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C3 and C4 photosynthetic performance in cold stress

C3 i C4 fotosintetska učinkovitost u uvjetima niskih temperatura

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ABSTRACT

Early sowing to avoid summer stresses poses a significant risk of cold stress for warm-season crops such as soybean and maize in Croatia. To address the aforementioned issues, a study was conducted to investigate the effects of low-temperature treatment on early growth of soybean (C3) and maize (C4), highlighting the differences in photosynthetic responses and biomass changes. The findings revealed a significant low-temperature effect on the minimum fluorescence (F_0), the maximum fluorescence (F_m) and the maximum quantum yield of PSII photochemistry (F_v/F_m), with notable distinctions between C3 and C4 photosynthesis. Low temperatures had the most pronounced effect on the average performance index of overall photochemistry (PI_{total}). The PI_{total} of C4 maize was 41.5%, 34.4% and 42.9% higher than the PI_{total} of C3 soybean at the first (D1), second (D2) and third (D3) measurements under optimal environmental conditions. The difference increased to 140.3%, 104.8% and 52% in D1, D2 and D3 of the imposed low-temperature treatment, respectively. Maize exhibited greater PSII damage at low temperatures, indicating a weaker coping and repair mechanism compared to soybean. Soybean demonstrated a better adaptive response by reducing overall photosynthetic efficiency. The better adaptation to low temperatures in soybean compared to maize was evidenced by a lower loss of water tissue and dry matter.

Keywords: PI_{total}, photosynthesis, soybean, maize, climate change

SAŽETAK

Rana sjetva kako bi se izbjegli ljetni stresovi predstavlja značajan rizik od negativnog učinka niskih temperatura za proljetne usjeve poput soje i kukuruza u Hrvatskoj. Kako bi se dao odgovor na navedeni problem, ispitan je učinak tretmana niskim temperaturama na rani rast soje (C3) i kukuruza (C4), ističući razlike u fotosintetskim odgovorima i promjenama biomase. Rezultati su pokazali značajan utjecaj niskih temperatura na minimalnu fluorescenciju (F_0), maksimalnu fluorescenciju (F_m) i maksimalni kvantni prinos fotokemije fotosustava II (F_v/F_m), s primjetnim razlikama između C3 i C4 fotosinteze. Niske temperature najviše su utjecale na indeks ukupne fotosintetske učinkovitosti (PI_{total}). Vrijednosti parametra PI_{total} kod C4 kukuruza bile su za 41,5%, 34,4% i 42,9% veće od vrijednosti kod C3 soje u prvom (D1), drugom (D2) i trećem (D3) mjerenju u optimalnim okolišnim uvjetima. Razlika se povećala na 140,3%, 104,8% i 52% u D1, D2 i D3 nakon tretmana niskim temperaturama. Kukuruz je pokazao veće oštećenje fotosustava II pri niskim temperaturama, ukazujući na slabiji mehanizam prilagodbe i popravka u usporedbi sa sojom. Soja je pokazala bolju prilagodbu niskim temperaturama smanjenjem ukupne fotosintetske učinkovitosti. Bolja prilagodba soje na niske temperature u usporedbi s kukuruzom dokazana je manjim gubitkom vode i suhe tvari.

Ključne riječi: PI_{total}, fotosinteza, soja, kukuruz, klimatske promjene

INTRODUCTION

Early sowing dates in spring-sown crops represent a strategy often used in Europe to avoid water and heat stresses during the most susceptible growth periods by shifting them later in the cycle (Pardo et al., 2015; Schoving et al., 2022). This practice will become even more common as the occurrence of droughts and heat waves is expected to rise in southern and continental Europe in the near future (Allen et al., 2018; Rojas et al., 2019). Among warm-season crops soybean and maize are the most significant. They are also the most significant agricultural products in Croatia overall. In the period from 2015 to 2021, soybean accounted for more than 50% of total oilseed production in Croatia, expressed quantitatively, while maize made up more than 60% of total grain production. In 2021, Croatia's share of EU soybean production was 9.2%, and 3.2% for maize, compared with less than 1% for all other crops (Zeleno izvješće, 2021). Furthermore, both crops were among the most important agricultural and food export products in 2020 (Zeleno izvješće, 2020).

Although there is a tendency of early sowing to avoid stresses later in the crop season, temperatures below the optimum during early spring can pose significant challenges to agricultural production. In plant physiology, low temperatures are non-optimal temperatures above the freezing point (Theocharis et al., 2012), i.e. temperatures that are sufficiently low to suppress plant growth without ceasing cellular functions (Balestrasse et al., 2010), and trigger the processes of cold stress response, collectively referred to as cold or chilling acclimation (Kleine et al., 2021, Hussain et al., 2023). Cold stress can adversely affect seed germination and plant establishment (Lamichhane et al., 2020a; Lamichhane et al., 2020b), reduce the uptake of water and nutrients, resulting in cell desiccation and starvation (Miura and Tada, 2014), alter the fluidity of cellular membranes and cause their damage (Xing and Rajashekar, 2001), reduce the rate of metabolic processes (Chinnusamy et al., 2007), reduce cellular respiration (Lee et al., 1997), increase accumulation of osmolytes and cryoprotectants (Bhandari and Nayyar, 2014) and promote generation of reactive oxygen species (Lee et al., 1997; Nouri et al., 2011; Abdel Latef and Chaoxing, 2011). Low temperatures causing stress have a detrimental effect on symbiotic nitrogen fixation (Zhang et al., 1995) and photosynthesis, especially in warm-season crops (Allen and Ort, 2001; Mehrotra et al., 2020; Gao et al., 2022; Hussain et al., 2023).

Negative effects of different abiotic and biotic stressors altering the plant's morpho-physiological status are reflected in plant biomass reduction (Galić et al., 2019; Luo et al., 2021; McMillan et al., 2022). Fresh and dry weight of plant biomass are determined destructively. To increase the efficiency of plant evaluation for stress tolerance and accelerate the decision-making, reliable parameters that indicate stress and can be measured more easily are needed. Among the biochemical processes that are affected by abiotic and biotic stressors, photosynthesis is the most easily quantified by non-destructive methods. It is, therefore, often used for rapid determination of plant response under drought stress, high-temperature stress, cold stress, salt stress, etc. (Umar and Siddiqui 2018; Galić et al., 2019; He et al., 2019; Zhao et al., 2020; Mehmood et al., 2021; Markulj Kulundžić et al., 2022). Low temperatures impair photosynthesis by affecting the stomata's pore diameter, the biosynthesis of photosynthetic pigments, the activity of photosystems I and II, the Calvin cycle-related enzymatic activity, and CO_2 acquisition and fixation (Hajihashemi et al., 2018). It is known that response to cold stress differs between plants with C3 photosynthetic pathway and plants with C4 photosynthetic pathway. The C4 pathway of maize is efficient in reducing photorespiration and water loss, making it suitable for hot and dry conditions, while the C3 pathway of soybean is less effective in minimizing water loss and photorespiration, making it adaptable to temperate climates (Ward et al., 1999). Nevertheless, both crops are highly sensitive to low-temperature conditions, particularly during early growth stages, with growth and development impairment and potential yield loss that can occur when temperatures fall below 15 °C for soybean

(Gass et al., 1996) and below 12 °C for maize (Yun et al., 2022). It is reported that C4 photosynthetic pathway plants, such as maize, have greater photosynthetic efficiency at optimal temperatures (20-25 °C), but they are considered to have lower photosynthetic efficiency at low temperatures and lower freezing resistance compared to C3 photosynthetic pathway plants such as soybean (Ehleringer and Björkman, 1977; Long, 1983; Liu and Osborne, 2008; Ibrahim et al., 2008; Osborne et al., 2008).

Photosynthetic performance as well as plants' response to environmental stressors and their ability to adapt are quantified and evaluated with non-invasive chlorophyll fluorescence (ChlF measurement (Strasser et al., 1995), which can therefore be used in screening for stress-tolerant genotypes (Strasser et al., 2004; Kalaji et al., 2016). Among the parameters resulting from the ChlF measurement, the maximum quantum yield of photosystem II (F_v/F_m) has been commonly used to quantify photosynthetic activity under cold stress (He et al., 2019; Aazami et al., 2021; He et al., 2021; Mehmood et al., 2021; Hussain et al., 2023). Minimal (F_0) and maximal fluorescence (F_m) are considered to be good indicators for estimating stress-induced damage to the plant photosynthetic system as well (Roháček et al., 2008; Roosta and Sajjadinia, 2010; Murchie and Lawson, 2013; Aazami et al., 2021). Nevertheless, the performance index for energy conservation from exciton to the reduction of PSI end acceptors (PI_{total}) is known to have higher sensitivity to unfavorable environmental changes compared to other fluorescence parameters (Oukarroum et al., 2007; Tsimilli-Michael and Strasser, 2008; Yusuf et al., 2010; Pavlović et al., 2019; Mihaljević et al., 2021).

In future climate scenarios, the successful cultivation of crops hinges on a comprehensive grasp of how plants react to their environment. This will allow us to proactively address requirements related to breeding, crop management, and cultivar selection. Understanding how soybean with C3 photosynthetic pathway and maize with C4 photosynthetic pathway respond to cold stress in their early developmental stages is essential for breeding cold-tolerant crops, addressing the climate change challenges and aiding global food security. Therefore, the aims of this study were: i) to investigate the impact of low temperatures on the photosynthetic apparatus in the early vegetative development of C3 (soybean) and C4 (maize) model plants; ii) to evaluate the differences in the cold stress response of the photosynthetic apparatus and biomass reduction between C3 and C4 model plants.

MATERIAL AND METHODS

Plant material

The plant material included 12 0–I maturity group (MG) soybean cultivars (C3 photosynthetic pathway type) and 12 FAO 500 and 600 maize parental lines (C4 photosynthetic pathway type), previously not tested for cold stress tolerance, all developed and in the property of Agricultural Institute Osijek (AIO, Osijek, Croatia). The 0-I MG soybean genotypes were chosen as it is the most common MG for soybean grown in the area in which the experiment was conducted. Furthermore, FAO 500 and 600 maize genotypes were chosen to represent common parental components for creating hybrids grown in the area in which the experiment was conducted.

Growth conditions

The plant experiment was set up in an Aralab Bio single-tier plant growth chamber (Fitoclima 10.000 HP, Aralab, Rio de Mouro, Portugal) in fully controlled ambient conditions. The experiment consisted of the control group with optimal ambient conditions (C) and a low-temperature treatment group (T) in four replications for each genotype per treatment and five plants per replication. Control and cold-stressed plants were grown in two separate time sets. The C conditions for day/night were: 16/8 h photoperiod, 25/18 °C temperature, 70/90% relative humidity (RH), 300 µmol m^2/s light intensity. The T conditions were the same as for control until the full development of the first trifoliate for soybean (25 days after sowing – DAS; V2; Fehr and Caviness, 1977) and the first real leaf for maize (17 DAS), at which point low-temperature treatment was induced and kept for three days. Low-temperature treatment conditions for day/night were: 16/8 h photoperiod, 10/5 °C temperature, 70/90% RH, 300 µmol m^2/s light intensity.

The plants were grown in trays (510 x 350 x 200 mm). Each tray was filled with 5.5 kg of soil (pH ($CaCl_3$) = 5.7, N (NH_4^+ + NO_3^-) = 70 mg/L, P (P_2O_5) = 50 mg/L, K (K_2O) = 90 mg/L, EC = 40 mS/m) and divided into 12 rows with 3 and 2 planting spaces placed interchangeably for soybean, and 7 rows with 5 planting spaces for maize. There were six genotypes per tray, two trays per replication and eight trays per treatment for both crops. The order of the genotypes per replication was randomised and trays were randomly shuffled in the growth chamber every day before the lights turned on.

The available water holding capacity (AWC) of the soil used in this experiment was determined by weighing the air-dried soil within a pot with drainage holes, saturating the soil with water and leaving it to drain for 7 hours, at which point the pot was weighed again. The difference between the air-dried soil and the soil saturated with water was considered as 100% AWC. All plants were watered with tap water continuously, every other day. The amount of water was determined by weighing the pots every day to determine the amount of water consumed by the plants, i.e., the amount of water that needed to be compensated by watering. Reference trays planted with soybean and maize were used so that the increasing plant biomass during the plant growth could be taken into consideration.

Photosynthetic performance

The ChlF was determined on 2 plants per genotype in each repetition by the saturation pulse method (Kalaji et al., 2014) on a middle leaflet of the last fully developed trifoliate for soybean and the first developed leaf from the top for maize with Fluorpen FP 110 (Photon Systems Instruments, Drásov, Czech Republic). The measurements were taken in both, C and T for three consecutive days, starting when the first soybean trifoliate and the second maize leaf were fully developed, i.e. at 26 DAS for soybean and 18 DAS for maize. In T, the measurements were taken 24 (D1), 48 (D2) and 72 (D3) hours after the onset of the low-temperature treatment. Before measuring, the leaves were adapted to dark with the light exclusion clips for a minimum of 30 minutes. The data recorded by measuring ChlF, expressed in relative units, were used for calculating the parameters according to Strasser et al. (2004) and Yusuf et al. (2010; Table 1).

Biomass determination

The aboveground parts of three equally developed plants per genotype in each replication for the control and treated groups were harvested and weighed on a precise four-decimal scale to obtain fresh weight (FW, g). Samples were oven-dried at 80 °C and weighed again to obtain dry weight (DW, g). Dry matter content (DMC, %) was calculated as (DW/FW) x 100.

Statistical analyses

Analysis of variance (ANOVA) was performed for four chosen ChlF parameters (F_0, F_v, F_v/F_m, PI_{total}). Genotype data were pooled separately for soybean and maize, and factorial ANOVA including photosynthetic pathway type (PPT), time of measurement (M) and treatment (T) as sources of variation was followed by the Bonferroni posthoc test, which corrects the false positives possibly occurring in multiple comparisons. The differences between the control and low-temperature treatment per individual crop in biomass parameters (FW, DW and DMC) were tested with Student's t-test ($P < 0.05$). The relationships between ChlF and biomass parameters for soybean and maize were evaluated based on Pearson's correlation coefficients. The strength of the correlation was determined based on the scale reported by Evans (1996). All statistical analyses were conducted in Statistica 12.0 software (StatSoft Inc., 2013).

RESULTS

The research conducted on soybean (C3 photosynthetic pathway type) and maize (C4 photosynthetic pathway type) in control with optimal ambient conditions (C) and low-temperature treatment (T) in the early stages of plant development included four ChlF parameters (F_0, F_v, F_v/F_m, PI_{total}) and three biomass parameters (FW, DW, DMC).

Table 1. Chlorophyll *a* fluorescence parameters: recorded and calculated values, definitions and equations according to Strasser et al. (2004) and Yusuf et al. (2010)

The recorded chlorophyll a fluorescence parameters	
F_0	Fluorescence intensity at 50 µs – step O; minimum fluorescence
F_m	Maximum fluorescence – step P
The chlorophyll *a* fluorescence parameters calculated from the recorded data	
F_v / F_m $(TR_0 / ABS) = 1 – (F_0 / F_m)$	The maximum quantum yield of PSII photochemistry
$PI_{total} = PI_{ABS} \text{ x } RE_0 / ET_0 / (1 – RE_0 / ET_0)$	Performance index for energy conservation from exciton to the reduction of PSI end acceptors

Almost all sources of variation, including most interactions, proved significant for tested ChlF and biomass parameters (Table 2 and 3), indicating low temperatures caused stress in both crops with noticeable differences in stress response between C3 and C4 photosynthetic pathway types.

Significant differences for all tested ChlF parameters were determined between C and T per PPT for each measurement (D1-D3) of soybean and maize. As a result of low-temperature treatment, C3 soybean F_0 initially dropped below control values, but then it started to increase, surpassing the control values in the third measurement (Figure 1a). The initial decrease of C3 soybean F_m was followed by a slight increase, but the values remained well below the control values for D2 and D3 (Figure 1b). The same was true for C3 soybean F_v/F_m (Figure 1c), while PI_{total} initially decreased and remained at the same level until the end of the low-temperature treatment (Figure 1d). In contrast, C4 maize F_0 increased initially as a result of low-temperature treatment and it remained above the control values at D2 and D3 (Figure 1a). Maize F_m reacted differently from soybean as well, i.e. it continued to decrease with the increasing length of the low-temperature treatment (Figure 1b). Maize F_v/F_m (Figure 1c) and PI_{total} (Figure 1d) had the same trend.

The average F_0 exhibited the smallest differences between C and T in both tested crop species (8.07%, 1.73%, 7.96% in D1, D2 and D3 for soybean with 0.73% average increase for all three times of measurement; 18.93%, 12.71%, 6.1% in D1, D2 and D3 for maize with 12.47% average increase for all three times of measurement).

Table 2. Mean squares and degrees of freedom (df) for different sources of variation from the three-way ANOVA for chosen chlorophyll *a* fluorescence parameters (F_0, F_m, F_v/F_m, PI_{total}) tested in soybean and maize. The descriptions for the chlorophyll *a* fluorescence parameters can be found in Table 1.

Source of variation	Mean squares				
	df	F_0	F_m	F_v/F_m	PI_{total}
Photosynthetic pathway type (PPT)	1	$1.15x10^{7\,*}$	$6.86x10^{8\,*}$	0.075^{*}	319.9^{*}
Time of measurement (D)	2	$1.62x10^{7\,*}$	$1.09x10^{7\,ns}$	0.108^{*}	9.414^{*}
Treatment (T)	1	$5.92x10^{7\,*}$	$7.89x10^{10\,*}$	18.38^{*}	1885.2^{*}
PPT*D	2	$1.39x10^{6\,ns}$	$5.84x10^{8\,*}$	0.342^{*}	12.95^{*}
PPT*T	1	$4.72x10^{7\,*}$	$1.57x10^{9\,*}$	0.101^{*}	16.21^{*}
D*T	2	$4.21x10^{5\,ns}$	$3.97x10^{8\,*}$	0.086^{*}	29.08^{*}
PPT*D*T	2	$2.17x10^{7\,*}$	$1.4x10^{9\,*}$	0.260^{*}	15.76^{*}

* – Significant ($P < 0.05$); ^{ns} – Non significant ($P > 0.05$)

Table 3. Mean squares and degrees of freedom (df) for different sources of variation from the two-way ANOVA for fresh weight (FW, g), dry weight (DW, g), and dry matter content (DMC, %) tested in soybean and maize.

Source of variation	Mean squares			
	df	FW	DW	DMC
Photosynthetic pathway type (PPT)	1	2724.7*	794.240*	3025.04*
Treatment (T)	1	6845.9*	34.476*	25.52*
PPT*T	1	1808.0*	0.207^{ns}	25.63*

* – Significant (*P* < 0.05); ^{ns} – Non significant (*P* > 0.05)

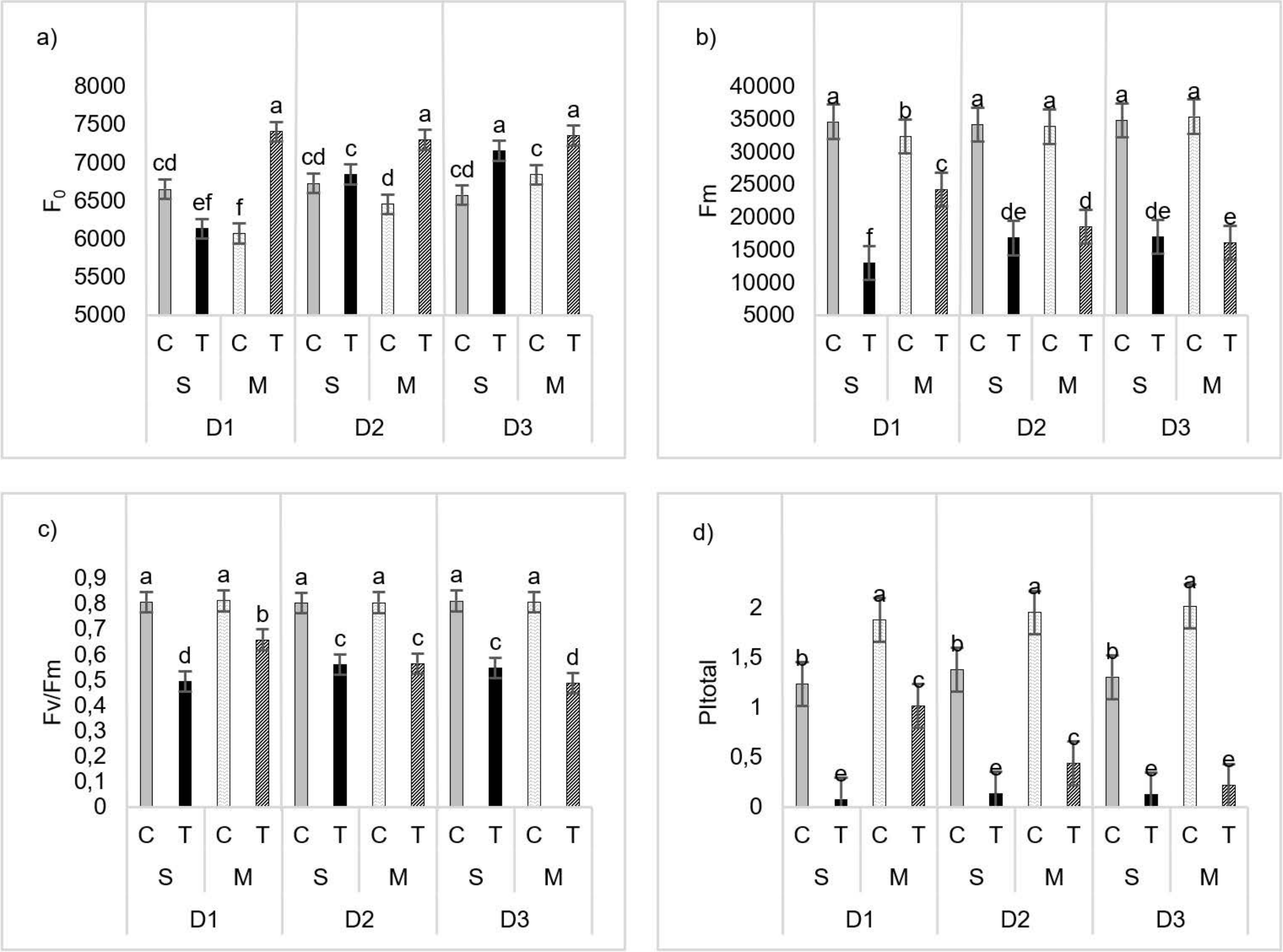

Figure 1. (a) Minimal fluorescence (F_0), (b) maximal fluorescence (F_m), (c) maximum quantum yield of photosystem II (F_v/F_m), and (d) performance index for energy conservation from exciton to the reduction of PSI end acceptors (PI_{total}) measured during three consecutive days (D1, D2, D3) on C3 soybean (S) and C4 maize (M) plants grown in control with optimal ambient conditions (C) and low-temperature treatment (T). Results are expressed as the mean value ± the standard error, and values with the same letter in the superscript are not significantly different (ANOVA, Bonferroni test, *P* < 0.05).

The differences between average CF_m and TF_m were 89.24%, 67.2%, 69.78% on D1, D2 and D3 for soybean and 28.69%, 57.71%, 75.69% on D1, D2 and D3 for maize. The F_m average decrease for all three times of measurement was 75.07% for soybean and 53.22% for maize. The differences between average CF_v/F_m and TF_v/F_m were 47%, 35.55%, 38.82% on D1, D2 and D3 for soybean and 20.81%, 34.91%, 48.05% on D1, D2 and D3 for maize. The F_v/F_m average decrease for all three times of measurement was 40.37 % for soybean and 33.98% for maize. The differences between average CPI_{total} and TPI_{total} were 150%, 163.53%, 164.15% on D1, D2 and D3 for soybean and 60.73%, 126%, 160.87% on D1, D2 and D3 for maize. The average PI_{total} decrease for all three times of measurement was 159.37% for soybean and 111.36% for maize.

In optimal ambient conditions (C), only PI_{total} differed significantly ($P < 0.05$) between PPT (soybean and maize) for all three times of measurement (D1-D3), and it was higher for maize than for soybean (Figure 1). C4 maize PI_{total} was higher than C3 soybean PI_{total} by 41.5%, 34.4% and 42.9% in CD1, CD2 and CD3, respectively. Although the values significantly ($P < 0.05$) differed between soybean and maize at the beginning of the low-temperature treatment (T D1-D2 for F_0, F_m, PI_{total}; D1 for F_v/F_m) for all tested ChlF parameters, they equalized at the end for all except F_v/F_m. Initial (D1) differences between soybean and maize were the highest for TPI_{total} (140.3%), but they decreased with the length of the imposed low-temperature stress (104.8% in D2, 52% in D3). In general, the differences between C and T were larger for C3 soybean in D1 and D2 compared to C4 maize for all ChlF parameters except F_0, but in D3 the trend was the opposite.

If considering biomass parameters (Figure 2), both, the average CFW for C3 soybean (45.95 g) and C4 maize (44.55 g) were significantly greater ($P < 0.05$) than the respective average TFW values (40.14 g, 26.45 g). The average CDW for soybean (7.3 g) and maize (3.3 g) were significantly greater ($P < 0.05$) than the respective average TDW (6.6 g, 2.4 g). Furthermore, the difference between soybean's average CFW and TFW (13.5%) was less than for maize (50.9%). The same was true for DW, as the difference between soybean's average CDW and TDW (11.3%) was less than the difference for maize (32.1%). On the other hand, the average CDMC and TDMC for soybean were the same (16.3%), but CDMC for maize (7.6%) was less than TDMC (9.1%), with the difference of 17.6%.

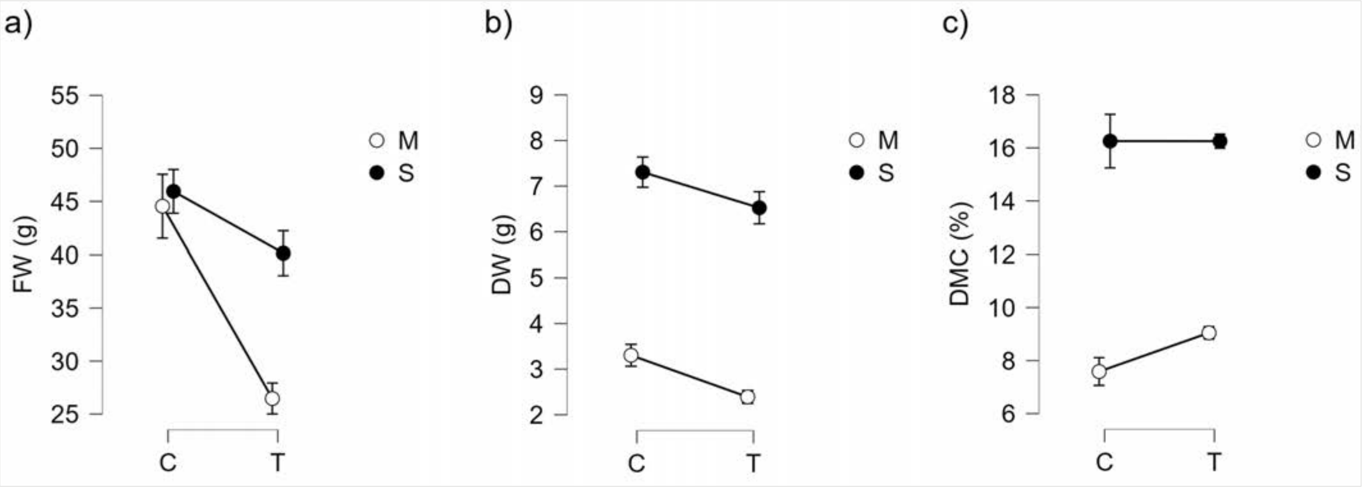

Figure 2. (a) Fresh weight (FW), (b) dry weight (DW), and (c) dry matter content (DMC) measured for C3 soybean (S) and C4 maize (M) plants grown in control with optimal ambient conditions (C) and low-temperature treatment (T). Results are expressed as the mean value ± standard error.

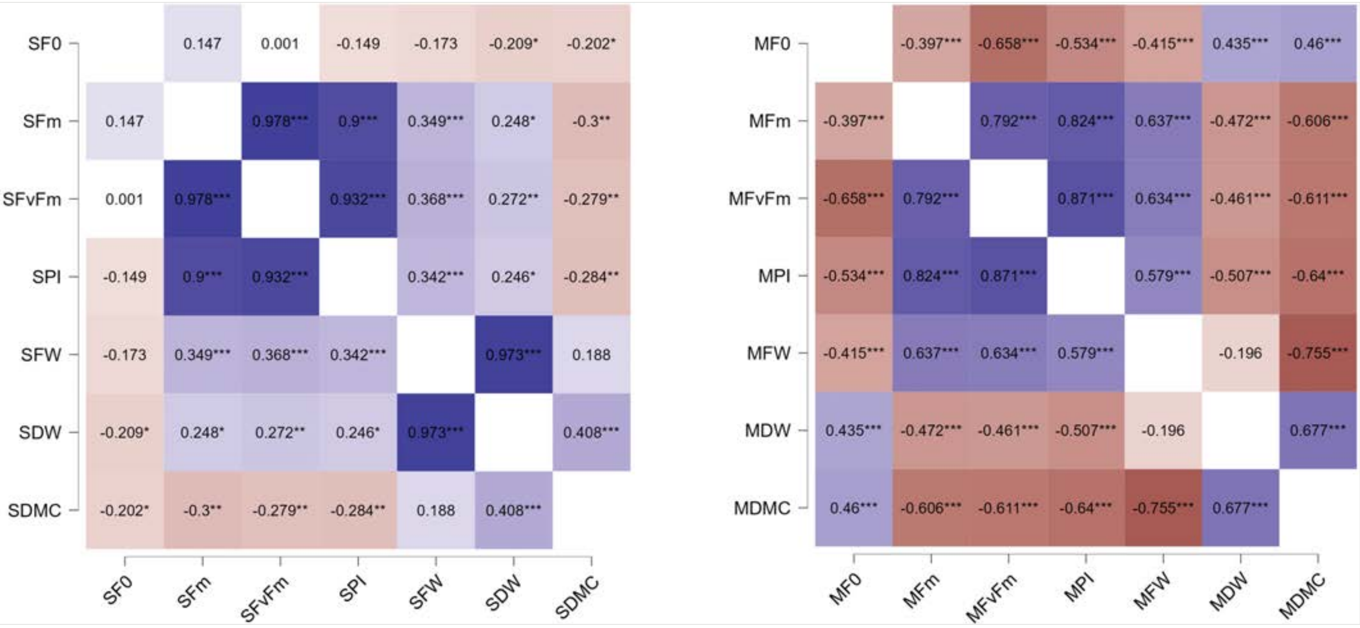

Figure 3. Heatmaps of correlation between the average chlorophyll a fluorescence parameters (F_0, F_m, F_v/F_m, PI_{total} – descriptions can be found in Table 1) and the average biomass parameters (fresh weight – FW; dry weight – DW; dry matter content – DMC) for C3 soybean (S, left) and C4 maize (M, right). Pearson's coefficient of correlation (r) is noted inside the quadrants. Statistical significance is indicated with * (*P* < 0.05), ** (*P* < 0.01) and *** (*P* < 0.001).

Among all average parameters, the strongest significant positive correlation for soybean was expectedly found between F_m, F_v/F_m and PI_{total} (r ≥ 0.9), and between DW and FW (r = 0.973). FW and DW were in a weak significant positive correlation with F_m, F_v/F_m and PI_{total} (r = 0.246-0.368). On the other hand, DMC was in a weak but negative correlation with the same parameters and F_0 was in weak significant negative correlation with DW and DMC (Figure 3).

In comparison, maize had F_0 in a significant moderate positive correlation with DW and DMC (r = 0.435, 0.46, respectively), but in a significant weak to moderate negative correlation with all other parameters. DW was in a significant moderate negative correlation with F_m, F_v/F_m and PI_{total} (r ≥ -0.461), DMC was in a significant moderate to strong negative correlation (r ≥ - 0.61) while FW was in a significant moderate to strong positive correlation (r ≥ 0.579) with the same parameters. The correlation between DMC and FW was significantly strongly negative (r = -0.755), and between DMC and DW significantly strongly positive (r = 0.677). The correlation between F_m, F_v/F_m and PI_{total} was less strong than for soybean (r ≥ 0.792).

DISCUSSION

Avoiding summer water and heat stresses from occurring during the most susceptible growth periods of warm-season crops by early sowing poses a considerable risk of cold stress. As the occurrence of droughts and heat waves is expected to rise in southern and continental Europe in the near future (Allen et al., 2018; Rojas et al., 2019), early sowing could become a common mitigating strategy. Below optimal temperatures that characterize early sowing emphasize the need for cold-tolerant spring-sown crop genotypes.

Low spring temperatures have a negative impact on many different physiological processes in plants. Among others, they have a detrimental effect on photosynthesis, especially in warm-season crops (Allen and Ort, 2001; Mehrotra et al., 2020; Gao et al., 2022; Hussain et al., 2023). Low daily temperatures have the potential to induce chronic photoinhibition of PSII, partly because lowering the temperature usually reduces reaction rates and can, therefore, limit the sinks for the absorbed excitation energy (light), particularly CO_2 fixation and photorespiration. Smaller sinks for absorbed excitation energy increase the potential for oxidative damage to

PSII (Huner et al., 1998; Allen and Ort, 2001). Although C4 photosynthetic pathway plants, such as maize, have greater photosynthetic efficiency compared to C3 plants at optimal temperatures (20-25 °C), at low temperatures, where photorespiration, which accounts for a significant fraction of assimilated carbon, is limited, the energetic requirements of the C4 cycle make C4 photosynthetic pathway less efficient than the C3 photosynthetic pathway (Ehleringer and Björkman, 1977; Liu and Osborne, 2008). Therefore, cold acclimation may be costlier and less effective in C4 than in C3 plants (Sage and McKown, 2006; Osborne et al., 2008). This was evident in the here presented research as C4 maize had a higher performance index of overall photochemistry (PI_{total}) values than C3 soybean in optimal conditions, but PI_{total} decreased more after 72 hours of low-temperature treatment in C4 maize than in C3 soybean. Furthermore, C4 maize PI_{total} changed gradually as a result of low-temperature treatment, while C3 soybeans' remained stable after the initial more substantial change. Nevertheless, a substantial PI_{total} reduction in both tested crops indicated an overall downregulation of PSII-related specific energy fluxes and efficiencies as a physiological response to stress (Živčák et al., 2017; Umar and Siddiqui, 2018; Liang et al., 2019).

The initial substantial drop in PI_{total}, as witnessed for C3 soybean, may suggest that the stress has caused irreversible damage to chlorophyll molecules, reaction centres, or other critical components involved in the conversion of light energy to chemical energy, affecting the electron transport chain within both PSII and PSI. It may also suggest a chronic stress response with the sustained low PI_{total} as an adaptive response to the continued stress, resulting in a reduced overall photosynthetic efficiency. According to Liu and Osborne (2008), a coordinated decrease in the PSII electron flux and CO_2 assimilation is an avoidance mechanism for an increase in the excitation pressure and PSII chilling-induced photodamage. This acclimation response, suggesting the effective non-photochemical quenching mechanisms and protective down-regulation of PSII efficiency, is common in C3 species (Sage and Kubien, 2007). On the other hand, C4 maize showed a continuous decrease of PI_{total} with the duration of stress, suggesting a sustained and progressive impact of the stress on the efficiency of the photosynthetic apparatus, i.e. a progressive breakdown of chlorophyll molecules, reaction centres, or other essential elements involved in the conversion of light energy to chemical energy. This may indicate that the repair mechanisms may be insufficient to counteract the ongoing damage, leading to a continuous decline in photosynthetic efficiency. A similar response to low temperatures was previously reported by Ibrahim et al. (2008) and Osborne et al. (2008), concluding that cold acclimation is negligible in C4 compared to C3 subspecies of African grass (*Alloteropsis semialata*). Furthermore, Sage and McKowan (2006) indicate that certain features unique to C4 photosynthesis may reduce the potential for phenotypic plasticity and photosynthetic acclimation to environmental change relative to what is possible with C3 photosynthesis.

The reduction of F_v/F_m, a widely accepted index for plant cold stress tolerance evaluation (Ehlert and Hincha, 2008; He et al., 2019; Gao et al., 2022), can indicate inactivation of RCs (Mathur et al., 2011; Liang et al., 2019), redox state imbalance, ROS overproduction and PSII photoinhibition (Harvaux and Kloppstech, 2001; Adams et al., 2013; Hussain et al., 2023). The reduction of F_v/F_m is considered to be among the immediate physiological responses of plants to low temperatures (Gao et al., 2022). Furthermore, Hussain et al. (2023) determined a significant negative correlation between F_v/F_m and leaf injury levels under cold stress, meaning cellular injuries and even death can be expected in leaf tissues with determined F_v/F_m reduction. As F_v/F_m is usually approximately 0.85 for most healthy plant species (Kalaji and Guo, 2008), an acute F_v/F_m decrease determined in the here presented research suggests that plants were, in fact, under stress (Roháček et al., 2008; Roosta and Sajjadinia, 2010; Murchie and Lawson, 2013). F_v/F_m decrease as a result of low temperatures was previously reported for both soybean (Van Heerden and Krüger, 2000; Yildiztugay et al., 2017; Hussain et al., 2023) and maize (Savitch et al., 2009; Sobkowiak et al., 2016; Bilska-Kos et al., 2018; Li et al., 2018; Li et al., 2019; Salesse-Smith et al., 2020). Although low temperatures caused a F_v/F_m decrease compared to the control for both tested crops, C4 maize F_v/F_m continuously decreased with the length of the imposed stress, while C3 soybeans had a more substantial drop after 24 hours of low temperatures, after which it bounced back slightly and remained at the similar level. As with the PI_{total}, the C3 soybean's F_v/F_m values indicate a slight recovery of PSII efficiency, suggesting that the photosynthetic system has acclimated or adjusted to the stress to some extent. The slight recovery may indicate a dynamic stress response where the organism attempts to mitigate the impact of the stress over time. On the other hand, a continuous decrease in the C4 maize's F_v/F_m typically indicates progressive damage to the PSII.

The decrease of F_v/F_m commonly implies an F_0 increase, F_m decrease or both (Allen and Ort, 2001; Guo et al., 2018; Meng and Sui, 2019; Faseela et al. 2020). F_0 has been widely used as a thermo-injury index (Feng et al., 2014), but both parameters are known to be indicative of different abiotic stresses. For example, F_0 increased in high light, NaCl, polyethylene glycol (PEG)-induced osmotic stress in rice (*Oryza sativa* L.) seedlings but decreased in heavy metal stress conditions (Faseela et al., 2020). In the same research, F_m decreased as a result of all previously mentioned abiotic stressors, except NaCl in which it remained the same. F_0 increased, and F_m decreased as a result of short-term (5-30 minute) heat stress (40 °C) in senescent leaves of *Vitis vinifera* L. cv. Red Globe (Zhang et al., 2018) and in winter wheat as a result of different levels of heat stresses (Brestič et al., 2012). Under cold stress, F_0 was increased in three grapevine cultivars (Aazami et al., 2021), basil (*Ocimum basilicum* L.) and lettuce (Lactuca sativa; Roosta and Sajjadinia, 2010). F_m decreased under cold stress in three grapevine cultivars (Aazami et al., 2021) and tomatoes (*Solanum lycopersicum*; Roosta and Sajjadinia, 2010). Although, on average, F_0 increased as a result of low-temperature treatment compared to control for both tested crops in the here presented research, C3 soybean and C4 maize had a different initial F_0 reaction: after 24 hours of low temperatures, F_0 increased in maize, but it decreased in soybean. On average, the F_0 increase was larger for maize than for soybeans. F_0 changes as a result of stress depend on the dominant factor between the energy dissipation and the PSII damage (Guo et al., 2018). An increase in F_0 may suggest destruction or irreversible inactivation of the RCs in PSII (Krause, 1988; Faseela et al., 2020), accumulation of ROS and alterations in the electron transport processes that lead to impaired efficiency or functionality of PSII and a decrease in the photosynthetic capacity of the organism (Aazami et al., 2021). On the other hand, a reduction in F_0 indicates nonphotochemical energy dissipation of antenna pigments in PSII (Krause 1988; Müller et al., 2001; Tietz et al., 2017). Therefore, a larger average increase in F_0 can indicate greater PSII damage as a result of low temperatures in maize compared to soybean, i.e. a better coping mechanism mitigating excessive excitation energy in soybean compared to maize (Guo et al., 2018). A significant F_m decrease that occurred in the here presented research for both tested crops is considered to be caused by a decrease in the activity of the water-degrading enzyme complex as well as the electron transfer cycle in/or around PSII (Roosta and Sajjadinia, 2010; Murchie and Lawson, 2013). It is a sign of the inhibition of electron transfer rates from the reaction centre to the quinone pool that produces an excess of excitation energy, which gets dissipated as heat (Brestič et al., 2012; Faseela et al., 2020).

Cold stress is known to disrupt root water uptake and cause imbalanced water relations, resulting in tissue dehydration (Aroca et al., 2012, Nayyar and Chander, 2004, Yildiztugay et al., 2017). It has been recorded that plants adapted to colder climates, such as plants native to high latitude and altitude areas, can extract water from soils near the freezing point, whereas species growing at lower latitudes often struggle below 10 °C (Larcher 2003). Reduced water uptake at low temperatures can be due to increased water viscosity and decreased hydraulic conductivity of root cell membranes (Baxter, 2014). Disturbed water relations negatively affect the uptake and transport of nutrients across plant tissue, disrupting the metabolic processes and affecting the synthesis of key molecules such as proteins, carbohydrates, and lipids (Nezhadahmadi et al., 2013). Furthermore, plant dehydration induces stomatal closure leading to lower CO_2 availability and a decline in photosynthesis rate (Rosales et al., 2012; Mahdieh et al., 2015). The lower rate of photosynthesis results in decreased carbon assimilation, and lower dry matter accumulation, i.e. it reduces biomass accumulation, plant growth and, eventually, the yield (Kingston-Smith et al., 1997). According to the results of the here presented research, C4 maize had a substantial fresh weight loss. Although dry weight decreased as well, the dry matter content increased, indicating that the weight reduction is primarily due to a reduced tissue water content. On the other hand, C3 soybean lost less fresh and dry weight than C4 maize, and its dry matter content remained the same. Given the results of the here presented research and previous investigations of the effects of cold stress in plants, it can be argued that soybean had a more efficient cold acclimation compared to maize, as it was able to maintain the balance between tissue water and dry matter content by adjusting photosynthetic and metabolic processes leading to lower dry matter accumulation reduction.

CONCLUSION

According to the results, low-temperature treatment in the early vegetative development of C3 soybean and C4 maize had a negative effect on photosynthesis, reducing PSII and overall photosynthetic efficiency.

C3 soybean and C4 maize differed in their photosynthetic apparatus response to low-temperature treatment. Results indicated a greater PSII damage caused by low temperatures in maize compared to soybean, i.e. a better coping mechanism mitigating excessive excitation energy in soybean compared to maize. A better adaptive response to the continued stress in soybean was evident as a reduced overall photosynthetic efficiency, i.e. an avoidance mechanism for an increase in the excitation pressure and PSII chilling-induced photodamage. Maize, on the other hand, had a continuous decrease in the efficiency of the photosynthetic apparatus with the duration of stress, suggesting that the repair mechanisms may be insufficient to counteract the ongoing damage. Furthermore, C4 maize had a more substantial loss of dry matter content as well as tissue dehydration compared to C3 soybean indicating that soybean had a more efficient cold acclimation.

The presented study is a part of ongoing research aiming to identify parental material that could be included in breeding programs aimed at developing low-temperature tolerant soybean and maize genotypes, ensuring optimal development earlier than conventional sowing dates. Therefore, the next steps will include determining the differences between individual soybean and maize genotypes and investigating the low-temperature priming effect and stress recovery.

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