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Cold tolerance of maize seedlings as determined by root morphology and photosynthetic traits

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Abstract

Mild chilling stress and slow soil warming are common causes for a retarded early development of maize (*Zea mays* L.). The objective of this study was to evaluate cold tolerance of a divers set of 14 inbred lines with respect to root morphology as well as the function of the photosynthetic apparatus. Plants were grown until the 2-leaf stage under growth chamber conditions at air and soil temperatures of 15/13 °C and 24/20 °C (day/night). Four contrasting genotypes were tested at 15/13 °C and 17/13 °C (day/night) in the topsoil simulating temperature differences as occurring in no-tillage in comparison with conventional tillage systems. The small variation in the day temperature of 15 °C versus 17 °C in the topsoil affected plant growth and a significant genotype-by-temperature interaction was detected for the chlorophyll content (SPAD) and the operating efficiency of photosystem II (Φ_{PSII}). At 15/13 °C compared to 24/20 °C, differences between genotypes for the primary lateral root (PrLat) length and its portion on the embryonic root system were hardly affected by temperature. Φ_{PSII} and the lateral root length were closest related to plant dry weight at 15/13 °C ($r^2 = 0.56$ and 0.75, respectively), the axile root length and the leaf area were closest related to plant dry weight at 24/20 °C ($r^2 = 0.46$ and 0.83, respectively). Therefore, the selection for long PrLat roots holds promise for the improvement of early vigour in environments and cropping systems with reduced soil warming in spring but might be disadvantageous under warmer conditions.

Keywords: Chlorophyll content; Chlorophyll fluorescence; Cold tolerance; Corn; Chilling; Root morphology; Primary root; Seminal root; Soil temperature; *Zea mays*

1. Introduction

Strong seedling performance is a desired goal for the adaptation of maize to the cold and wet conditions of central and northern Europe as well as for its integration in soil-conservation tillage systems of temperate climates where soil warming is comparably slow (Tollner et al., 1984; Arshad and Azooz, 1996). In no-tillage systems, the temperature is probably the main physical stress factor which impairs the early development of maize (Chassot, 2000), the shoot apex of which remains below the soil surface until about the 6-leaf stage (Blacklow, 1972; Erbach et al., 1986; Stone et al., 1999). Consequently, both the shoot and root meristems are directly influenced by the soil temperature. It is well established that the early leaf development is controlled mainly by the soil temperature, both under controlled conditions (Beauchamp and Lathwell, 1966) and in the field (Giauffret et al., 1995; Stone et al., 1999). The shoot development can be limited by a direct effect of temperature on the shoot meristem or by a reduced nutrient supply through the roots (Engels and Marschner, 1990). Genotypic differences in cold tolerance exist for the development of the root (Stamp, 1984; Richner et al., 1997) and the shoot (Lee et al., 2002). Genotypes differ strongly in photosynthesis at the threshold air temperatures of around 15 °C (Fracheboud et al., 1999; Lee et al., 2002). While genotypic variation in the leaf-tip appearance rate in response to soil temperature has been reported (Giauffret et al., 1995), there is no information about a comparable response of photosynthesis to soil temperatures. In an earlier study using 21 inbred lines Hund et al. (2007) found that among all studied root traits the length of the lateral roots on the primary root was strongest

Abbreviations: CrAx, crown axile root; DW, dry weight; PPFD, photosynthetic photon flux density; PrLat, primary lateral roots; SeLat, seminal lateral root; SPAD, chlorophyll content (Soil Plant Analysis Development); Φ_{PSII}, operating efficiency of photosystem II

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correlated with traits related to photosynthesis (SPAD, Φ_{PSII}) and to shoot dry weight. This was surprising, since lateral roots represent a comparably small portion of the root dry weight. For example, even for genotypes with a rather high proportion of thick lateral roots (74% of the overall root length) the weight amounted to only 20% of the root dry weight (Hund et al., 2004). Therefore, other mechanisms than just a "heavy plants have heavy roots" relationship must be responsible for this correlation. There are three hypotheses: (i) photosynthetic carbohydrate supply affects lateral root growth, (ii) larger root surface area enhances nutrient uptake and thus photosynthetic performance, and (iii) both are similarly affected by a third factor. Addressing the third hypothesis, a factor like membrane integrity could influence both photosynthesis and lateral root growth. However, it was not in the scope of the study to test this. The relationship between lateral root length and density on the one hand and carbohydrate supply on the other, was demonstrated using dark grown seedling and those with removed endosperm (Enns et al., 2006). Both shading and endosperm removal reduced lateral root growth and density, supporting the first hypothesis. On the other hand, Chassot and Richner (2002) reported that phosphorus concentration in the shoot at the early 2-leaf stage (V2) was mainly derived from the growth substrate, supporting the second hypothesis.

The objective of this study therefore was to evaluate (i) the degree of cold tolerance of root morphology as determined by the length of different root types and branching orders in comparison to photosynthetic performance of diverse genotypes, and (ii) the effect of small changes in topsoil temperature on these traits.

2. Materials and methods

2.1. Genotypes

A set of 14 inbred lines (Ac7643 (a), Ac7729/TZSRW (b), CM105 (c), *ETH*DeH1 (g), *ETH*DeH7 (h), *ETH*DeL3 (i), Lo 1016 (k), Lo 964 (l), S335 (m), D167 (n), D171 (o), *ETH*FlH1 (s), *ETH*FlL8 (u), and Z7f (v)) was analysed at different temperatures. The lines were selected out of a set of 21 inbred lines, based on the estimated photosynthesis per plant at 15/13 °C (Hund et al., 2007). The letters in brackets refer to the individual lines in Figs. 3 and 4. The lines (a) to (m) are dent kernel type, and lines (n) to (v) are flint kernel type. The letter labels used for the lines are consistent with those used earlier (Hund et al., 2007). The genotypes were derived from several breeders and from our own experimental breeding material (*ETH*).

2.2. Experimental conditions

The experiments were carried out in growth chambers (PGW36, Conviron, Winnipeg, Canada) at 12 h photo- and thermoperiod, 60/70% (day/night) relative air humidity, 500 $\mu mol\,m^{-2}\,s^{-1}$ photosynthetic photon flux density (PPFD). The growth substrate was a mixture of quartz sand (particle size 0.08–0.2 mm) and 5%, w/w vermiculite powder (Vermex Pulver E, Vermica AG, Bözen, Switzerland), with a volumetric nutrient solution content of 15%. The nutrient solution was a modified Hoagland solution containing 7.0 mM $Ca(NO_3)_2$, 2.0 mM $MgSO_4$, 1.0 mM H_3PO_4, 1.5 mM K_2SO_4, 0.16 mM FeNa-EDTA, 0.05 mM KCl, 18.0 μM $MnSO_4$, 12.0 μM H_3BO_3, 1.5 μM $ZnSO_4$, 0.6 μM $CuSO_4$, and 4.2 μM MoO_3. A pH of 7 was obtained by adding H_2SO_4 to the nutrient solution. Moist substrate was packed into PVC growth columns (5.6 cm diameter and 50 cm height) to a bulk density of 1.25 $Mg\,m^{-3}$; after planting, it was covered with a 1 cm isolation layer of Perlit (PePe® Pflanzen Perlit, Otto Hauenstein Samen AG, Rafz-Biberist-Landquart-Orbe, Switzerland).

Seeds were surface-sterilised for 12 min with 2.5% NaOCl, pre-germinated at 25 °C and planted at a depth of 2 cm. Once the coleoptile had reached a length of ∼1 cm, the growth columns were covered with aluminium foil in the main experiment to prevent warming of the upper zone of the substrate due to the light. In the first experiment (see below) some tubes were not covered, which was proven to raise the temperature in 5 cm substrate depth by 2 °C.

2.3. Temperature treatments

In a first set of experiments the low temperature was slightly varied by elevating the topsoil temperature to 17/13 °C compared to that of homogenous 15/13 °C and tested on the four genotypes CM105, Lo 1016, Lo 964, and D171. In a second set of experiments, the 14 inbred lines were evaluated at low 15/13 °C (day/night) and high 24/20 °C (day/night) air and soil temperature.

2.4. Measurements

Photosynthesis-related measurements were performed on the second leaf between the collar and the leaf tip. The operating efficiency of photosystem II (Φ_{PSII}) was measured at 380 $\mu mol\,m^{-2}\,s^{-1}$ PPFD with a pulse-amplitude modulated fluorometer (PAM-2000, Walz, Effeltrich, Germany) at leaf temperatures of 16 °C (low and high topsoil temperatures) or 24 °C (high overall temperatures). The chlorophyll content of the second and third leaf was measured with a SPAD-502 Chlorophyll Meter (Minolta Corporations, Ramsey, NJ, USA).

The leaf areas of the first, second, and partially developed successive leaves were measured with a leaf-area meter (LI-COR 3100, Lincoln, NE, USA).

Plants were harvested 29 days (low temperature, with or without elevated topsoil temperature) or 12 days (high temperature) after imbibition, when more than half of the plants had reached the 2-leaf (V2) stage. The stage was defined by the number of leaves with visible collars (Ritchie et al., 1992). The roots were removed from the growth columns, washed under pressurised tap water, and separated into primary, seminal, and crown roots. The axile roots, i.e. the main axes of the different root types, were counted and their length measured on a cm scale. For the digital measurement of the root morphology, the roots were cut and distributed evenly on a glass tray in a thin layer of water. The tray was placed on a flatbed scanner (Scanjet 4c, Hewlett Packard, CA, USA) to obtain 8-bit greyscale images (resolution 600 by

Table 1
Effect of a 2 °C change in topsoil temperature (measured at 5 cm depth) on the performance of four inbred lines, grown under controlled conditions until the 2-leaf stage

Treatment main effect	Plant DW (mg)	Leaf area (cm^2)	Lat. length (cm)	Ax. length (cm)	Lf/Rt (cm)	Pr. port. (%)	SPAD (units)	Φ_{PSII} (e^-/γ)[a]	SLA ($m^2 * kg^{-1}$)
Inbred line									
D171	358	27.2	380	83	0.064	80.7	36.2	0.498	32.2
CM105	159	25.4	59	150	0.136	32.2	17.7	0.146	40.3
Lo964	270	25.1	326	80	0.078	82.7	27.3	0.303	37.3
Lo1016	254	31.1	109	99	0.177	34.6	27.0	0.358	36.8
Standard error	19	1.9	28	9	0.015	4.0	1.2	0.029	2.0
Temperature									
15/13	224	23.2	180	86	0.122	58.2	25.6	0.255	36.2
17/13	297	31.1	256	120	0.104	56.9	28.5	0.397	37.1
Standard error	14	1.3	20	6	0.010	2.6	0.9	0.02	1.4
Anova									
Inbred line (I)	***	*	***	***	***	***	***	***	**
Temperature (*T*)	***	***	***	***	ns	ns	***	***	ns
I × T	ns	ns	ns	ns	ns	ns	***	***	*

Examined traits are: plant DW, leaf area, lateral root (Lat.) length, axile root (Ax.) length, leaf area/root length ratio (Lf/Rt), and the portion of the primary root length on the embryonic root system (Pr. port.).*, ***: comparison of line mean values significant at $P \leq 0.05$ and 0.001, respectively, ns = not significant.
[a] Electrons/photon.

600 dpi) and covered with a black box to obtain a uniform background. The root images were analysed with the digital image analysis programme RD (Root Detector, ETH Zurich, Switzerland) (Walter and Bürgi, 1996). The dry matter of the leaves, shoots and roots was determined separately after drying at 65 °C for 42 h.

2.5. Experimental design and statistics

The experimental design for the study with different topsoil temperatures was a split plot randomized complete block design with two growth chamber replications with four blocks. The main factor was inbred line, the sub-factor was topsoil temperature. The experimental design for the overall temperature differences was a randomised complete block design with two growth chamber replications for the cold treatment and one for the warm treatment. Each replication consisted of four blocks, each containing a whole set of genotypes. The experimental unit within block and replication was one growth column with one plant. The data were analysed using a linear mixed effect model fit by restricted maximum likelihood (REML) in the 'nlme' package of R 1.8.1 (Ihaka and Gentleman, 1996). A tolerance index for the overall temperature treatments was calculated as TI = (mean value cold/mean value warm × 100)-100. A hierarchical cluster analysis of the correlation distance matrix among $\log_2$-transformed TI values was performed using the 'hclust' function of the 'mva' package of R 1.6.2. According to the recommendations of Backhaus et al. (1994), two agglomeration methods were used successively, the single linkage method to detect outliners and Ward's minimum variance method for the final model. Simple Pearson correlation coefficients (r) were calculated between the traits using the means of the inbred lines. The significance of the correlation coefficient at $P \leq 0.05$, 0.01, and 0.001 is indicated as *, **, and ***, respectively.

3. Results

3.1. Response to slightly varied suboptimal topsoil temperatures

A set of four divergent inbred lines was studied with regard to their response to low temperature with just an additional small variation in still suboptimal topsoil temperatures. Significant differences among lines were found for all the measured traits (Table 1). Significant temperature effects were found for all traits except for the organisation of the root system, measured as the portion of the primary root on the embryonic root system and the leaf/root length ratio. At 15/13 °C, compared to 17/13 °C day/night, the plant growth was reduced significantly by 25–30%, depending on the trait. Genotypic differences in the degree of cold tolerance, measured by the genotype-by-temperature interaction, were found only for the SPAD values and Φ_{PSII}. The genotype performance with regard to these two traits is shown in Fig. 1. Line D171 was the

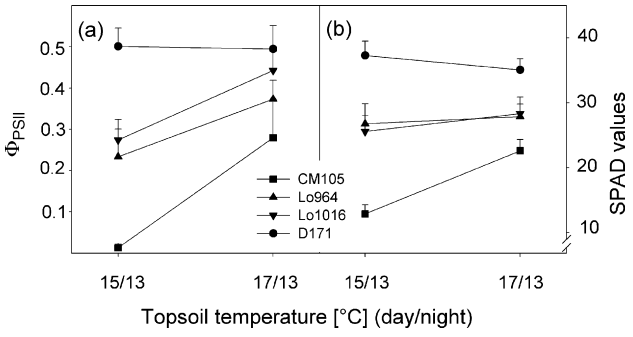

Fig. 1. Response of four inbred lines to a 2 °C change in topsoil temperatures (measured at 5 cm depth) for Φ_{PSII} (a) and SPAD values (b) showing highly significant genotype-by-temperature interaction (see Table 1): Vertical bars show the 95% confidence intervals.

most tolerant genotype of the four tested lines and did not respond within this small range of topsoil temperatures. In contrast, Φ_{PSII} of CM105 increased from close to zero to 0.27, and the SPAD values doubled by a 2 °C temperature increase.

3.2. Response to cold versus warm temperatures

The impact of two overall air and substrate temperatures (15/13 °C versus 24/20 °C (day/night)) on morpho-physiological traits was studied on 14 inbred lines. Differences in the response of the genotypes to temperature are expressed in a tolerance index (TI) (Table 2). The strongest mean reduction of the trait values was observed for the structural traits (root length and leaf area), while a strong mean increase was found for the leaf area/root length ratio (Table 2, Trait TI). Correlations between the line averages at low and high temperatures elucidate their stability across environments. High coefficients of determination (r^2) indicate stability across temperature treatments and, thus, constitutive expression among lines.

Significant correlations between the performance of the lines at high and low temperatures were observed for the portion of the primary root on the embryonic root system ($r^2 = 0.69$***) (Fig. 4f), the leaf area/root length ratio ($r^2 = 0.58$*), and the lateral root length ($r^2 = 0.40$*) (Table 2), indicating a low genotype-by-temperatures interaction. In contrast, coefficients of determination close to zero, observed for Φ_{PSII} and the axile root length, indicate a strong genotype-by-temperature interaction. According to the absolute mean values over all the tolerance indices of the lines (Table 2, line TI), CM105 responded most sensitively to temperature (mean change = 69%), while FlH1 responded least (mean change = 23%).

According to the hierarchical cluster analysis (Fig. 2a) of the tolerance index of root and shoot traits, two main clusters were distinguished. One cluster contained all the structural data and the other contained the two photosynthesis-related traits together with SeLat length. Low clustering height indicates that traits are similarly affected by the cold stress. Genotypes showing a strong decrease in Φ_{PSII} are also showing a strong decrease in SeLat length ($r = 0.68$) and genotypes with a strong decrease in leaf area showed also a strong decrease in SeAx length ($r = 0.85$). Line CM105 (c) was excluded from the correlation and cluster analysis, because of its extreme temperature-dependent change in performance (Fig. 3b).

3.3. Trait correlations with plant dry weight

Close correlation of SPAD values and Φ_{PSII} with the daily increment in plant DW at 15 °C disappeared when the lines were grown at 24 °C (Fig. 3a and b). This was due mainly to the overall strong performance of the lines with regard to SPAD values and Φ_{PSII} at 24 °C. Φ_{PSII} was on average 0.33 for the low and 0.57 for the high-temperature treatment. The greatest change in photosynthetic performance was again observed for line CM105(c). The SPAD values at 24 °C were about four times higher and Φ_{PSII} rose from 0.01 to 0.56. The daily leaf-area increment of the lines was closely related to the daily plant DW increment at

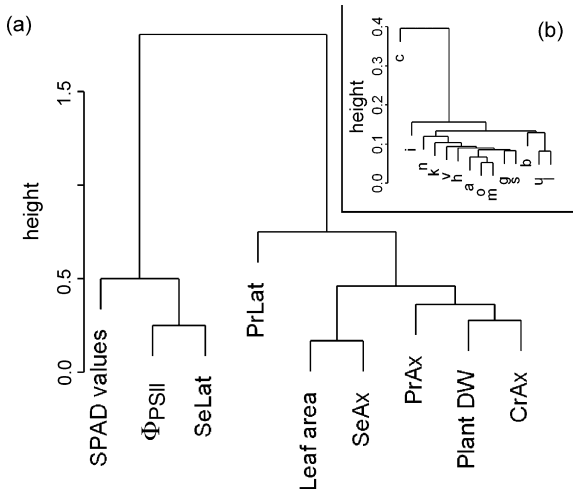

Fig. 2. Dendrograms obtained from hierarchical cluster analysis (HCA) on the log-transformed tolerance indices (TIs) of 14 inbred lines. HCA of traits (a) and genotypes (b) was performed on the correlation distance matrix using Ward's minimum variance (a) and the single linkage agglomeration method (b). Individual lines (in b) are identified by the letters (Table 2). The traits are: SPAD values; Φ_{PSII}; plant dry weight (DW); leaf area; length of the primary, seminal, and crown axile roots (Pr, Se, and CrAx, respectively); and of the primary and seminal lateral roots (Pr and SeLat, respectively). (TIs) for lengths, area, and weight were calculated on the basis of daily increments.

both temperatures (Fig. 3c). The line dependent leaf-area increment per unit DW was much higher in the warm than in the cold environment, as indicated by the higher slope of the regression (0.19 versus 0.05 $cm^2\ mg^{-1}$). A negative relationship observed between the leaf area/root length ratio and the plant DW at low temperatures was due mainly to the trait values of four lines; Lo1016(k), CM105(c), Ac7729/TZSRW(b), and FlL8(u). This negative relationship was not observed at high temperature. The root length can be divided according to the different root types (primary, seminal, and crown roots) or to the hierarchical order (axile versus lateral roots). The primary root made up the greatest portion (about 80%) of the lateral root length, while the seminal roots made up the greatest portion (about 50%) of the axile root length (data not shown). While at 15/13 °C the lateral root length was more closely related to plant DW ($r^2 = 0.75$*** versus 0.23), at 24/20 °C the axile root length was more closely related to the plant DW ($r^2 = 0.46$** versus 0.06). The length of the primary lateral roots (PrLat) and the portion of the primary root on the embryonic root system expressed constitutively (Fig. 4e and f) and were related to Φ_{PSII} and SPAD values at low but not at high temperature (Fig. 4a–d). Due to the constitutive expression of the primary root structure, its relationship to photosynthesis at low temperature was largely independent of the temperature at which the roots developed. The variability in primary root structure at 24/20 °C explained 16–24% of the variability in photosynthesis-related traits at 15/13 °C (Fig. 4). Thus, the relationship between the primary root structure and photosynthesis at low temperature must have causes other than the variability in autotrophic carbohydrates due to differences in photosynthetic performance of the lines. In contrast, the SeLat length changed with temperature in the same way as Φ_{PSII} and SPAD values (Fig. 2), which indicates that the same mechanisms

Table 2
Mean trait values of 14 inbred lines, grown at 24/20 °C (mean), tolerance index for trait reduction at 15/13 °C day/night (TI)

	Plant DW (mg d^{-1})		Leaf area (cm^2 d^{-1})		Lat. length (cm d^{-1})		Ax. length (cm d^{-1})		Lf/Rt (cm)		Φ_{PSII} (e$^-$/γ)[a]		Mean trait
Line	Mean	TI[b]	Mean	TI	Mean	TI	Mean	TI	Mean	TI	Mean	TI	|TI|[c]
Ac7643 (a)[d]	21.29	−54	3.36	−68	31.37	−70	15.14	−83	0.070	23	0.555	1	44
AC7729/TZSRW (b)	14.45	−42	2.42	−61	26.63	−83	11.54	−76	0.060	127	0.588	−54	66
CM105 (c)	17.60	−78	3.32	−79	11.51	−92	17.12	−75	0.104	45	0.574	−98	69
DeH1(g)	17.64	−5	2.55	−51	46.35	−59	12.75	−62	0.042	38	0.611	−21	34
DeH7 (h)	19.00	−42	3.09	−70	25.03	−71	16.93	−77	0.068	32	0.546	−30	49
DeL3 (i)	13.85	−23	2.53	−39	75.66	−74	9.04	−38	0.033	155	0.508	−48	57
Lo1016 (k)	16.02	−47	2.56	−61	11.53	−74	12.97	−76	0.092	89	0.599	−54	59
Lo964 (l)	14.43	−38	1.92	−62	41.31	−78	10.89	−81	0.036	70	0.622	−62	57
S335 (m)	23.54	−35	4.26	−62	63.37	−82	14.79	−76	0.052	123	0.567	−37	61
D167 (n)	12.77	−20	2.31	−63	40.72	−76	7.65	−70	0.044	81	0.530	−59	54
D171 (o)	15.12	−18	2.49	−68	45.44	−74	6.81	−66	0.045	42	0.535	−6	42
FlH1 (s)	15.33	5	2.44	−51	32.39	−36	11.01	−35	0.052	−17	0.574	−16	23
FlL8 (u)	15.65	−51	2.70	−63	15.83	−69	15.50	−76	0.072	79	0.564	−71	61
Z7 (v)	20.83	−18	3.90	−64	50.37	−73	14.32	−60	0.061	25	0.563	−24	42
Mean	16.96	−34	2.85	−62	36.97	−72	12.60	−70	0.059	65	0.57	−42	
Corr. warm/cold (r^2)	0.13		0.26		0.40*		0.03		0.58**		0.00		

Mean TI over traits (mean trait) and inbred lines (mean line), and correlation between trait values at 24/20 °C and 15/13 °C (corr warm/cold). Examined traits: plant dry weight (DW), Φ_{PSII}, leaf area, lateral root (lat.) length, axile root (ax.) length, and leaf area/root length ratio (Lf/Rt). Weight, area and length are given as increment per day (d). * and **: significant correlation at $P \leq 0.05$ and 0.01, respectively.

[a] Electrons/photon.

[b] Calculated from absolute values.

[c] *TI* = (trait value cold/trait value warm*100)−100 [%] were cold = 15/13 °C and warm = 25/20 °C day/night.

[d] Letter label to identify individual lines in Fig. 3.4 and 3.5. The lines (a) to (m) are dents, and lines (n) to (v) are flints.

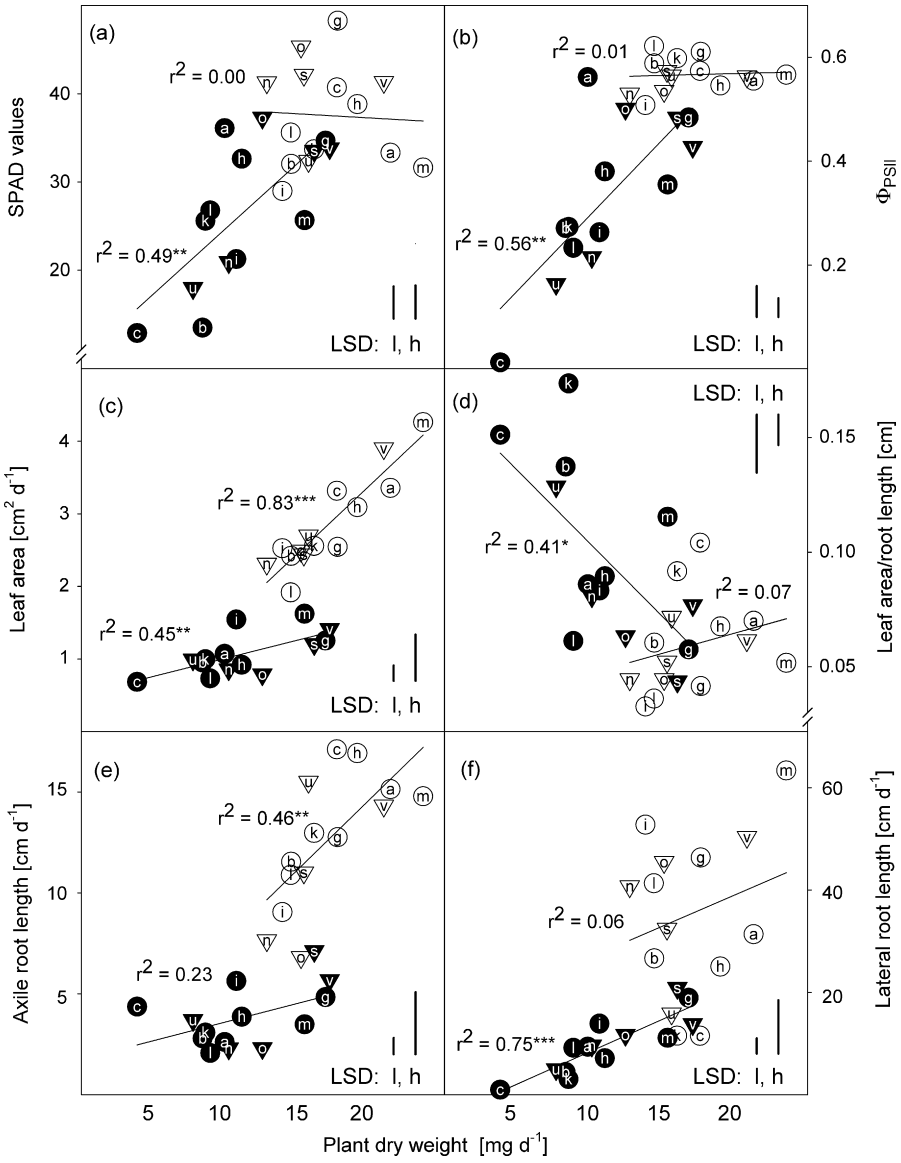

Fig. 3. Correlation between plant dry weight and leaf-chlorophyll content (a), operating efficiency of photosystem II (b), leaf area (c), leaf area/root length ratio (d), axile root length (e), and lateral root length (f). Length, area, and weight are expressed as daily increments. Flint (triangles) and dent (circles) lines were grown at 15/13 (closed symbols) or 24/20 °C (open symbols) day/night. Letters representing the individual lines are given in Table 2. Significance of the regression at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$ is indicated by *, **, and ***, respectively. Bars indicate Fisher's least significant difference (LSD) for the comparison of trait values at low (l) and high (h) temperature.

are involved in the cold tolerance of these traits. However, due to the large portion of the primary lateral roots of the embryonic root system, the overall lateral root length did not interact strongly with temperature (Table 2).

4. Discussion

4.1. Response to slightly varied suboptimal topsoil temperatures

About 2–3 °C lower soil temperatures in no-tillage compared with tillage systems decrease the performance of maize seedlings (Chassot et al., 2001). However, it is not clear which trait is most severely affected by the temperature. There are two contrasting hypotheses: (i) the temperature acts directly on the shoot development, and (ii) the weak plant performance is due to the indirect effect of poor root growth and, thus, of an insufficient supply of nutrient and water to the shoot. The slight temperature changes of 2–3 °C in the apex region significantly influenced the overall performance of the plant (Table 1), which is in agreement with previous studies on traits such as leaf area (Beauchamp and Lathwell, 1966; Giauffret et al., 1995; Stone et al., 1999) and root development (Stamp, 1984; Engels, 1994). Engels and Marschner (1990) reported that the shoot growth of maize seedlings at suboptimal root zone temperature was limited both by a reduced supply of nutrients through the roots and by the direct influence of temperature on the shoot meristem. In this study, significant genotype-by-temperature interactions,

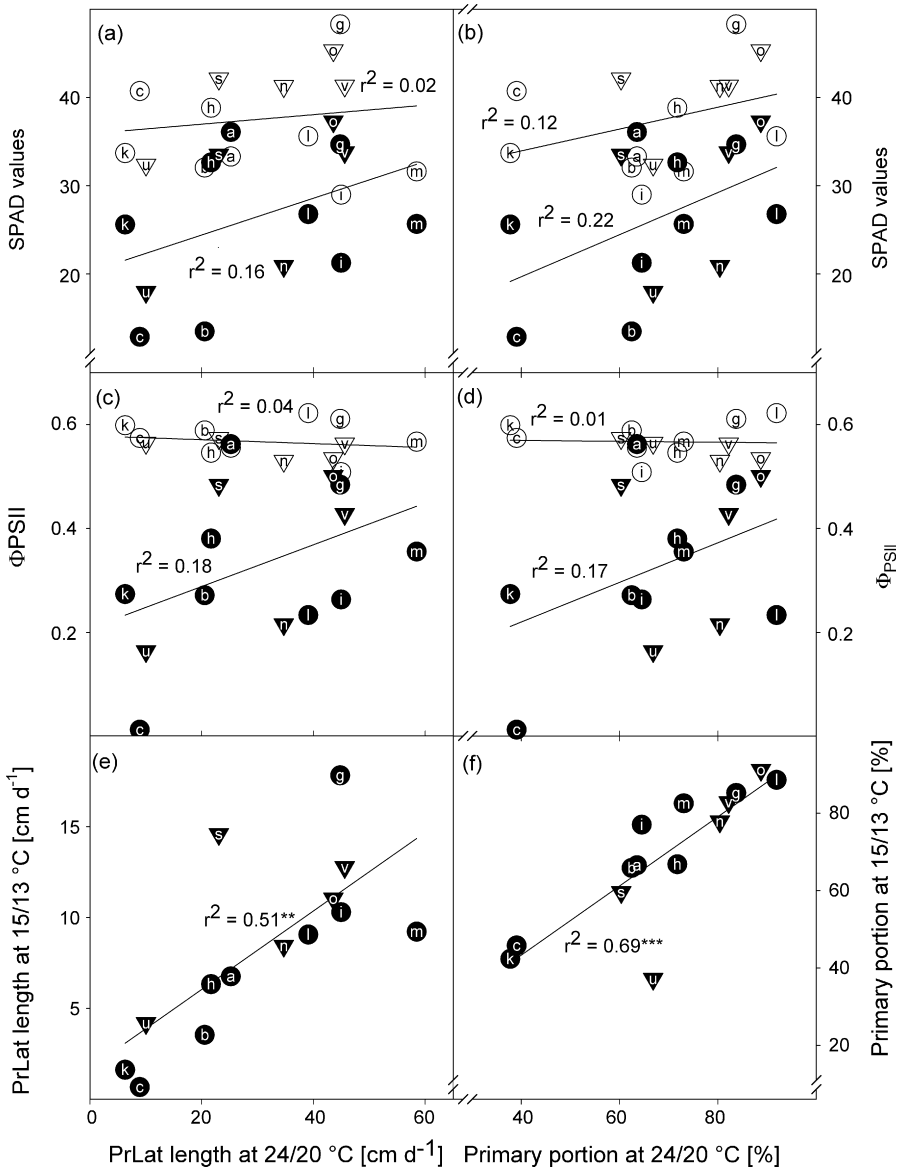

Fig. 4. Correlation between primary lateral root (PrLat) length (left) or the portion of the primary root on the embryonic root system (primary portion) (right) at 24/20 °C and leaf chlorophyll content (a, b) and the quantum yield of electron transport at PSII (c, d). Flint (triangles) and dent (circles) lines were grown at 15/13 (closed symbols) or 24/20 °C (open symbols) day/night. Correlation across temperatures (15/13 °C vs. 24/20 °C) for the PrLat length (e) and the primary portion (f). For further information see Fig. 3.

indicating differences in tolerance to low topsoil temperatures among the inbred lines, was observed only for SPAD values and Φ_{PSII}. The strong influence of the slight differences in topsoil temperature on photosynthesis indicates that the direct effect of temperature on the growing meristem of the shoot apex may play an important role in the development of a functional photosynthetic apparatus in maize. It is concluded that the stability of the photosynthetic apparatus is among the most important traits indicating the adaptation of maize to low topsoil temperature.

4.2. Response to cold versus warm temperatures

At overall temperature differences of 15/13 and 24/20 °C (day/night) compared to slightly varied suboptimal topsoil temperatures, the response of the lines with regard to Φ_{PSII} and SPAD values was more pronounced. While the lines differed strongly at low temperatures, the differences almost disappeared at high temperatures (Fig. 3). Since the performance of the lines at optimal temperatures was generally high, they can be characterized by the percentage of the decrease in photosynthetic performance at low temperatures compared to high temperatures. According to the small decrease in Φ_{PSII} the lines D171 and Ac7643 were most tolerant while of the lines CM105 and FlL8 with a big decrease in Φ_{PSII} were most sensitive (Table 1). At the threshold temperature for maintenance of well balanced functions of about 15 °C in maize lines, this strong genotype-by-temperature interaction is consistent with the literature (Fracheboud et al., 1999). The carbon partitioning between the roots and shoots at low temperature interfered with the photosynthetic performance: the leaf area/root length ratio increased

drastically for most of the lines which were cold sensitive with regard to photosynthesis (*c.f.* Fig. 3b and d). At low temperature, the lateral root length, the SPAD values, and Φ_{PSII} were closely correlated with the plant DW. This close relationship disappeared at high temperature (Fig. 3). In contrast, the correlation of the leaf area and the axile root length with the plant DW was closer at high than at low temperature. This may reflect different ecophysiological strategies of the genotypes. The ability to form a highly structured root system might be of major importance for growth at low temperature while it might not be significant at high temperature. In contrast, a large framework of axile roots ensures the fast exploration of a large soil volume and might be advantageous at optimal temperatures.

5. Conclusions

The data suggest that correlation between photosynthesis and the length of PrLat at low temperatures was not an effect of different carbohydrate supply by the shoot, but merely a constitutive, i.e. temperature independent, dominance of the PrLat roots, supporting the hypothesis of a better early nutrient supply. Therefore, the selection for a strong primary root, i.e. a high density of long lateral roots, holds promise for the improvement of early vigour under chilling conditions. However, at close-to-optimal conditions, the axile root development was of greater importance. Since early cold stress is restricted to a limited period of time, genotypes with a strong performance at both high and low temperature are desirable for vigorous early development. Therefore, it will be necessary to combine knowledge of root morphology under controlled conditions with field evaluations in order to determine an optimal balance between axile and lateral roots for a given target environment.

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