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Original scientific paper

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSE OF MAIZE SEEDLINGS TO CHILLING STRESS

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Although accompanied with adverse low temperatures, early maize sowing could be used to avoid drought during flowering and diminish yield losses. Herein, a small-scale experiment of low temperature stress (LTS) on maize lines L1 (tolerant), L2 (medium tolerant) and L3 (susceptible) is presented. Plants were grown in pots exposed to exterior suboptimal (March) and optimal (late April) temperatures until three leaf stage. Chlorophyll (CH), flavonoids (FL), anthocyanins (AN) and nitrogen balance (NBI) indices were measured using Dualex Scientific optical device. Growth parameters were also determined. Under LTS, number of plants was unchanged for L1 and halved for L2 and L3. Compared to L2 and L3, L1 had significantly higher ($p<0.05$) shoot fresh weight (0.649 g vs. 0.406 g and 0.303 g), AN (0.17 vs. 0.13) and FL (1.47 vs. 1.38 and 1.36). For recovery evaluation, plants were transplanted into the field. Transplanted stressed L1 plants showed the highest grain yield per plant (55g) in the field. Due to high correlations ($p<0.01$) between FL in three leaf stage and grain yield per plant, FL could be used as an indicator of plant recovery of maize genotypes exposed to LTS during early sowing.

Keywords: chlorophyll, growth, low temperature, phenolic compounds, plant recovery

INTRODUCTION

Climatic changes can cause severe summer droughts in temperate regions worldwide, often leading to serious maize yield losses. One way of surpassing this problem is earlier sowing to avoid negative effects of drought during the flowering period (KUCHARIK, 2006). However, temperatures in March and early April are very low for seed germination and early stages of plant development, contrary to the optimal conditions in the second half of April and the beginning of May. Reduction in growth and biomass production capacity can be found under suboptimal temperatures (10–15°C), while irreparable damage and loss of plants can occur under

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low temperatures (2–8°C) (reviewed in: LEIPNER and STAMP 2009). Moreover, cold intolerance of parental components can affect plants emergence, leading to flowering incompatibility or poor stand, thus causing reduction in maize hybrid seed production.

Maize is generally sensitive to low temperatures, but there is a considerable variation within its germplasm regarding cold sensitivity. Physiological research related to the mechanisms underlying maize cold sensitivity concerned mostly the photosynthetic apparatus (FOYER *et al*., 2002; JOŃCZYK *et al*., 2017), root functioning (HUND *et al*., 2004), water relations (JOŃCZYK *et al*., 2017), and transport processes (SOBKOWIAK *et al*., 2014). Several QTL and gene expression experiments were performed with the aim to provide a set of candidate genes for use in breeding for tolerant maize genotypes. It was shown that dozens of genes are involved in stress response through cell processes including photosynthesis, metabolism, regulation of gene expression and cell wall organization (SOBKOWIAK *et al*., 2014; MAO *et al*., 2017).

Herein, a small-scale experiment on three elite lines differing in low temperature tolerance is presented. The aim of the experiment was to 1) identify morphological and physiological traits at early seedlings stage involved in low temperature stress response, and 2) evaluate recovery of the stressed lines through grain yield achieved under field conditions.

MATERIALS AND METHODS

Plant material and experimental design

Elite maize lines, L1 (tolerant), L2 (medium tolerant) and L3 (susceptible) were tested for low temperature tolerance. L1 belongs to BSSS, while L2 and L3 belong to Lancaster heterotic groups. Considering maturity groups, L1 is FAO 650, L2 is FAO 550 and L3 is FAO 500. Moreover, L1 is flint, L2 dent and L3 semi-dent kernel type. The level of tolerance was noted according to the breeders′ field experience. Plants were grown in jiffy pots until three leaf stage, on a mixture of quartz sand (particle size 0.17–0.32 mm) and field soil (ratio 1:3). In order to comply with the environmental conditions, two experimental sets were laid out in a randomized complete block design (RCBD) with three replications and 40 seeds in jiffy pots each, placed outside and sheltered from the rain and watered after planting. Afterwards, plants were watered as needed.

The low temperature stress (LTS) experiment lasted from the 6th of March till the 11th of April. First ten days, daily temperatures were below 10°C (average of 7.6°C) and air humidity was 43.2%. From mid-March to the 11th of April, daily temperatures were between 10°C and 15°C (average of 13.3°C), with seven days between 16.8°C and 19.8°C and four days between 7.7°C and 9.8°C. The average air humidity was 29.2%. Plants started to emerge on the 27th of March. The third leaf of all three lines was fully developed on the 11th of April.

The optimal condition (OC) experiment lasted from the 26th of April till the 15th of May. The average temperature was 16.9°C and air humidity 34.8%. Temperatures were between 9.7°C and 14.9°C six days, and 14 days between 15.6°C and 20.8°C. Plants started to emerge on the 4th of May and the third leaf of all three lines was fully developed on the 15th of May.

Morphological and physiological traits measured

Number of plants (NP), leaf area per plant (LA) and physiological traits were measured on randomly chosen 10 plants per replication, the 1st, 4th and 7th day since more than half plants were at the third leaf stage until they had fully developed third leaf. Number of leaves, length and maximum width of each leaf were used for calculating leaf area per plant (cm^2) using the formula: Σ (length x maximum width x 0.75)/number of plants. Chlorophyll (CH), flavonoid (FL) and anthocyanin (AN) indices were determined using Dualex Scientific (Force-A, Orsay, France) optical leaf sensor. Nitrogen balance index (NBI), calculated as the ratio between chlorophyll and flavonoid content, was also recorded.

At three leaf stage, root and shoot characteristics were recorded on 15 plants per line (five per replication). After measuring root and shoot lengths (RL and SL), and their fresh weights (RFW and SFW), plant samples were oven-dried at 105°C for 24 h for root and shoot dry weight (RDW and SDW) measurement. Data on lengths were expressed in cm and on weights in g.

Plant recovery estimation

For plant recovery estimation, 30 plants per line (10 per replication) previously sown in jiffy pots under LTS and OC, were transplanted into the field on the 13th of April and 17th of May, respectively. Sowing/transplanting was done in three replications according to RCBD. As a control, lines were sown in the field on the 25th of April (regular sowing). Plants were harvested manually and dried to 14% of grain water content. Yield was expressed as average grain yield per plant (YP in g $plant^{-1}$).

Statistical analysis

For both OC and LTS, two-way analysis of variance (ANOVA) for RCBD was done for all traits using MSTAT-C software and Fisher's LSD at 0.05 probability level was performed. Student's *t*-test was done for morphological and physiological traits between OC and LTS, as well as between measurements for physiological traits. Pearson correlations were determined between seedlings morphological and physiological traits with YP, separately for OC and LTS.

RESULTS AND DISCUSSION

Maize seedlings are very sensitive to cold stress during germination, emergence and transition phase from heterotrophic to autotrophic growth (HUANG *et al*., 2013). In the experiment presented herein, plants started to emerge 12 days after the temperature rose above 10°C. Number of plants was significantly different ($p<0.01$) under OC and LTS for L2 (120 *vs* 68) and L3 (112 *vs* 72), opposite to L1 (112 plants in both OC and LTS). Germination at low temperatures requires phospholipid remodelling to prevent loss of membrane integrity and cold tolerant seeds accumulate polyunsaturated chains associated with lower electrolyte leakage (NOBLET et al., 2017). The unaltered NP of L1 indicated its tolerance to LTS during germination, possibly due to accumulation of polyunsaturated fatty acids. Also, previously in field noted different response to cold stress of L2 and L3 inbred lines most probably does not refer to exposure to low temperatures during germination, but during later phases of development.

ANOVA showed that genotype and replication had no impact on root and shoot traits under LTS, while genotype had significant impact on RFW ($p<0.05$), SL ($p<0.001$) and SDW ($p<0.05$) under OC (data not shown). Under OC, LA, RFW, SL and SDW were significantly different ($p<0.05$) between the genotypes (Table 1). However, significant difference between the lines was found only for SFW between L1 and L3 ($p<0.05$) under the stress, indicating the ability of the tolerant line to absorb more water and nutrients under LTC. Several QTLs for SFW at early growth stages under contrasting temperature conditions in the field were identified in PRESTERL *et a*l. (2007). Student's *t*-test revealed significant changes in all morphological traits but RFW, being more pronounced in stressed shoots (data not shown).

Table 1. Results of Fisher's LSD test for morphological and physiological traits under optimal and stress conditions

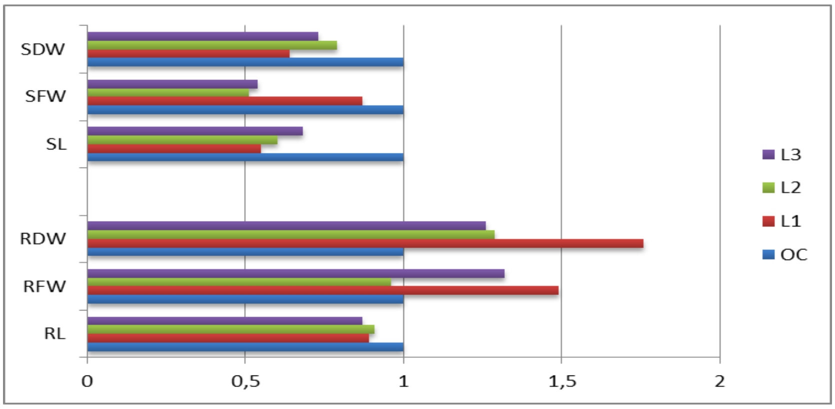
Trait	Optimal conditions				Low-temperature stress			
	L1	L2	L3	*LSD*	L1	L2	L3	*LSD*
Morphological traits								
LA	14.95a[1]	13.19b	10.23c	*1.57*	9.73 a	10.37a	9.00a	*1.95*
RL	23.59a	21.05a	20.32a	*7.18*	21.05a	20.09a	18.18a	*6.29*
RFW	0.507b	0.701a	0.503b	*0.176*	0.758a	0.676a	0.636a	*0.617*
RDW	0.030a	0.044a	0.035a	0.023	0.054a	0.057a	0.043a	*0.023*
SL	15.49a	12.69b	11.02c	*0.91*	8.48a	7.58a	7.27a	*2.64*
SFW	1.741a	0.789a	0.585a	*0.424*	0.649a	0.406ab	0.303b	*0.336*
SDW	0.102a	0.085a	0.062b	*0.023*	0.065a	0.068a	0.043a	*0.072*
Physiological traits								
FL	1.29a	1.15b	1.28a	*0.06*	1.47a	1.38b	1.36b	*0.07*
AN	0.14a	0.12b	0.12b	*0.009*	0.17a	0.13b	0.13b	*0.007*
CH	23.90b	26.52a	24.16b	*0.84*	23.19b	27.86a	26.94a	*2.073*
NBI	19.27b	23.62a	19.21b	*1.23*	16.08b	20.66a	20.4 a	*2.33*

LA – leaf area per plant (cm^2); RL – root length (cm); RFW – root fresh weight (g); RDW – root dry weight (g); SL – shoot length (cm); SFW – shoot fresh weight (g); SDW – shoot dry weight (g); FL – flavonoids; AN – anthocyanins; CH – chlorophyll; NBI – nitrogen balance index.

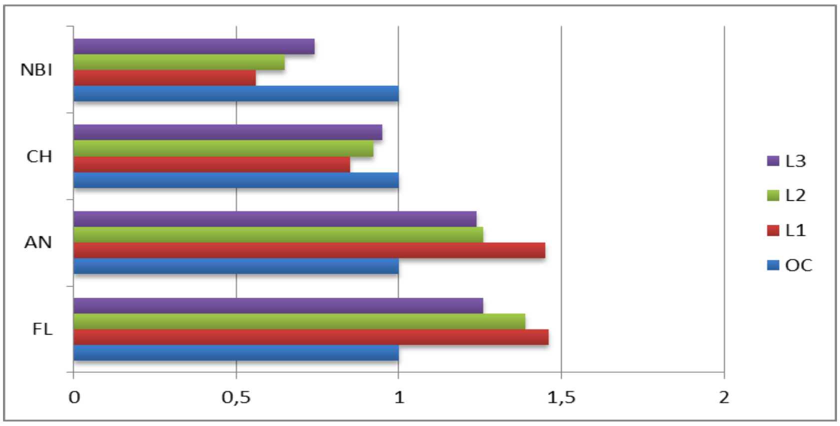
[1] – values with different letters in a row for different conditions are significantly different at $p<0.05$.

The level of changes of morphological traits under LTS is illustrated in Fig. 1a.

Analysis of variance for physiological traits revealed significant impact of genotype and measurement on all traits under both OC and LTC ($p<0.001$), except of measurement insignificance on CH under LTS (data not shown). Tolerant L1 had significantly higher content of pigments and lower CH and NBI ($p<0.05$) compared to L2 and L3 under LTC (Table 1). Student's *t*-test for these traits showed significant changes under LTS (data not shown), with the highest number of them found in the third measurement (fully developed third leaf) for all traits in L1, FL and NBI in L2 and NBI in L3 (Table 2). Thus, the number of significant changes increased with the time of exposure to the stress, primarily in the most tolerant L1 line. Similar results were found for chlorophyll fluorescence parameters in maize under cold conditions (RIVA-ROVEDA *et al*., 2016). The level of physiological changes under LTC is illustrated in



1a



1b

Figure 1. Percentage of changes of morphological (1a) and physiological traits in the third measurement (1b) under low-temperature stress compared to the optimal conditions in L1, L2 and L3. OC – values measured under optimal conditions given as 1 (100%). FL – flavonoids; AN – anthocyanins; CH – chlorophyll; NBI – nitrogen balance index. RL – root length (cm); RFW – root fresh weight (g); RDW – root dry weight (g); SL – shoot length (cm); SFW – shoot fresh weight (g); SDW – shoot dry weight (g)

Table 2. Significances of Student's t-test of physiological traits for measurements between optimal and low-temperature conditions

Genotype	L1			L2			L3		
Measurement	I	II	III	I	II	III	I	II	III
FL	ns	ns	*	ns	ns	*	ns	ns	ns
AN	ns	*	**	ns	ns	ns	ns	ns	ns
CH	ns	ns	*	ns	ns	ns	ns	ns	ns
NBI	**	ns	***	ns	ns	**	ns	ns	*

FL – flavonoids; AN – anthocyanins; CH – chlorophyll; NBI – nitrogen balance index. *,**,*** – significant at $p< 0.05$, 0.01 and 0.001, respectively; ns – non-significant.

In plants, LTS strongly increases flavonoids (KORN *et al*., 2008; BECKER *et al*., 2014) and differences found in FL between L1, L2 and L3 support its role in response to LTC. Since seedling leaf tissues are developmentally unable to synthesize structurally protective compounds in their cell walls, they often increase vacuolar solutes, like anthocyanin, to remain turgid under low water potential conditions (GOULD, 2004). Higher synthesis and vacuolar sequestration of anthocyanins as a considerable metabolic investment for plant cells, implies a more preserved overall status of cold tolerant L1 compared to L2 and L3 inbreds. This is opposite to RODRIGUEZ *et al*. (2014), where a susceptible line accumulated two times more anthocyanins under cold conditions. However, none of the QTLs referring to anthocyanins were identified in their work.

Chlorophyll content reflects plant photosynthesis efficiency and under suboptimal temperatures the photosynthetic capacity is low (ZAIDI *et al*., 2010). In the third measurement, decrease in CH under LTS was found in all three lines, but it was significant only in tolerant L1 (Table 2), the genotype with the highest anthocyanins accumulation. Similar results were reported in studies on a variety of plant species that significant decrease of photosynthetic pigments coincided simultaneously with an increase of anthocyanin biosynthesis, which is determined by inherited factors and enhanced by low temperature conditions (PIETRINI *et al*., 2002). Significant change in the third measurement in all lines was shown only by NBI. As leaf flavonoids can be considered as an indicator of N availability, NBI could relate to N status of the plant (CARTELAT *et al*., 2005). The influence of the stress on NBI was significant, indicating temperature effect on crop N status of maize seedlings.

After the pot experiment, plants were transplanted to the field to evaluate their recovery through YP. ANOVA showed that genotype ($p<0.05$), sowing/transplanting dates ($p<0.001$) and genotype x sowing/transplanting dates ($p<0.05$) had significant impact on YP (data not shown). The highest YP was achieved in regular sowing (Table 3).

The tolerant L1 had the highest YP after the stress treatment (B). However, YP was significantly reduced in L1 and L3 in plants transplanted after the OC (C), indicating their susceptibility to drought, which occurred during flowering and early grain filling in 2017 (http://www.hidmet.gov.rs/podaci/meteorologija/latin/l2017.pdf). Significant correlations were found between YP and physiological traits (Table 4), opposite to insignificant correlations between YP and morphological traits (data not presented).

Table 3. LSD for mean values of the lines, treatments (sowing/transplanting dates) and line x treatment interaction of morphological parameters and grain yield calculated from the two-way ANOVA

	YP (g $plant^{-1}$)
Genotype (G)	
L1	55.74a
L2	56.17a
L3	41.10b
$LSD_{0.05}$	*10.46*
Sowing/Transplanting date (STD)	
regular sowing (A)	65.40a
transplanting after LTS (B)	47.68b
transplanting after OC (C)	39.93b
$LSD_{0.05}$	10.46
G x STD	
L1xA	83.20a
L1xB	55.03bc
L1xC	29.00d
L2xA	60.40bc
L2xB	44.60cd
L2xC	63.50b
L3xA	52.60bc
L3xB	43.40cd
L3xC	27.30d
$LSD_{0.05}$	18.17

Values with different letters in a column for each section are significantly different at $p<0.05$.

Table 4. Pearson's correlations for YP and physiological parameters for three measurements (I, II and III) under optimal and low-temperature stress conditions

	Optimal conditions				Low-temperature stress			
	YP:FL	YP:AN	YP:CH	YP:NBI	YP:FL	YP:AN	YP:CH	YP:NBI
I	-0.843**	-0.208	0.563	0.820**	0.735*	0.560	-0.537	-0.783*
II	-0.882**	-0.301	0.605	0.868**	0.801**	0.310	-0.060	-0.335
III	-0.643	-0.105	0.250	0.857**	0.759**	0.445	-0.302	-0.481

YP – yield per plant (g); FL – flavonoids; AN – anthocyanins; CH – chlorophyll; NBI – nitrogen balance index. *,** – significant at $p< 0.05$ and 0.01, respectively.

Although drought effect hindered the precise estimation of recovery, significant and positive correlations between FL in early phases of development under the stress and YP were found in all three measurements, indicating that FL observed at three leaf stage could be used for predicting recovery of a maize genotype exposed to low temperatures during germination, emergence, heterotrophic growth phase and/or transition to autotrophic growth phase.

CONCLUSIONS

Unchanged number of plants under both optimal and cold conditions observed in tolerant inbred, could suggest high relevance of this indicator for cold tolerance stress. Among the morphological traits evaluated under cold stress, shoot fresh weight contributed the most to separation of cold tolerant line from medium and susceptible ones. Due to observed high correlation with grain yield per plant, flavonoid index measured at three leaf developmental stage could be used as a potent indicator of plant recovery for maize inbreds exposed to low temperature stress during early sowing.

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MORFOLOŠKI I FIZIOLOŠKI ODGOVOR KUKURUZA U RANIM FAZAMA RAZVIĆA NA STRES NISKIM TEMEPERATURAMA

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Izvod

Ranom setvom kukuruza se može izbeći efekat suše u fazi cvetanja i tako preduprediti smanjenje prinosa uprkos nepovoljnim temperaturama u tom periodu. U ovom istraživanju prezentovani su rezultati efekta niskih temperatura na tri linije kukuruza: L1 (tolerantna), L2 (srednje osetljiva) i L3 (osetljiva). Biljke su gajene do faze trećeg lista u saksijama izloženim suboptimalnim (mart) i optimalnim (april) spoljnim temperaturama. Sadržaj hlorofila, flavonoida i antocijana kao i *nitrogen balance index* (NBI) su mereni korišćenjem uređaja Dualex Scientific (Force-A, Orsay, France). Takođe, mereni su i parametri rasta. U poređenju sa L2 i L3, L1 je imao značajno veću ($p<0.05$) svežu masu nadzemnog dela biljke (0.649 g vs. 0.406 g i 0.303 g), antocijana (0.17 vs. 0.13) i flavonoida (1.47 vs. 1.38 i 1.36). Biljke su presađene u polje radi procene oporavka. Presađene biljke genotipa L1 su pokazale najveći prinos po biljci u polju (55g). S obzirom na visoku korelaciju između sadržaja flavonoida u fazi trećeg lista i prinosa po biljci ($p<0.01$), flavonoidi mogu biti korišćeni kao indikator oporavka biljke kukuruza izloženih niskim temperaturama u fazi rane setve.

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