl (MPa) in relation to soil water content θw (%); experiment in containers. Values of ψl calculated from the model ln(ψl) = a + bθw are also presented.

Potentiel hydrique foliaire ψl (Méga Pascals, MPa) en fonction du contenu en eau du sol θw (%). Les valeurs de ψl prédites à partir de ln(ψl) = a + bθw sont également indiquées.

■ : Zea diploperennis - - - - - - ■ : Zea mays

![Figure 3](image3.png)

Leaf diffusive conductance

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Only a sample of control values for G are presented in figure 3 to improve readability. G values started from similar values and showed the same trend with time in
both species. An increase of G with time, associated with the reproductive stage, has been reported in other species such as millet (HANSON et al., 1983). In maize plants growing in pots complete stomatal closure (G = 0) was observed at the 4th DCW. In Z.D. on the contrary G remained little affected until the 6th day, when a drop was recorded, but even at that stage stomata were not completely closed (G ≠ 0). Plots of G versus ψᵣ for the period starting after cessation of watering are presented in figure 4 (plants in containers). Linear regression fitted to the data in figure 4 gave a higher slope in the case of maize (b = 0.17** cm s⁻¹ MPa for maize and b = 0.09** for Z.D.). Moreover the relationship was looser in the case of Z.D.: corresponding coefficients of correlation were indeed r = 0.89** and 0.59** (for maize and Z.D. respectively). Comparable results were obtained with plants growing in pots: b = 0.18** and 0.12 N.S.; r = 0.90** and 0.57 N.S. (maize and Z.D. respectively). Thus a decrease in ψᵣ had less effect on G in Z.D. than in maize.

D. Recovery

When watering was resumed, recovery was very fast for ψᵣ and its components: for both species return to control values took less than 2 days. Recovery was also fast for G values in Z.D. but not in maize (fig. 3).

E. CO₂ exchange rate

CER of maize decreased rapidly after cessation of watering (plants in pots). It reached nil values the 4th day after the onset of treatment. In Z.D. the decrease was more gradual and the last day of measurement CER still reached 50% of the rate observed in the controls.

In maize where stomatal conductance (G) was drastically affected by cessation of watering a relatively close association existed between CER and G (r = 0.81**, d.f. 13).

In Z.D. where stomatal opening was less affected the corresponding correlation was not significant (r = 0.26 N.S.; d.f. 28). Correlations between CER and ψᵣ gave similar results (r = 0.82**, and 0.26 N.S. for maize and Z.D. respectively).

Plots of CER as a function of G or ψᵣ showed a great dispersion of CER values at some G or ψᵣ values. Heterogeneity within the leaf (small assimilation chamber: 8 mm diameter) and sampling of leaves differing in positions and therefore age and microclimate might explain partly this result. To homogenize the results CER values obtained for second uppermost leaves were discarded if they differed more than 30% from the value obtained for uppermost leaves, moreover we
discarded data from pots where a difference of more than 30% was observed between the shoots (tillers or plants within the same pot). The screened data are presented in figure 5 (relationship of CER vs \( \psi_t \)) and figure 6 (relationship of CER with \( G \)). Correlations calculated on screened data were 0.93** (maize) or 0.31 N.S. (Z.D.) for the relation CER, G, and 0.78** (maize) or 0.49* (Z.D.) for the relation CER, \( \psi_t \). They lead to the same conclusions as those reached from the correlations on rough data.

Figure 5 indicates that CER of maize was completely inhibited when \( \psi_t \) was about – 1 MPa (~10 bar).

Similar (BEADLE et al., 1973) but also lower values (~2 MPa, MCPHERSON & BOYER, 1977) are found in the literature hence these numbers should not be taken as applying generally.

CER of Z.D. was less affected since at Bjft values of –1 MPa it still reached about 50% of the control value. The same result is obtained with G.

F. Leaf area and dry matter

Drought reduced total shoot dry weight by 42% in maize and by 22% in Z.D. (plants growing in containers, table 2). The interaction treatment × species was highly significant. Therefore dry matter was more reduced by drought in maize than in Z.D., a result found also for stomatal conductance. Leaf area was also more reduced in maize (29% in maize, versus 23% in Z.D.). The higher leaf area values for Z.D. were associated with its tillering capacity (3-6 tillers per plant in containers and pots respectively) and occurred despite a smaller leaf area per shoot (a mean surface area per leaf lamina of 2.1 dm\(^2\) (maize) and 0.6 dm\(^2\) (Z.D.) was observed on plants in pots. Number of tillers in Z.D. was reduced 14-20% by drought.

Table 2

<table>
<thead>
<tr>
<th></th>
<th>Zea mays</th>
<th>Zea diploperennis</th>
<th>LSD (ppds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf area/plant (dm(^2))</td>
<td>17.1</td>
<td>12.2</td>
<td>25.3</td>
</tr>
<tr>
<td>Surface foliace/plante (dm(^2))</td>
<td>21.5</td>
<td>12.5</td>
<td>20.8</td>
</tr>
<tr>
<td>Total shoot dry weight (g)</td>
<td>17.3</td>
<td>12.2</td>
<td>25.3</td>
</tr>
<tr>
<td>Nb tillers/plant</td>
<td>0</td>
<td>0</td>
<td>3.6</td>
</tr>
</tbody>
</table>

Dead plant material was carefully harvested separately. The very low amounts obtained indicate that the drought treatments had little effect on tissue death in these experiments.

IV. CONCLUSIONS

Higher leaf diffusive conductances (G) were maintained in Z.D. than in maize, when watering was withheld. This result was observed although, during the drought period, soil in containers with Z.D. reached lower soil water content (\( \theta_w \)) than in containers with maize. In fact the lower soil water content obtained with Z.D. appears to be the result of a higher transpiration of Z.D., in relation with higher G and larger leaf area. Higher G in Z.D., despite higher loss of water, indicates a better maintenance of turgor in this species. Whether this may be attributed to differences in elasticity of cell walls or to other mechanisms such as osmotic adjustments etc... remains an open question.

The maintenance of a higher transpiration rate when water becomes limited is not, per se, an advantage.
Maintenance of photosynthetic rates is. Higher CER were observed in Z.D. during the stress period.

The final dry weights obtained were consistent with the lesser reduction of CO₂ exchange rate (CER) in Z.D. plants subjected to water shortage. Maintenance of higher G was favourable to CER and dry matter production.

The disadvantage of maize, as far as CER is concerned, seems to be associated with greater effect of water shortage on G, affecting growth through a close association of CER with G.

Such a close association is not observed in Z.D., but this is probably because of its higher G values, corresponding to the part of the response curve of CER to G which tends to plateau.

Reduction of photosynthesis at low water potentials is known to be due to stomatal closure, but also to other factors related to chloroplast activity and structure (Vieira da Silva, 1976; Farquhar & Sharkey, 1982; Krieg & Hutmacher, 1986).

Measurements of fluorescence induction seemed to indicate, however, that the primary photochemistry of photosystem II was not affected and was not a cause for the reduction of CER in these experiments (Golberg et al., 1986).

Under our conditions and with the material we used Z.D. (Zea diploperennis) appeared to be more drought-tolerant than maize: leaf diffusive conductance was better maintained and less reduction in dry matter occurred. Field-grown plants of different age might however differ markedly from plants grown indoors in pots or containers because of root systems, stomatal behaviour, etc... Our results should therefore not be extrapolated. It can be concluded, however, that the species appears to present some interest and it seems worthwhile to continue the investigations with interspecific crosses and field trials.

REFERENCES


