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Changes in photosynthesis in inbred maize lines with different degrees of chilling tolerance grown at optimum and suboptimum temperatures

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Abstract

The effects of growth temperature on changes in net photosynthetic rate (P_N) and the chlorophyll fluorescence induction parameter F_v/F_m were investigated after cold stress in inbred maize lines with different degrees of cold tolerance. There was no significant difference between lines grown at optimum temperatures of 25/23 and 20/18 °C as regards P_N and F_v/F_m determined at the growth temperature, but these parameters were lower for plants grown at a suboptimum temperature of 15/13 °C. After cold treatment, the decrease in P_N was more pronounced in chilling-sensitive lines. The higher the growth temperature was, the more pronounced decrease occurred in P_N and F_v/F_m. Thus at low growth temperature both damaging and adaptive processes occur.

Additional key words: chlorophyll fluorescence; gas exchange; intercellular CO_2 concentration; low temperature stress; stomatal conductance; *Zea mays*.

Introduction

As is the case for most C_4 plants, maize requires a relatively high temperature if it is to develop well. If growth and development take place at below-optimum temperature, several important life functions suffer inhibition, including the photosynthetic apparatus (Baker *et al.* 1983, Long *et al.* 1983). In maize a reduction in the activities of several enzymes has been described. The most important of these are the enzymes responsible for the C_4 reaction pathway, such as pyruvate P_i dikinase or phosphoenolpyruvate carboxylase (Long 1983). In various chilling-sensitive plants a reduction in activity has been demonstrated for ribulose-1,5-bisphosphate carboxylase (Brüggemann *et al.* 1992), $NADP^+$-malate dehydrogenase (Stamp

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1987a), and phosphofructokinase (Stamp 1987b) as the result of cold stress. In cold-tolerant maize lines the dry matter production and leaf growth rate are generally greater than in the cold-sensitive types. A larger net growth is associated with higher P_N (Stamp *et al.* 1993). At low growth temperature an alteration in pigment content and arrangement, and an inhibition of electron flow occur (Csapó *et al.* 1991). Numerous chlorophyll (Chl) fluorescence induction and CO_2 fixation parameters indicate that photoinhibition also plays an important role in cold injury to young maize plants (Janda *et al.* 1994a, Szalai *et al.* 1996).

The aim of this study was to evaluate how certain parameters related to photosynthetic activity change as the result of low temperature treatment in maize lines with various degrees of cold tolerance, and whether the growth temperature has any influence on their response to low temperature.

Materials and methods

Plants: Inbred maize lines (cold-tolerant Z7 and KW1074; cold-sensitive CM109, Mo17, and Penjalinan) in the 4-leaf stage were used in the experiments. The plants were grown in a *Conviron PGR-15* chamber at 25/23, 20/18 or 15/13 °C at PPFD of 250 μmol m^{-2} s^{-1} (16/8 h light/dark period), and relative humidity of 75 % in a mixture of loamy soil, *Vegasca* (humus-containing additive, manufactured by *Florasca*), and sand (3 : 1 : 1, v : v : v). The cold treatment was carried out in the same chamber.

Gas exchange measurements: P_N was measured with a *LI-6400* infrared gas analyser operated with a *6400-02* LED light source (*LI-COR*, Lincoln, Nebraska, USA) providing 250 μmol m^{-2} s^{-1} PPFD. Measurements were carried out at the ambient temperature on the youngest fully developed leaves. The gas exchange parameters were determined using the method described by Caemmerer and Farquhar (1981).

Chl fluorescence induction parameters were measured at room temperature after 30 min dark adaptation on the youngest fully developed leaves using a fluorometer of the *PAM-2000* type (*Walz*, Effeltrich, Germany). The saturating irradiance (acting for 8 s) was approx. 5000 μmol m^{-2} s^{-1}.

Statistical analysis: Values represent the means of at least 3-5 measurements; they were evaluated using the *t*-test method.

Results

Plants grown at optimum temperatures: In the first experiment, the chilling-tolerant inbred maize lines KW1074 and Z7, and the chilling-sensitive CM109, Mo17, and Penjalinan lines (Stamp *et al.* 1993) were grown at 25/23 or 20/18 °C under identical irradiance. Both growth temperatures can be regarded as optimum for young maize plants. There were no significant differences in P_N between the lines and between the two growth temperatures (Table 1). As a cold treatment the plants were kept first for

Table 1. Changes in net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mmol(H_2O) m^{-2} s^{-1}], and intercellular carbon dioxide concentration (C_i) [μmol(CO_2) mol^{-1}(air)] in 5 inbred maize lines grown at optimum temperatures (25/23 and 20/18 °C with 16 h photoperiod) after 1 d of cold treatment at 15/13 °C followed by 1 d at 10/8 °C. The measurements were made on the youngest fully developed leaves at the ambient temperature. The results are the means of at least 3 measurements. *, **: significant at $p \leq 0.05$, 0.01 compared to the control values, respectively.

	KW1074		Z7		CM109		Penjalinan		Mo17	
	25/23	20/18	25/23	20/18	25/23	20/18	25/23	20/18	25/23	20/18
P_N										
Control	12.5 ±0.8	11.9 ±1.2	12.5 ±.6	11.7 ±0.3	12.8 ±0.7	12.1 ±0.3	11.5 ±1.3	11.9 ±0.4	11.9 ±0.6	11.9 ±0.8
1 d 15/13 °C	8.4 ±0.6**	10.3 ±0.1	8.4 ±1.2**	9.0 ±0.8**	7.3 ±0.3**	9.8 ±1.4*	6.7 ±0.6**	9.4 ±1.2*	6.7 ±0.2**	9.8 ±1.0*
+1 d 10/8 °C	5.5 ±0.5**	8.9 ±0.7*	4.5 ±0.3**	7.2 ±0.6**	3.9 ±0.7**	7.8 ±0.4**	2.6 ±1.2**	6.6 ±1.7**	1.9 ±2.1**	3.6 ±2.0**
g_s										
Control	100.6 ±4.1	81.2 ±10.1	100.5 ±13.8	71.7 ±4.7	120.0 ±16.7	93.1 ±8.5	83.5 ±16.3	87.5 ±13.5	97.8 ±5.4	93.6 ±25.5
1 d 15/13 °C	58.6 ±2.7**	65.8 ±4.4	61.7 ±16.7*	57.1 ±10.3	71.4 ±16.9*	71.6 ±22.6	63.3 ±17.3	57.8 ±15.8	77.8 ±29.7	66.5 ±7.2
+1 d 10/8 °C	70.0 ±17.8*	80.9 ±10.1	88.7 ±3.4	79.7 ±13.3	84.3 ±4.2*	90.1 ±10.3	64.4 ±23.5	49.1 ±24.1	50.7 ±19.6*	36.1 ±11.5*
C_i										
Control	194 ±21	82 ±23	189 ±38	131 ±10	219 ±17	110 ±20	172 ±19	174 ±29	197 ±16	181 ±35
1 d 15/13 °C	225 ±20	201 ±16**	237 ±40	200 ±26*	284 ±45	229 ±36**	272 ±69*	184 ±36	294 ±72	216 ±42
+1 d 10/8 °C	282 ±27*	230 ±19**	335 ±4**	271 ±17**	336 ±13**	265 ±21**	354 ±11**	191 ±44	352 ±46**	262 ±57

1 d at 15/13 °C and then for a further day at 10/8 °C. These cold treatments induced a reduction in P_N in all genotypes. The extent of this reduction, however, depended greatly on the growth temperature: plants of all genotypes grown at the lower temperature (20/18 °C) exhibited a less severe loss of photosynthetic activity after cold treatment than those grown at the higher temperature (25/23 °C) (Table 1). Thus although both growth temperatures can be regarded as optimum for young maize plants, the plants grown at the lower temperature were more resistant to chilling. The P_N of the cold-sensitive lines was generally lower than that of lines tolerant to low temperatures. The two-sample *t*-test showed significant differences at $p \leq 0.05$ for the following treatments: When grown at 25/23 °C, KW1074 > CM109, Mo17, and Penjalinan; Z7 > Mo17 and Penjalinan at 15/13 °C; and KW1074 > Z7, CM109, Penjalinan, and Mo17 at 10/8 °C. When grown at 20/18 °C, KW1074 > Z7 and Mo17; Z7 > Mo17; CM > Mo17 at 10/8 °C.

Stomatal conductance (g_s) usually decreased during cold treatment in plants which were grown at 25/23 °C, but in plants grown at 20/18 °C a significant decrease occurred only in the cold-sensitive line Mo17 (Table 1). This decrease may play a role in the reduction of P_N, though the fact that the P_N values of plants grown at 20/18 °C decreased less due to cold treatment than the P_N of plants grown at 25/23 °C cannot be explained purely by changes in g_s.

Intercellular carbon dioxide concentration (C_i) was usually smaller in plants grown at 20/18 °C than at 25/23 °C (Table 1). The exceptions were the control treatments of lines Penjalinan and Mo17, where the C_i values were relatively high for both growth temperatures. As a result of cold treatment, C_i increased, but a close correlation was not found between cold tolerance and C_i.

Table 2. Changes in F_v/F_m in 5 inbred maize lines grown at optimum temperatures (25/23 and 20/18 °C with 16 h photoperiod) after 1 d of cold treatment at 15/13 °C followed by 1 d at 10/8 °C (*A*) or after 8 h cold treatment at 5 °C in the light (*B*). The measurements were made on the youngest fully developed leaves after 30 min dark adaptation at room temperature. The results are the means of at least 4 measurements. *, **: significant at $p \leq 0.05$, 0.01 compared to the control values, respectively.

	KW1074		Z7		CM109		Penjalinan		Mo17	
	25/23	20/18	25/23	20/18	5/23	20/18	25/23	20/18	25/23	20/18
Control	0.779 ±0.014	0.769 ±0.013	0.791 ±0.010	0.785 ±0.011	0.794 ±0.014	0.808 ±0.010	0.799 ±0.009	0.795 ±0.012	0.802 ±0.010	0.799 ±0.012
A	0.675 ±0.028**	0.729 ±0.018**	0.623 ±0.063**	0.726 ±0.039*	0.666 ±0.048**	0.747 ±0.014**	0.610 ±0.047**	0.720 ±0.044**	0.597 ±0.065**	0.709 ±0.024**
B	0.466 ±0.058**	0.646 ±0.039**	0.477 ±0.063**	0.562 ±0.042**	0.463 ±0.033**	0.575 ±0.100**	0.357 ±0.034**	0.460 ±0.067**	0.367 ±0.038**	0.544 ±0.050**

The F_v/F_m, indicative of the maximum photochemical efficiency of photosystem 2, was measured for each line after an 8 h cold treatment at 5 °C, and also after the combined cold treatment (1 d at 15/13 °C + 1 d at 10/8 °C) used for determining the P_N, g_s, and C_i (Table 2). Similarly to other Chl fluorescence induction parameters (Janda *et al.* 1994a, Szalai *et al.* 1996), there was very little change in F_v/F_m after cold treatment in the dark. Similarly to P_N, there was no significant difference in F_v/F_m for the control plants, while after cold treatment the ratio declined to different extents for plants grown at different temperatures: the decrease was much greater for plants grown at 25/23 °C than for those grown at 20/18 °C. However, if the different lines are compared, it is difficult to demonstrate such a direct correlation between the F_v/F_m and the cold tolerance of the plant as in the case of P_N. After the combined cold treatment only the KW1074 > Penjalinan and KW1074 > Mo17 differences were significant ($p \leq 0.05$) for plants grown at 25/23 °C, while for those grown at 20/18 °C the greatest value was found for CM109, and only this was significantly greater than that of Mo17 ($p \leq 0.05$). After cold treatment at 5 °C for 8 h, significant differences were observed: For plants grown at 25/23°C, KW1074 > Mo17 and Penjalinan; Z7 > Mo17 and Penjalinan; CM109 > Mo17 and Penjalinan. For plants grown at 20/18 °C, KW1074 > CM109, Z7, Penjalinan, and Mo17; Z7 > Penjalinan;

CM109 > Penjalinan; Mo17 > Penjalinan. This reduction was smaller for plants grown at 20/18 °C than for those grown at 25/23 °C.

Plants grown at suboptimum temperature: In the second experiment the same lines were germinated for a week at 20/18 °C and then grown at suboptimum temperature (15/13 °C). The other parameters were the same as those described above. Lines grown at suboptimum temperature were unable to maintain the P_N observed for plants grown at higher temperatures (Table 3). Nevertheless, these P_N values were greater than those found for plants grown at 25/23 °C during the 1 d cold treatment at 15/13 °C, indicating that adaptation processes also took place. A similar conclusion can be drawn for the effect of a 1 d treatment at 10/8 °C.

Table 3. Changes in the net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mmol(H_2O) m^{-2} s^{-1}], and intercellular carbon dioxide level (C_i) [μmol(CO_2) mol^{-1}(air)] in 5 inbred maize lines grown at 15/13 °C after 1 d of cold treatment at 10/8 °C. The measurements were carried out on the youngest fully developed leaves at the ambient temperature. The results are the means of 5 measurements. *, **: significant at $p \leq 0.05$, 0.01 compared to the control values, respectively.

	KW1074	Z7	CM109	Penjalinan	Mo17
P_N					
Control	8.2 ± 2.5	8.9 ± 2.2	9.1 ± 2.1	7.7 ± 1.6	7.1 ± 1.2
1 d 10/8 °C	7.4 ± 0.6*	6.9 ± 0.6	5.2 ± 1.7*	4.6 ± 1.0*	5.6 ± 1.1
g_s					
Control	49.7 ± 21.6	57.9 ± 23.8	59.5 ± 2.1	43.8 ± 16.0	43.4 ± 9.5
1 d 10/8 °C	60.2 ± 6.6	52.6 ± 5.7	72.1 ± 42.0	36.3 ± 11.3	45.2 ± 18.1
C_i					
Control	188 ± 49	203 ± 46	195 ± 36	175 ± 56	167 ± 18
1 d 10/8 °C	254 ± 13	253 ± 20	330 ± 46**	253 ± 48	229 ± 84

The g_s at a growth temperature of 15 °C was lower than at optimum temperature, while a non-significant change was observed as the result of 1 d at 10/8 °C (Table 3). By contrast, the C_i was higher and a slight increase occurred as the result of cold treatment (Table 3).

Table 4. Changes in F_v/F_m in 5 inbred maize lines grown at 15/13 °C with 16 h photoperiod after 1 d of cold treatment at 15/13 °C followed by 1 d at 10/8 °C or after 8 h cold treatment at 5 °C in the light. The measurements were made on the youngest fully developed leaves after 30 min dark adaptation at room temperature. The results are the means of 5 measurements. *, **: significant at $p \leq 0.05$, 0.01 compared to the control values, respectively.

	KW1074	Z7	CM109	Penjalinan	Mo17
Control	0.688±0.009	0.713±0.025	0.743±0.022	0.675±0.089	0.741±0.023
1 d 10/8 °C	0.662±0.042	0.662±0.038*	0.687±0.058	0.672±0.013	0.679±0.023**
8 h 5 °C	0.626±0.032*	0.640±0.058*	0.617±0.053*	0.576±0.045	0.566±0.145**

The lower P_N than in the control for lines grown at optimum temperature was due partly to the lower measurement temperature. P_N was always determined at the growth temperature, but the fact that this temperature was really experienced as stress is indicated by the F_v/F_m which was always lower for control plants grown at 15 °C than for control plants grown at optimum temperature. F_v/F_m was measured at room temperature after 30 min of dark adaptation (Table 4). The values obtained after cold treatment for 8 h at 5 °C were generally higher than those measured for plants grown at either 25/23 or 20/18 °C.

Discussion

The chilling susceptibility of the photosynthetic system of maize is one of the most important limiting factors for the production of maize over wider areas. Besides the high temperature optimum of the enzymes responsible for CO_2 fixation (Long 1983), low temperature-induced photoinhibition is also important in the cold damage of young maize plants (Janda *et al.* 1994b). In cold-tolerant plants, as was demonstrated for spinach (Somersalo and Krause 1989) or winter rye (Öquist and Huner 1993), growing at low, but not freezing temperatures leads to an increased resistance to both low temperature and photoinhibition. Growing maize at suboptimum temperature, but above the threshold of 10-12 °C (Miedema 1982), causes increased tolerance to high irradiance at low temperature. However, in maize exposed to extremely low temperature (0.5 °C) the susceptibility of plants to low temperature-induced photoinhibition increases (Szalai *et al.* 1996). The present study demonstrated that not only in chilling-tolerant (KW1074, Z7), but also in chilling-susceptible maize lines (CM 109, Mo17, Penjalinan), the lower the growth temperature, the less reduction occurred in the photosynthetic activity after cold stress. The effect of cold hardening can be seen in both the P_N and F_v/F_m, especially after a short low-temperature (5 °C) stress in the light (this parameter does not change at low temperature in the dark). Of course, the negative effect of a brief low temperature exposure of maize may be restored by a subsequent warmer period (Kościelniak *et al.* 1996). Exposure of young maize plants to low temperature in the light causes a decrease in g_s (Szalai *et al.* 1997). A correlation between stomatal closure at low temperature and cold sensitivity was demonstrated in maize (Vígh *et al.* 1981) and black-currants (Jefferies and Brennan 1994). Generally, genotypes tolerant to low temperature exhibit a greater reduction in g_s. For the maize lines tested in the present work, however, such a correlation was not found. Although g_s was usually lower at low growth temperature, it decreased in all lines when grown at 25/23 °C, and in the most chilling-sensitive lines Mo 17 and Penjalinan when grown at 20/18 °C. There was no significant change after cold treatment in lines CM109, KW1074, and Z7 when grown at 20/18 °C, or in any plants grown at sub-optimum temperature (15/13 °C).

The F_v/F_m showed similar changes after cold treatment in plants grown at various temperatures: the lower the growth temperature the less pronounced was the decrease in F_v/F_m. Verheul *et al.* (1993) found similar changes when measuring another Chl fluorescence induction parameter, the maximum rate of rapid fluorescence increase (F_R).

Generally, the cold sensitivity of a plant is well correlated with the photoinhibition sensitivity induced at low temperature. When the genotypes do not differ much from each other (*e.g.*, cultivars or lines within a species) this is not always the case (Janda *et al.* 1994b). Chilling temperatures increase the likelihood of photoinhibition, characterized by a decrease in F_v/F_m, in the leaves of both chilling-sensitive and chilling-tolerant plants, and while photoinhibition during low temperature stress generally occurs more rapidly in cold-sensitive plants, it is not directly related to chilling sensitivity (Hetherington *et al.* 1989). There may be various reasons for this: adaptation to low temperature does not necessarily mean adaptation to high irradiance. Photoinhibition is not simply a degradation process, but in a certain sense it is also part of a regulating mechanism. The acceleration of the electron transport as the result of high irradiance may lead to the production of various injurious oxygen radicals. In the course of a down regulation mechanism, however, there may be a reduction in the efficiency of radiant energy utilisation, leading to a decrease in the damaging effect of photoinhibition, though at the expense of photosynthesis (Baker *et al.* 1994). While the reduction in the quantity of D1-protein during photoinhibition can usually be described by a linear equation, changes in F_v/F_m are the result of both the D1-protein degradation and the above-mentioned down-regulation mechanism (Tyystjärvi *et al.* 1994).

Our results suggest that at low growth temperature, in addition to stress injury, adaptation processes take place in maize plants, which may induce tolerance to low temperature stress and to low temperature-induced photoinhibition.

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