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Thermal stability changes of photosynthesis during osmotic and salt stress in wheat varieties cultivated in Central Europe and Mediterranean North Africa

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Abstract

The thermal stability of photosynthetic apparatus under osmotic/salt stress was examined in wheat cultivars grown under different climatic conditions. The thermostability of nonstressed plants did not differ significantly from each other and it was not improved by osmotic treatment in the absence of light. In contrast, the salt stress resulted in better thermostability. This was also manifested in the temperature dependence of maximal quantum yield of PSII photochemistry. The temperature dependence of steady-state fluorescence and other photosynthetic parameters indicated a moderate reduction in thermal sensitivity of photosynthesis in well-watered plants which was further enhanced by osmotic, but even more by salt treatment. It seems likely that the osmotic stress-induced thermal stability increase of PSII occurs only in energized thylakoids. The temperature dependence of quantum yield of regulated energy dissipation seems to suggest that the secondary effects of lumen pH might have a role in the protective mechanisms concerning these stresses, but salt stress can also affect thermal stability in other ways as well.

Keywords: chlorophyll fluorescence; osmotic stress, photosynthesis; salt stress; thermal tolerance; wheat.

Introduction

Water deficit, salt stress, and high temperature often limit plant growth and crop production (Wang *et al*. 2018) by impairing photosynthesis (Ashraf and Harris 2013) which is the key process for energy transformation, thus growth, development and productivity (Yang *et al*. 2020, 2021; Lu *et al*. 2023, Zahra *et al*. 2023, Wang *et al*. 2024). Photosynthetic electron transport is considered a high temperature-sensitive process, especially the efficiency of electron flow at the acceptor and donor side of PSII (Pshybytko *et al*. 2008, Jat *et al*. 2024, Moloi *et al*. 2025).

Highlights

- Osmotic and salt stress enhances the thermal stability of photosynthesis
- Water deficit-induced PSII heat stability increase happens only in the presence of light
- Effects of low lumen pH may be important in protection against simultaneous stresses

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Abbreviations: AL – actinic light; F_0 – initial chlorophyll fluorescence determined in the dark-adapted state; F_m – maximum chlorophyll fluorescence determined in the dark-adapted state; F_m' – maximal fluorescence determined in the light-adapted state; F_s – steady-state fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; FTC – fluorescence (F_0, F_s) temperature curve; NPQ – nonphotochemical quenching of chlorophyll fluorescence; P_N – net assimilation rate; P_{Nmax} – maximum net assimilation rate; *Tc* – critical temperature for photochemical damage; Tc_0 – critical temperature of control (well-watered) plants; Tc_1 – critical temperature of plants treated with 21% PEG and 300 mM NaCl; Tc_1–Tc_0 – phenotypic plasticity to high temperature; Tc_{200}, Tc_{1000} – critical temperature for photochemical damage determined by the F_sTC at 200 and 1,000 µmol(photon) m^{-2} s^{-1} actinic light (AL) intensity; Tc_{dark} – critical temperature for photochemical damage determined by the F_0TC; Φ_{NO} – quantum yield of nonregulated energy dissipation; Φ_{NPQ} – quantum yield of regulated energy dissipation; Φ_{PSII} – effective quantum yield of PSII photochemistry.
Conflict of interest: The authors declare that they have no conflict of interest.

High-temperature stress-induced disorganisation of the oxygen-evolving complex (Vani *et al*. 2001, Shanker *et al*. 2022) can be one of the main reasons for the disruption of the donor side while the inability to transfer electrons from Q_A to Q_B results in the acceptor side limitation above the optimum temperature (Allakhverdiev *et al*. 2008). The degradation of the D1 protein by high temperature, as well as the disorganization and increased permeability of the thylakoid membrane, also lead to the disturbance of the photochemical processes (Havaux *et al.* 1996, Yamane *et al.* 1997, Vani *et al.* 2001). The high temperature-induced damages and the structural stability of the thylakoid membrane have often been tested by the heat responses of the initial fluorescence level (F_0) (Schreiber and Berry 1977, Schreiber and Bilger 1987). Rising in F_0 can be caused by the detachment of light-harvesting protein complexes (LHCII) from the PSII cores (Yamane *et al*. 1997) and/or by the accumulation of the reduced Q_A molecules (Kouřil *et al*. 2004). The thermal sensitivity of PSII can be examined by the determination of the *T*c (critical temperature) point based on F_0 (initial chlorophyll fluorescence) and F_s (steady-state fluorescence) *vs*. *T* (FTC, Nauš *et al.* 1992) curves. In this context, the fluorescence rise in FTC curves is also attributed to the reversed electron donation between Q_A and Q_B or the light-induced Q_A reduction (Kouřil *et al*. 2004). The critical temperature for PSII inactivation and disorganization of thylakoid membranes is indicated by the sharp rise in F_0 of the heated sample (Havaux 1992, Hill *et al*. 2009).

The thermal tolerance of photosynthetic apparatus may be influenced by additional environmental stress factors such as light (Molnár *et al*. 1998), water deficit, and/or salinity (Lu and Zhang 1999, Dulai *et al.* 2006, Yan *et al*. 2012, Jiang *et al*. 2025). The effects of water deficit and salt stress on photosynthesis may be quite varied. Based on these observations, inhibition of photosynthesis could be primarily attributed to stomatal limitation or nonstomatal disturbance (Centritto *et al*. 2003, Medrano *et al*. 2003, Dulai *et al*. 2014, Szopkó *et al*. 2017, dos Santos *et al*. 2022, Bellasio 2025). The latter may be associated with altered PSII functions, such as poor quantum efficiency of PSII or the over-reduction of the linear electron transport chain, leading to oxidative damage resulting in reduced PSII activity (Smirnoff 1993, Flexas *et al*. 2006, Kalaji *et al*. 2011, Stefanov *et al*. 2024). In contrast, others did not observe significant changes in the maximal quantum yield of PSII photochemistry indicating no considerable PSII damage during a period of osmotic or salt stresses (Dulai *et al*. 2014, Szopkó *et al*. 2017). CO_2 assimilation is more sensitive to water deficit and salt stress than electron transport processes around PSII (Darkó *et al*. 2015) resulting in oxidative damage by the over-reduction of the photosynthetic electron transport chain (Asada 2006). Under these circumstances, the downregulation of PSII by light-induced nonphotochemical quenching (NPQ) may be essential to avoid photooxidative damage (Demmig-Adams *et al*. 2020). The protective/regulative function of NPQ plays an important role not only in osmotic/salt stress but also under heat and excess light intensity. Tang *et al.* (2007) described a linear relationship between the aggregated LHCII and NPQ in high-temperature-stressed plants. Since this association between LHCII occurred at lower temperatures than the decrease of F_v/F_m therefore aggregated LHCII represented a protective mechanism in plants at high temperatures.

Although the negative effects of osmotic and salt stresses are widely recognised (Chaves *et al*. 2009, Urban *et al*. 2017, El Sabagh *et al.* 2021, Atta *et al*. 2023, Zahra *et al*. 2023, Rehman *et al*. 2025), these may enhance the thermal stability of PSII (Touchette *et al*. 2020). Osmotic/salt stress-induced increase in thermal tolerance can be associated with distinct mechanisms. Some studies observed increased thermal tolerance on the main targets of heat such as oxygen-evolving complex and PSII reaction centre (Chen *et al*. 2004, Wen *et al.* 2005, Yan *et al*. 2012, Mathur *et al*. 2013) because of salt adaption, and salt treatment may partially protect the physical separation of LHCII from the PSII core complex (Wen *et al*. 2005). Osmolytes that accumulate during water deficit and salt stress, such as glycine betaine or proline, may also be useful against high temperature stress through their membrane stabilizing function (Murata *et al.* 1992, Chen and Murata 2008, Yan *et al.* 2012, Ozturk *et al.* 2021, Kaur *et al.* 2024). Denaturation of PSII at high temperatures also relates to physical changes affecting the lipid matrix of the thylakoid membrane, and the modified lipid composition during dehydration can help to strengthen the interaction between PSII proteins and surrounding lipids (Havaux 1992). The reduction of polyunsaturated fatty acids or zeaxanthin accumulation in the photosynthetic membranes may be induced by osmotic/salt stress, thus resulting in lower membrane fluidity (Tardy and Havaux 1997, Demmig *et al*. 1988, Shu *et al*. 2015). The maintenance of the integrity of the thylakoid membrane is also necessary for the development of NPQ (Dau 1994), which can protect plants against high light and high-temperature stress by the dissipation of excess absorbed energy (Demmig-Adams *et al*. 2020). LHCII trimers can be transformed into an aggregated form by conformational changes, which also require zeaxanthin (Horton *et al*. 1991, Jahns and Holzwarth 2012).

Under natural conditions drought and salinity are often accompanied by high light intensity and high-temperature stress (Jiang *et al.* 2025) not only in semi-arid regions but also in the increasingly arid and warming fields in Central Europe where the examined wheat varieties are cultivated. These regions are characterised by hot summers and nowadays a very rhapsodic distribution of precipitation. Therefore, wheat varieties grown in these habitats need to withstand periods of varying length, characterised by strong interacting stress factors. Thus, to maintain adequate dry matter production and growth rate, efficient photosynthesis is required even under such limiting factors (Jiang *et al.* 2025); the effect of these stress factors needs to be tolerated here at the same time, which requires photosynthetic functions with high thermal tolerance. In this paper, we would like to test the hypothesis that the thermal stability of photosynthesis and critical temperature for photochemical damage is increased by

prior osmotic/salt treatment in dark-adapted samples and after short preillumination of different light intensities. We also aimed to conduct a comparative study of wheat varieties grown in semi-arid and temperate continental, but continuously drying and warming habitats. For this purpose, the responses to high temperatures of several photosynthetic parameters were examined during osmotic/salt stress.

Materials and methods

Plant materials and treatments: The seeds of Hungarian winter wheat (*Triticum aestivum* L.) cultivars (Mv9kr1, MvBéres, MvNádor) required for the experiments were provided by the gene bank of the Agricultural Institute, Centre for Agricultural Research (Martonvásár, Hungary). GTA (Mexican), Ancomarzio and Semito (Italian) varieties, cultivated in Algeria and Mediterranean North Africa, were sourced from the Field Crop Research Institute, Agriculture Research Centre, Guelma, Algeria. All experiments were performed on intact leaves or leaf segments of *Triticum aestivum* cultivars. Seeds were germinated on filter paper moistened with distilled water in Petri dishes for two days. After germination, these plants were grown in half-strength modified Hoagland nutrient solution (Nagy and Galiba 1995) in 1,500-ml pots in a growth chamber with atmospheric CO_2 concentration at 20/25°C. The light intensity for growth was 200 μE m^{-2} s^{-1}. Sixty plants of each genotype (five plants/pot) were grown. Water deficit and salt stress were induced in 5-week-old plants by increasing the osmotic pressure and salt concentration of the hydroculture medium through the addition of nonpenetrating polymers of *PEG8000* (*Sigma*, St. Louis, MO) and NaCl (*Sigma*, St. Louis, MO). The solution was renewed twice a week. Measurements were made after the 7-d treatment with 15 (–0.72 MPa) and 21% (–1.8 MPa) PEG or 150 (–0.67 MPa) and 300 mM (–1.35 MPa) NaCl concentration and after 2 and 7 d of regeneration without PEG or NaCl. The relative water content (RWC) was determined as RWC = (FW – DW) × 100/(SW – DW), where FW is the fresh mass, SW is the water-saturated mass, and DW is the oven-dry mass for 12 h at 105°C.

Na^+ and K^+ analysis: For microwave-assisted digestion a *CEM* model *Mars Xpress* (North Carolina, USA) closed-vessel microwave system was used for sample and certified reference material digestion. Approximately 100 mg of powdered plant samples were directly weighed in PFA digestion vessels. A mixture comprising 5.0 mL of HNO_3 (68 m/m%, *Sigma*, St. Louis, MO), 3.0 mL of H_2O_2 (30%, *Sigma*, St. Louis, MO), and 2.0 mL of H_2O was added to each vessel. Analytical blanks were prepared in the same way. The heating program was performed in four successive steps: (*1*) a 2-min ramp to reach 120°C, (*2*) 8 min hold at 120°C, (*3*) a 5-min ramp to reach 180°C, (4) 15 min hold at 180°C. In all steps, the oven was kept at 1,600 W (maximum power). After the heating program, the vessels were cooled down for 15 min. Digested samples were diluted to 25.0 mL with ultrapure distilled water. As a reference procedure to evaluate digestion efficiency, an experiment was performed in triplicate, adding 5.0 mL of HNO_3 (65%) and 3.0 mL of H_2O_2 (30%) to the vessels using the same heating program. Measurements were carried out using a *Varian SpectrAA 55b* (*Varian*, Macquarie Park, Australia). Determination of sodium (589.0 nm), and potassium (766.5 nm) by flame atomic absorption spectrometry with an acetylene-air was used. The gas-flow rate and the burner height were adjusted to obtain the maximum absorbance signal for sodium and potassium elements.

Chlorophyll *a* fluorescence measurements: The *in vivo* chlorophyll *a* fluorescence was measured in dark-adapted intact leaves using a pulse amplitude modulation fluorometer (*Imaging PAM M-series*, *Walz*, Effeltrich, Germany). The initial level of fluorescence (F_0) was detected after 15-min dark adaptation. The maximal fluorescence level of the dark (F_m) and light (F_m') adapted leaves was determined by applying saturating flashes [15,000 μmol(photon) m^{-2} s^{-1}] lasting 0.8 s. Photosynthesis was induced by continuous actinic illumination of the leaf at 200 μmol(photon) m^{-2} s^{-1} for 15 min. The fluorescence parameters were calculated as described by Klughammer and Schreiber (2008) based on the following equations: maximal quantum yield of PSII photochemistry, $F_v/F_m = (F_m - F_0)/F_m$; effective quantum yield of PSII, $\Phi_{PSII} = (F_m' - F)/F_m' = \Delta F/F_m'$; quantum yield of regulated energy dissipation, $\Phi_{NPQ} = (F/F_m') - (F/F_m)$; quantum yield of nonregulated energy dissipation, $\Phi_{NO} = F/F_m$.

High-temperature-induced chlorophyll fluorescence: To determine the critical temperature values (*T*c) of the fluorescence temperature curves (FTC, Nauš *et al.* 1992) temperature induction of fluorescence method was applied as described by Schreiber and Berry (1977). For determination of F_0TCs the leaf segments were placed on a laboratory-made high-precision thermoelectric module and then were dark-adapted for 15 min. After that, F_0 and F_m were determined at 25°C, and the samples were heated gradually at a rate of 1°C min^{-1} to 60°C. The saturation light pulses were applied at 25, 30, 35, 38, 41, 43°C and then at any further 2°C temperature rise to detect F_m. Gradually heating of leaf segments for F_sTC measurements was started after reaching the steady-state fluorescence level (min. 15 min, 25°C) at actinic light (AL) intensity of 200 and 1,000 μmol(photon) m^{-2} s^{-1}.

The saturation light pulses were applied at the temperatures described above to detect F_m'. *T*c was determined as the interception of regression lines fitted to F_0 and F_s data. Phenotypic plasticity to high temperature was calculated as $Tc_1 - Tc_0$, where Tc_1 is the breakpoint for F_0TC or F_sTC in the treated state, and Tc_0 is the breakpoint for these curves in well-watered plants. "Absolute" phenotypic plasticity to high temperature was calculated as $Tc_1 - Tc_{0dark}$, where Tc_1 is the breakpoint for F_STC in the treated state, Tc_{0dark} is the breakpoint for F_0TC in well-watered plants. The temperature dependence of Φ_{PSII}, Φ_{NPQ}, and Φ_{NO} parameters is given at 200 μmol(photon) m^{-2} s^{-1} of AL intensity.

Gas-exchange measurements: The CO_2 assimilation of intact leaves was measured with an infrared gas analyser (*GFS-3000FL*, *Walz*, Effeltrich, Germany). The net assimilation rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were calculated in the light-saturated state of photosynthesis [1,000 μmol(photon) m^{-2} s^{-1}]. The gas-exchange chamber parameters were 25°C, and completely dry reference air. The CO_2 concentration of the reference air was 380 μL L^{-1}. The maximum net assimilation rate (P_{Nmax}) was determined at saturating PPFD [1,000 μmol(photon) m^{-2} s^{-1}] and CO_2 concentration (1,200 μL L^{-1}). The responses of P_N and P_{Nmax} to high temperature were measured at 45°C leaf temperature (after a gradual heating) under the above-mentioned conditions. After the high-temperature treatment, samples were cooled back to 25°C and P_N was determined again.

Statistical analysis: All the experiments were repeated three times. Ten measurements were performed on each cultivar and treatment for chlorophyll fluorescence and high temperature-induced fluorescence while four measurements were performed for CO_2 gas-exchange analyses. The RWC content was determined in ten replicates of each cultivar and treatment. Differences between treatments or genotypes within each treatment were determined using *Tukey*'s post hoc test ($p \leq 0.05$) using the *SPSS 16.0* software.

Results

Relative water content: Although the decrease in relative water content by PEG-induced osmotic stress was less pronounced in MvNádor and MvBéres than in the other varieties when the osmotic potential of the medium decreased to –1.8 MPa, it was statistically significant (Table 1). However, the decrease in water content was relatively moderate in all lines. The increase of salt stress induced a more definite but also relatively moderate water loss in the lines. At 300 mM NaCl treatment, the decrease in water content was statistically significant in all lines compared to the control (Table 1). In the regeneration period, the varieties which survived the treatments practically recovered their water contents completely by the 7th day except for Ancomarzio, where RWC was significantly lower than that in the control, at the end of the relaxation period from salt treatment.

Na^+/K^+ ratio in control and stressed plants: Although in some cases statistically significant differences were detected compared to the control, the Na^+/K^+ ratio remained low in both the shoots and roots under 21% PEG treatment (Table 1S, *supplement*). At the same time, the Na^+/K^+ ratio both in roots and shoots significantly increased under salt treatment (300 mM) in all varieties. The values written in the following order (Semito, Mv9kr1, GTA, MvNádor, Ancomarzio, MvBéres) were as follows: $2.16 \pm 0.13, 1.81 \pm 0.14, 1.76 \pm 0.10, 1.27 \pm 0.17, 1.26 \pm 0.08$, 1.19 ± 0.03 in the shoots. Similarly to the previous case, the Na^+/K^+ ratio in the roots also increased in the order of GTA > Semito > Mv9kr1 > MvNádor > MvBéres > Ancomarzio (Table 1S). By the end of the relaxation period, the Na^+/K^+ ratios decreased in both the shoots and roots except for GTA and Semito. In these, since they did not survive the experimental period, measurements were made on dead organs.

The critical temperature for photochemical damage under dark and light conditions: Tc_{dark} values determined by the F_0TC measurements did not differ from each other significantly (varied between 41.9–43.3°C) in nonstressed plants (Fig. 1*A*,*D*). Although *T*c values increased slightly with the severity of osmotic stress, this change in thermal stability was not significant, even in the case of the 21% PEG treatment. At the same time, treatment with 150 mM NaCl caused a substantially higher thermostability compared to the control in Ancomarsio, GTA, and Mv9kr1varieties under dark conditions. Raising the salt concentration (300 mM NaCl) further increased Tc_{dark} values and these were significantly higher than the control data in all varieties. Although during the regeneration period, high-temperature sensitivity increased by the 7th day in all plants compared to the Tc_{dark} values at 300 mM NaCl, except Nádor, these values were still significantly higher than the control. These plants did not lose fully their improved thermal stability caused by the two-week salt treatment.

*T*c values of F_sTCs were also determined at 200 μmol(photon) m^{-2} s^{-1} (Tc_{200}) and 1,000 μmol(photon) m^{-2} s^{-1} light intensity (Tc_{1000}). Fig. 1*B*,*E* presented that Tc_{200} values shifted towards significantly higher temperatures

Table 1. Effects of increasing polyethylene glycol (PEG) and NaCl concentrations followed by 7 d of regeneration on the relative water content (RWC) for leaves in the examined wheat cultivars. Each value (± SD) is the mean of the data of five plants per treatment. *The asterisks* indicate significant differences between untreated control and treatments within a cultivar at $p \leq 0.05$ level. Nonsignificant differences between the untreated control and treatments are marked by ns.

Cultivar	Control	PEG concentration/Recovery				NaCl concentration/Recovery			
		15%	21%	2 d	7 d	150 mM	300 mM	2 d	7 d
Mv9kr1	94.76 ± 1.40	88.41 ± 2.50*	84.71 ± 2.67*	88.10 ± 3.66*	95.59 ± 0.80ns	83.39 ± 2.15*	79.54 ± 5.23*	95.28 ± 3.76ns	92.41 ± 2.58ns
MvNádor	95.27 ± 2.60	93.47 ± 1.35ns	88.59 ± 1.46*	94.93 ± 5.53ns	95.78 ± 2.61ns	92.88 ± 1.21ns	86.99 ± 2.59*	94.99 ± 2.71ns	96.06 ± 0.59ns
MvBéres	94.53 ± 1.51	95.58 ± 0.62ns	91.51 ± 0.62*	95.95 ± 1.10ns	94.83 ± 2.20ns	93.70 ± 3.47ns	86.71 ± 3.51*	94.53 ± 1.47ns	95.13 ± 3.57ns
Semito	94.70 ± 4.12	86.50 ± 2.42*	82.87 ± 2.46*	91.61 ± 2.25ns	94.73 ± 2.28ns	84.90 ± 2.25*	84.87 ± 5.84*	88.76 ± 2.61ns	-
GTA	94.25 ± 1.44	86.37 ± 5.72*	89.39 ± 3.69*	85.19 ± 4.55*	-	85.58 ± 1.34*	81.95 ± 2.61*	90.25 ± 2.18ns	-
Ancomarzio	96.46 ± 0.87	82.51 ± 3.29*	86.19 ± 2.98*	90.87 ± 2.34*	93.18 ± 6.21ns	83.08 ± 3.37*	86.55 ± 1.24*	88.76 ± 4.18*	89.94 ± 3.91*

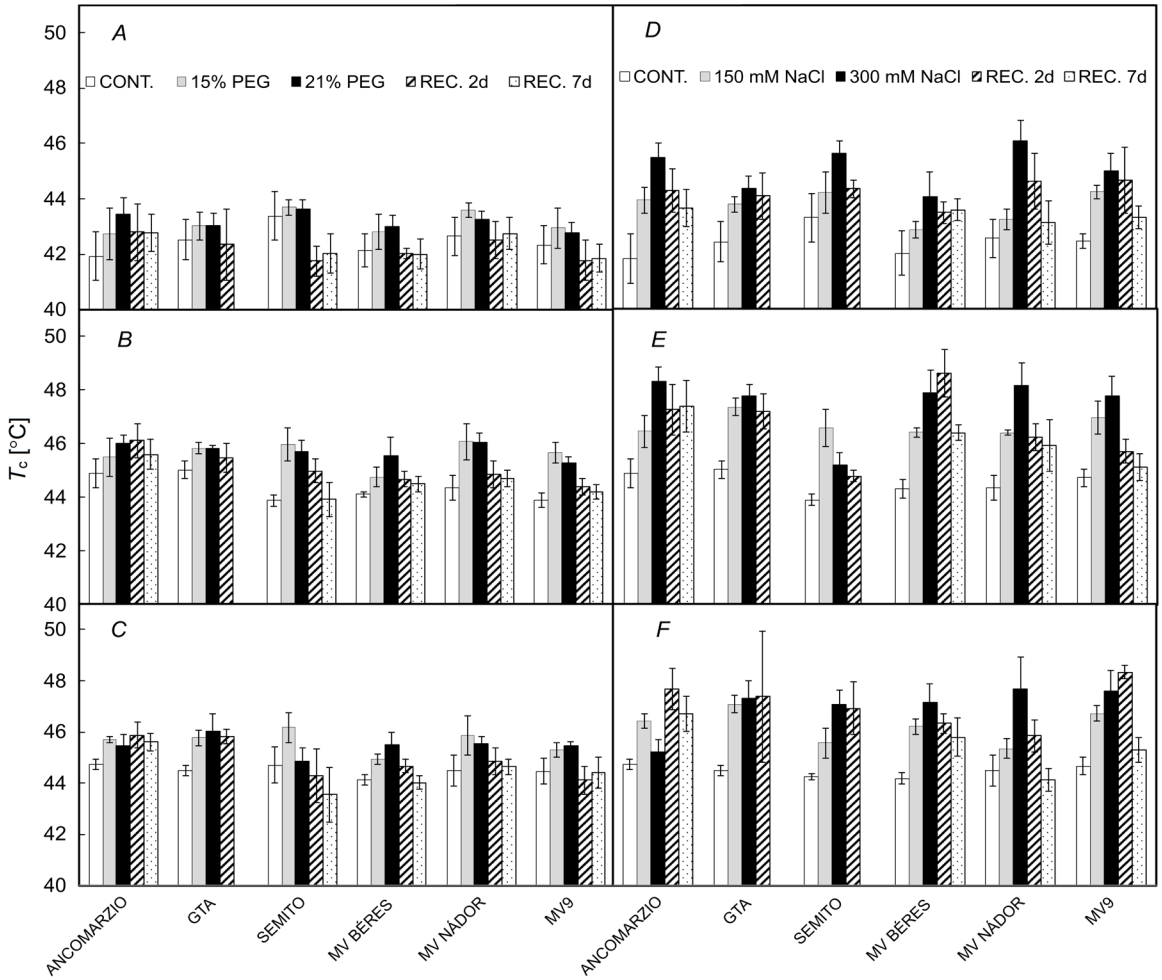

Fig. 1. Effects of increasing polyethylene glycol (PEG; *A*, *B*, *C*) and NaCl (*D*, *E*, *F*) concentration followed by seven days of regeneration on the critical temperature (*T*c) for F_0TC measurements (*A*, *D*), and F_sTC measurements at 200 μmol(photon) m^{-2} s^{-1} (*B*, *E*) and at 1,000 μmol(photon) m^{-2} s^{-1} (*C*, *F*) actinic light intensities in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment.

in all lines even in the well-watered samples concerning Tc_{dark} values. As a result of osmotic/salt treatments, in light-adapted samples the thermal stability of PSII was further enhanced, indicated by the higher *T*c values of the F_sTCs. Furthermore, the NaCl treatment resulted in stronger thermal stability than the osmotic stress. In the case of salt treatment, Tc_{200} values of wheat lines remained significantly higher than those in well-watered plants after the 7-d rewatering (except Mv9kr1), thus the salt-induced better thermal stability was not fully recovered. Two varieties (GTA and Semito) could not be measured at this stage because GTA dried out and Semito matured rapidly following spike development. In spite, the recovery of thermal stability was practically complete after the osmotic treatment except for Ancomarsio, where a residual high-temperature stability was detected. Similarly to salt stress, GTA could not be measured at this stage either. In comparison with Tc_{200} and Tc_{1000} values of wheat, except for Ancomarsio (at 300 mM salt treatment), did not differ significantly under both control and stressed/regeneration conditions (Fig. 1*C*,*F*).

The treatment by 21% PEG did not cause significant changes in phenotypic plasticity (Tc_1–Tc_0) in the dark, but it increased in the light-adapted state (Fig. 2). At same time, the 300 mM NaCl-induced changes of phenotypic plasticity to high temperature under dark and different light intensities were significant (Fig. 2). "Absolute" phenotypic plasticity (Tc_1 – Tc_{0dark}) showed a greater shift in the PEG/NaCl treated plants than the normal one. Moreover, these changes in phenotypic plasticity by both osmotic and salt stresses were roughly independent of the measure of excitation energy (AL intensity).

Temperature dependence of the chlorophyll fluorescence parameters: The responses of PSII photochemistry under dark-adapted conditions to elevated temperatures were investigated in control and osmotic/salt-treated leaves. The temperature responses of the maximum quantum yield of PSII photochemistry (F_v/F_m) for leaves of well-watered plants did not differ in a wide range of heating temperatures and significant decreases were registered above 41°C mostly without significant differences between the wheat

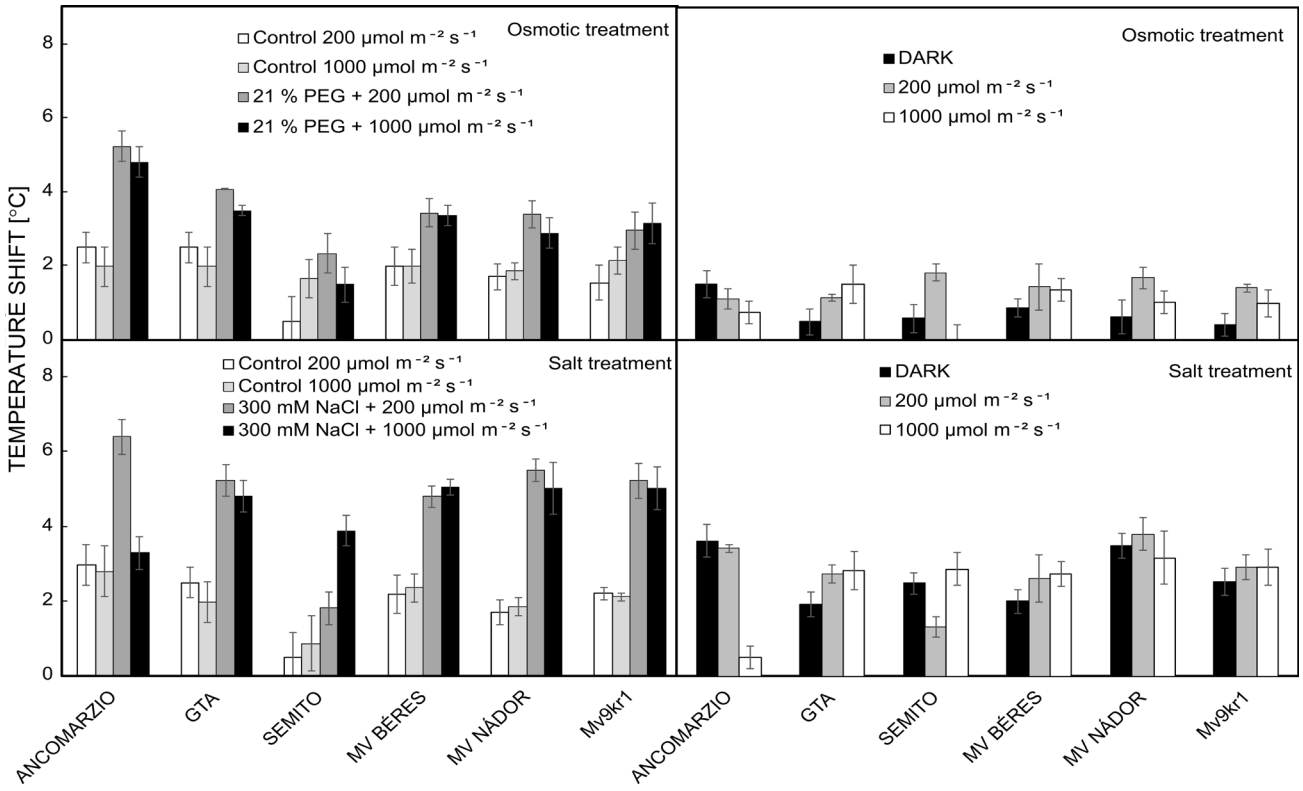

Fig. 2. Effects of increasing polyethylene glycol (PEG) and NaCl concentration followed by seven days of regeneration on the "absolute" phenotypic plasticity ($Tc_1 - Tc_{0dark}$, *on the left*) and phenotypic plasticity ($Tc_1 - Tc_0$, *on the right*) to high temperature, in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment.

cultivars (Fig. 3). Moreover, thermal stability of PSII was not improved by PEG treatment in absence of light since practically there was no upward shift in the temperature dependence of F_v/F_m. At the same time, the salt-stressed plants revealed that F_v/F_m values of NaCl-treated (150 mM) samples started going down and reached a minimum level at significantly higher temperatures compared to the control almost in all the examined lines. This upward shift was more strongly induced due to the severe salt treatment (300 mM) in all of the cultivars and it was not recovered fully by the end of the regeneration period.

We detected the responses of PSII photochemistry in light-adapted leaves to high temperatures further. As shown in Fig. 4, in control conditions, the effective quantum yield at 200 µmol(photon) m^{-2} s^{-1} ($\Phi_{PSII200}$) changed very similarly in the examined varieties: at moderately high temperatures, $\Phi_{PSII200}$ softly increased and the decrease of this parameter began to drop significantly at once above 38°C. When water deficit was applied besides the light, the heat resistance in the tested plants was more intense than in the control plants: the temperature dependence of $\Phi_{PSII200}$ was significantly improved by 15 and 21% PEG treatment. More pronounced differences were detectable when the control samples were compared to salt-stressed plants. It was observed that $\Phi_{PSII200}$ started decreasing and reached zero value at higher temperatures already at 150 mM NaCl in all cultivars which was further enhanced by the 300 mM salt treatment.

Fig. 5 shows the changes in quantum yield of regulated energy dissipation (Φ_{NPQ}) to elevated temperature in proportion to values measured at 25°C in the presence of actinic light intensity of 200 µmol(photon) m^{-2} s^{-1} (Φ_{NPQ200}). We observed that Φ_{NPQ200} began to rise at temperatures above 35°C both in the nonstressed and PEG-treated plants, but these increases were more pronounced in the well-watered plants. The 21% PEG treatment shifted the Φ_{NPQ200} maxima moderately higher in some lines and they were close to the *T*c values of F_sTCs. This shift was not detectable in all varieties because the Φ_{NPQ} determination was done in 2°C steps (at 45 and 47°C) in this temperature range (*see* "Materials and methods" section). Furthermore, compared to the osmotic treatment, the salt stress-induced temperature dependence of Φ_{NPQ} shifts upward to higher temperatures even more with maxima around *T*c values of F_sTCs.

As can be seen in Fig. 6, the quantum yield of nonregulated energy dissipation Φ_{NQ} in most cases started to increase from 43°C in well-watered plants. As a result of osmotic stress, these threshold temperatures were slightly elevated. In this respect, the effect of salt stress was even more pronounced at 150 mM treatment, which was further increased by stronger stress. Furthermore, the threshold temperature for the increase coincided with the *T*c values of F_sTCs with Φ_{NQ} maxima around the temperatures where the F_s was the highest (peak temperature, *T*p).

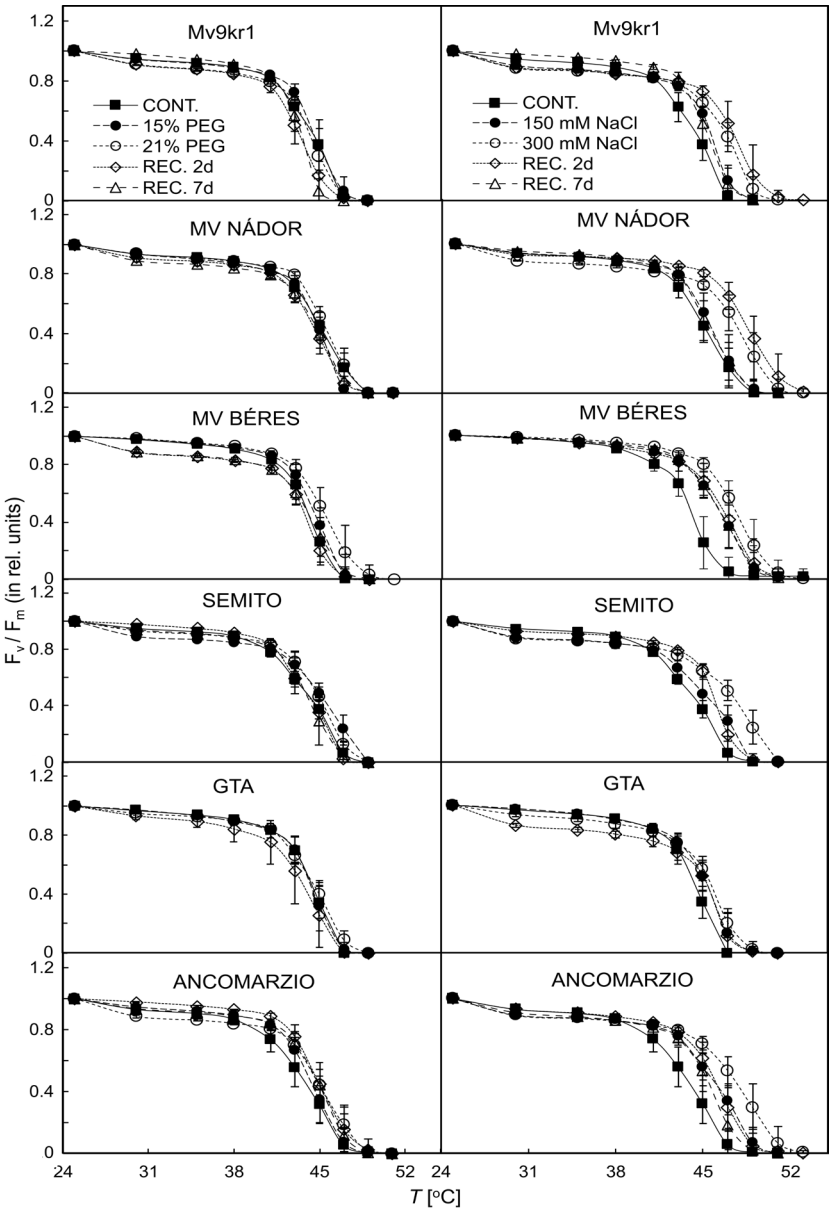

Fig. 3. Effects of increasing polyethylene glycol (PEG, *on the left*) and NaCl (*on the right*) concentration followed by seven days of regeneration on the temperature dependence of maximum quantum yield (F_v/F_m) of PSII in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment. The un-normalized values measured at 25°C, written in the following order (control, 21% PEG treatment, recovery 7 d, 300 mM NaCl treatment, recovery 7 d) were as follows: 0.76 ± 0.02, 0.77 ± 0.01, 0.72 ± 0.03, 0.8 ± 0.01, 0.79 ± 0.01 for Mv9kr1; 0.77 ± 0.01, 0.76 ± 0.01, 0.8 ± 0.01, 0.74 ± 0.01, 0.76 ± 0.01 for MvNádor; 0.74 ± 0.02, 0.74 ± 0.01, 0.79 ± 0.02, 0.71 ± 0.02, 0.74 ± 0.01 for MvBéres; 0.74 ± 0.01, 0.76 ± 0.01, 0.74 ± 0.09, 0.75 ± 0.05, -, for Semito; 0.73 ± 0.01, 0.76 ± 0.02, 0.79 ± 0.01, 0.65 ± 0.05, -, for GTA; 0.78 ± 0.01, 0.79 ± 0.01, 0.76 ± 0.02, 0.079 ± 0.01, 0.77 ± 0.02 for Ancomarzio.

Heat sensitivity of gas-exchange parameters: Osmotic and salt treatments affected the net assimilation rate (P_N) in different degrees, and significant differences were also detected between the tolerance of individual varieties for the given treatment, at a temperature of 25°C (Fig. 6). In well-watered plants at 25°C, leaf temperature values of P_N [μmol(CO_2) m^{-2} s^{-1}] were 15.24 ± 1.92 for Mv9kr1, 15.25 ± 2.16 for MvNádor, 13.37 ± 0.86 for MvBéres, 18.17 ± 4.06 for Semito, 14.51 ± 3.84 for GTA, and 19.12 ± 1.27 for Ancomarsio. Osmotic treatment had the most significant effect on P_N in Mv9kr1, while it was moderately reduced in MvNádor and Semito at 21% PEG concentration at the growth temperature. In this regard, MvBéres, GTA, and Ancomarsio did not show any obvious sensitivity. Although GTA could not be measured at the end of the treatment period (after 7-d recovery) because it was senesced and dried out, P_N did not decrease below the control level even at 21% PEG treatment.

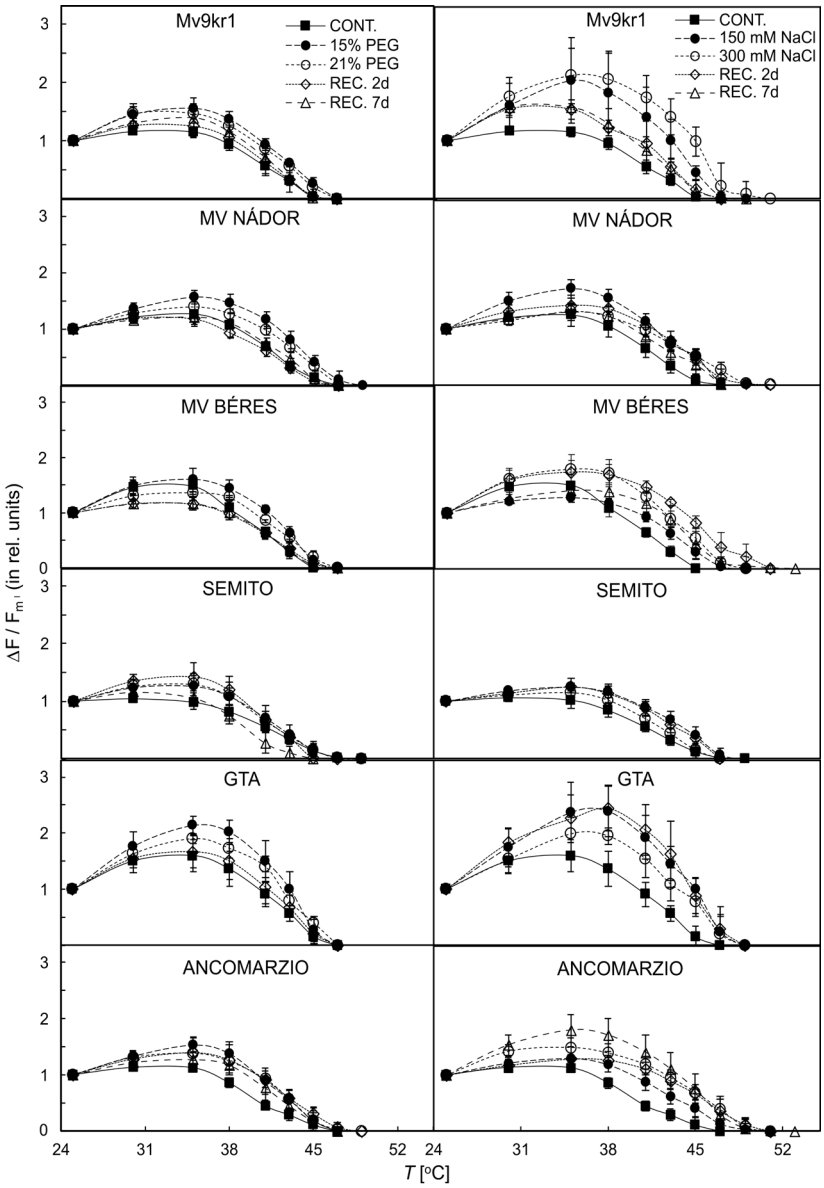

Fig. 4. Effects of increasing polyethylene glycol (PEG, *on the left*) and NaCl concentration followed by seven days of regeneration on the temperature dependence of effective quantum yield (Φ_{PSII}, expressed as $\Delta F/F_m'$) of PSII in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment. The un-normalized values measured at 25°C, written in the following order (control, 21% PEG treatment, recovery 7 d, 300 mM NaCl treatment, recovery 7 d) were as follows: 0.42 ± 0.04, 0.28 ± 0.06, 0.33 ± 0.05, 0.12 ± 0.05, 0.24 ± 0.04 for Mv9kr1; 0.35 ± 0.04, 0.34 ± 0.07, 0.42 ± 0.03, 0.16 ± 0.04, 0.37 ± 0.04 for MvNádor; 0.31 ± 0.06, 0.38 ± 0.03, 0.43 ± 0.04, 0.12 ± 0.04, 0.34 ± 0.06 for MvBéres; 0.48 ± 0.08, 0.38 ± 0.07, 0.39 ± 0.08, 0.17 ± 0.14, -, for Semito; 0.29 ± 0.09, 0.22 ± 0.03, -, 0.10 ± 0.06, -, for GTA; 0.43 ± 0.04, 0.36 ± 0.08, 0.38 ± 0.05, 0.22 ± 0.03, 0.25 ± 0.05 for Ancomarzio.

The recovery of P_N was practically complete in all varieties by the end of the recovery phase except GTA. The maximum net assimilation rate (P_{Nmax}) measured at 1,200 μL L^{-1} CO_2 concentration and saturation light intensity also significantly decreased in Mv9kr1, MvNádor, and Semito varieties, while this drop was not observed for MvBéres, GTA, and Ancomarsio. In well-watered plants, P_N at 45°C showed negative values in all cases, regardless of whether it was measured at normal or saturated CO_2 concentration (P_{Nmax}). Similarly, P_N after cooling back to 25°C was also negative. Although P_N remained negative values at high temperatures during osmotic treatments, P_{Nmax} was positive, indicating a moderate increase in the thermotolerance of the photosynthetic apparatus, which subsided by the end of the relaxation period (Fig. 6).

Salt stress significantly reduced net photosynthesis in all lines compared to osmotic stress. Semito and GTA responded most sensitively to this when plants dried out by the end of the regeneration phase, but Semito nevertheless developed ears. In addition, except for the MvNádor and MvBéres varieties, the recovery of P_N was not complete

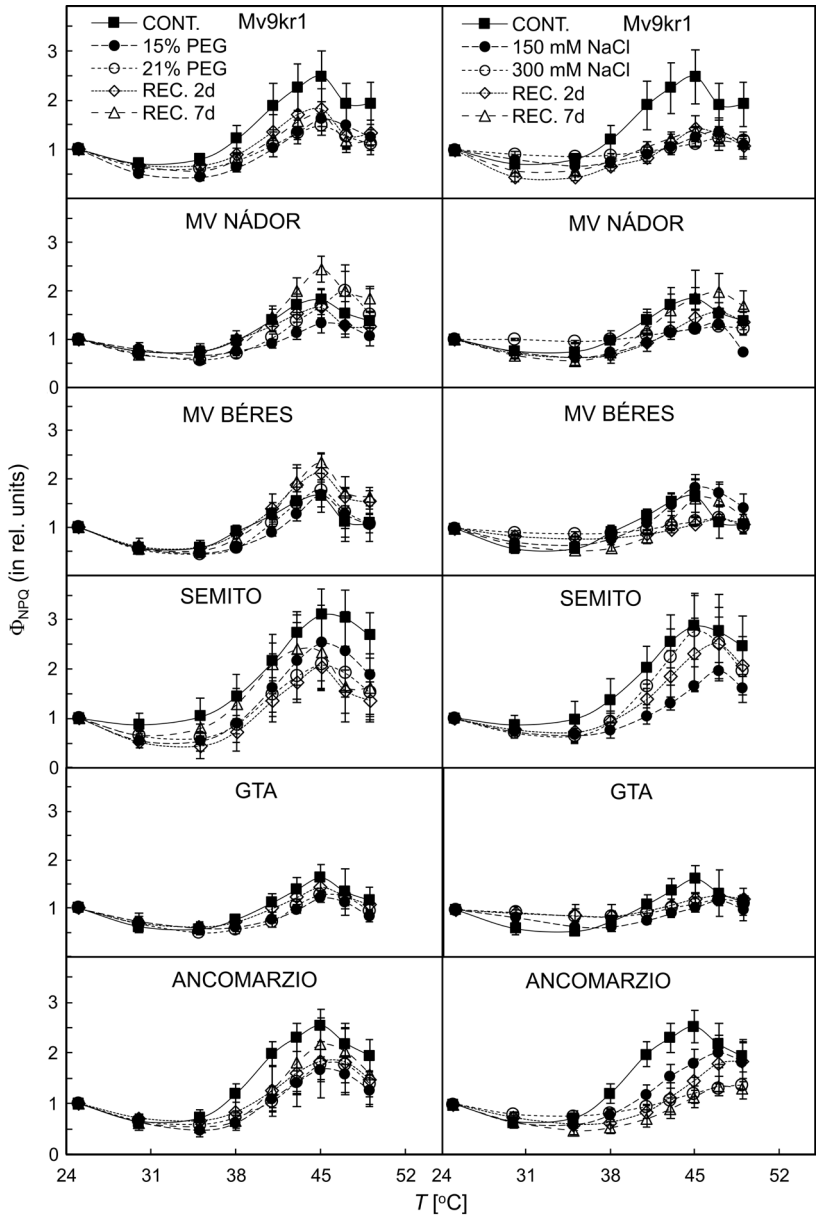

Fig. 5. Effects of increasing polyethylene glycol (PEG, *on the left*) and NaCl (*on the right*) concentration followed by seven days of regeneration on the temperature dependence of quantum yield of regulated energy dissipation (Φ_{NPQ}) of PSII in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment. The un-normalized values measured at 25°C, written in the following order (control, 21% PEG treatment, recovery 7 d, 300 mM NaCl treatment, recovery 7 d) were as follows: 0.28 ± 0.06, 0.42 ± 0.07, 0.39 ± 0.07, 0.54 ± 0.06, 0.49 ± 0.05 for Mv9kr1; 0.35 ± 0.04, 0.36 ± 0.09, 0.26 ± 0.03, 0.52 ± 0.04, 0.32 ± 0.07 for MvNádor; 0.43 ± 0.08, 0.34 ± 0.05, 0.29 ± 0.05, 0.59 ± 0.04, 0.36 ± 0.08 for MvBéres; 0.24 ± 0.08, 0.32 ± 0.08, 0.27 ± 0.1, 0.34 ± 0.09, -, for Semito; 0.43 ± 0.11, 0.45 ± 0.04, -, 0.54 ± 0.07, -, for GTA; 0.27 ± 0.05, 0.32 ± 0.13, 0.31 ± 0.07, 0.48 ± 0.04, 0.46 ± 0.05 for Ancomarzio.

at 25°C. Furthermore, 150 and 300 mM of salt treatment significantly increased the P_{Nmax} level at 45°C indicating a higher thermal stability of PSII, which was maintained in most of the lines until the end of the relaxation period. In addition, the effect of salt stress on the temperature stability of P_{Nmax} was much stronger than that of osmotic stress. P_N also showed low but positive values after cooling back to 25°C from 45°C temperature treatment at normal CO_2 concentration.

Discussion

In field conditions, drought and salinity often occur simultaneously with high-temperature stress under conditions of high light intensity. These stress factors may limit the processes of carbon metabolism simultaneously (Dulai *et al*. 2006, Chauhan *et al*. 2023, Jiang *et al*. 2025). During global climate change, it may become common for wheat to tolerate the combined effects of abiotic stress

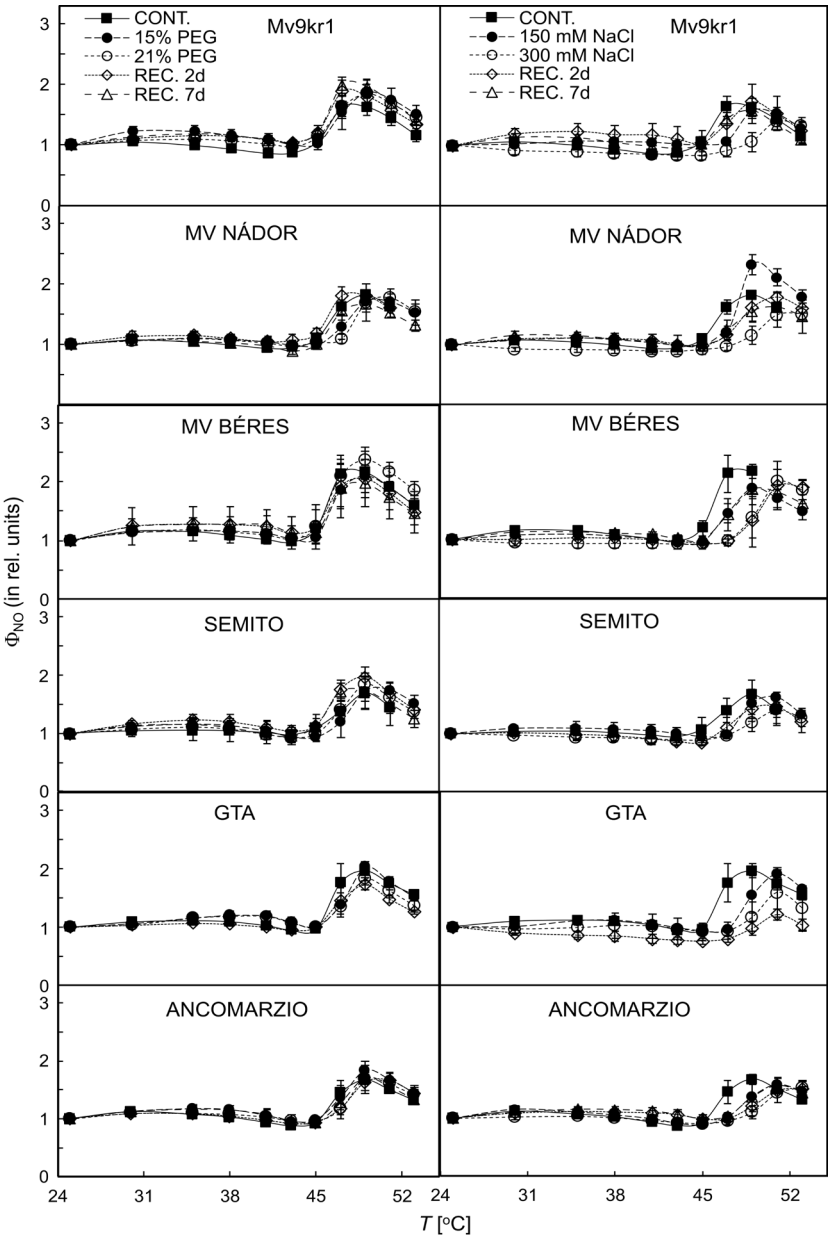

Fig. 6. Effects of increasing polyethylene glycol (PEG, *on the left*) and NaCl (*on the right*) concentration followed by seven days of regeneration on the temperature dependence of quantum yield of nonregulated energy dissipation (Φ_{NO}) of PSII in the examined wheat cultivars. Each value (± SD) is the mean of the data of ten samples per treatment. The un-normalized values measured at 25°C, written in the following order (control, 21% PEG treatment, recovery 7 d, 300 mM NaCl treatment, recovery 7 d) were as follows: 0.29 ± 0.02, 0.29 ± 0.07, 0.28 ± 0.02, 0.33 ± 0.04, 0.28 ± 0.02 for Mv9kr1; 0.28 ± 0.01, 0.28 ± 0.03, 0.31 ± 0.01, 0.31 ± 0.02, 0.30 ± 0.03 for MvNádor; 0.25 ± 0.02, 0.27 ± 0.02, 0.29 ± 0.05, 0.28 ± 0.02, 0.29 ± 0.02 for MvBéres; 0.27 ± 0.03, 0.28 ± 0.02, 0.33 ± 0.03, 0.38 ± 0.09, -, for Semito; 0.26 ± 0.02, 0.30 ± 0.01, -, 0.35 ± 0.01, -, for GTA; 0.28 ± 0.02, 0.31 ± 0.07, 0.31 ± 0.03, 0.30 ± 0.03, 0.28 ± 0.01 for Ancomarzio.

factors (Suzuki *et al.* 2014, Jiang *et al.* 2025). Consequently, the survival and productivity of wheat cultivars can be determined by their ability to synchronize the protecting/regulating mechanisms against multiple factors.

The thermal tolerance of PSII can be characterised by the critical temperature for photochemical damage (*Tc*) based on the F_0TC and F_STC measurements (Schreiber and Berry 1977, Molnár *et al.* 1998, Nauš *et al.* 1992, Hill *et al.* 2009, Coast *et al.* 2022, Mitchell *et al.* 2025). In dark-adapted state, Tc_{dark} values did not differ from each other significantly (varied between 41.9–43.3°C) in well-watered plants (Fig. 1*A*,*D*) confirming that thermal stability of PSII was similar for all wheat cultivars, which is a possible consequence of the same growth temperature (Dulai *et al.* 1998). Moreover, it was not further enhanced considerably even by the 21% PEG treatment, indicating that osmotic treatment did not improve significantly the temperature tolerance in the dark-adapted state (Dulai

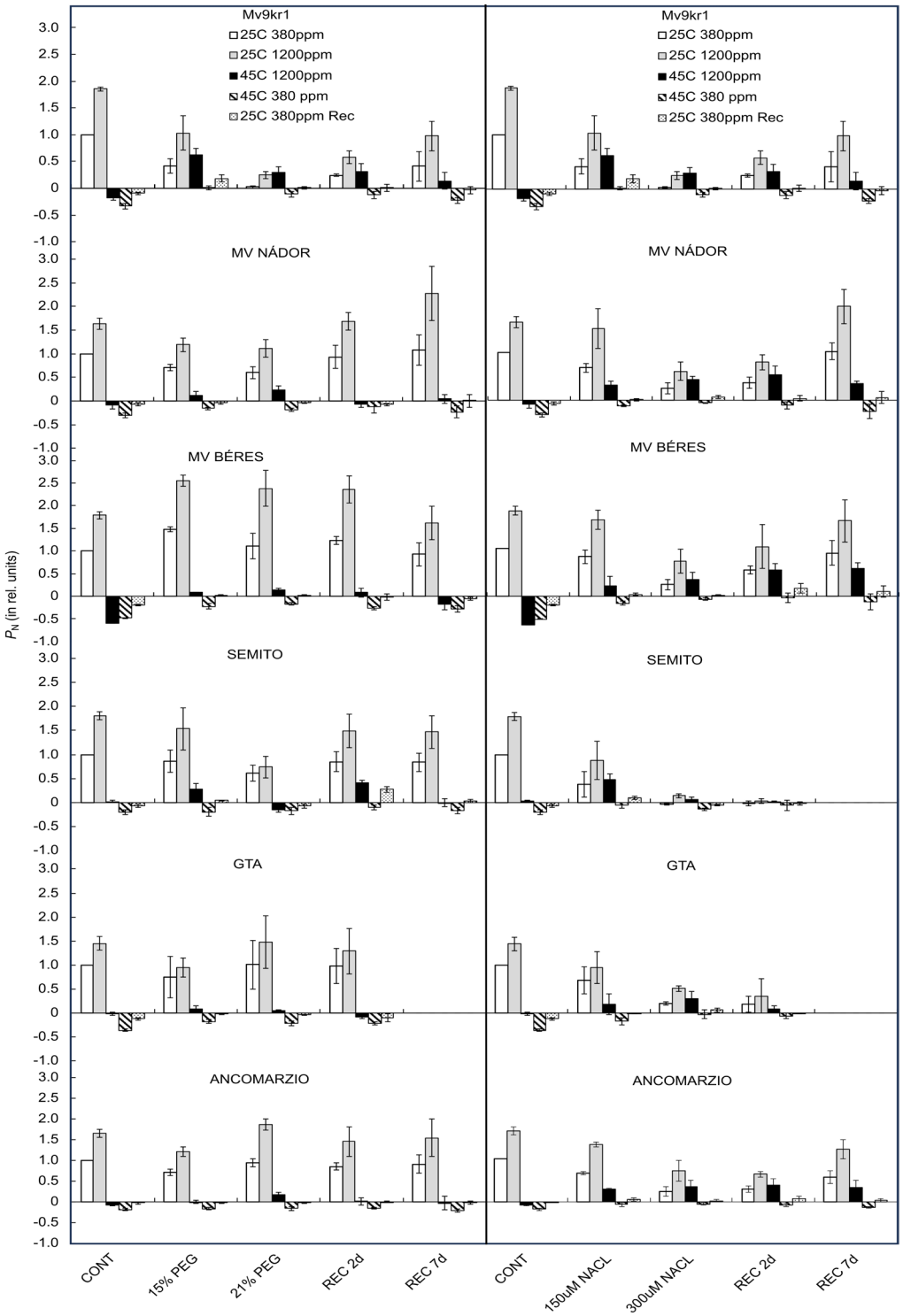

Fig. 7. Effects of increasing polyethylene glycol (PEG, *on the left*) and NaCl (*on the right*) concentration followed by seven days of regeneration on the net photosynthesis (P_N) measured under light-saturated state at 380 μL L^{-1} CO_2 concentration at 25°C (untreated), 45°C (temperature treated), and after cooling back from 45°C to 25°C (25°C 380 μL L^{-1} CO_2 Rec.) and maximum net photosynthesis (P_{Nmax}), measured at 1,200 mL L^{-1} CO_2 concentration at 25 and 45°C, in the examined wheat cultivars. Each value (± SD) is the mean of the data of four samples per treatment. The un-normalized values of P_N [μmol(CO_2) m^{-2} s^{-1}] measured at 25°C, written in the following order (control, 21% PEG treatment, recovery 7 d, 300 mM NaCl treatment, recovery 7 d) were as follows: 15.24 ± 1.92, 6.36 ± 0.25, 14.41 ± 2.08, 0.34 ± 0.25, 6.0 ± 3.48 for Mv9kr1; 15.24 ± 2.13, 8.92 ± 0.79, 15.94 ± 2.34, 3.67 ± 1.22, 15.47 ± 2.73 for MvNádor; 13.37 ± 0.47, 14.81 ± 3.43, 12.37 ± 3.25, 2.83 ± 2.02, 12.18 ± 3.89 for MvBéres; 18.47 ± 4.06, 10.62 ± 0.82, 14.65 ± 0.18, 0.74 ± 0.17, -, for Semito; 14.51 ± 2.84, 13.38 ± 2.85, -, 2.8 ± 0.32, -, for GTA; 19.21 ± 1.27, 18.01 ± 1.72, 17.21 ± 3.72, 4.76 ± 2.04, 11.12 ± 2.5 for Ancomarzio.

et al. 2006). At the same time, salt stress strongly decreased the thermal sensitivity of photosynthesis for the examined plants already at 150 mM NaCl, and PSII was mostly more thermal tolerant under severe treatment. In this regard, some other authors also support the observation that osmotic and salt tolerance are not necessarily linked and do not always act through the same pathways (Nagy and Galiba 1995). As it has been reported, the value of Tc_{dark} is influenced by the fluidity of photosynthetic membranes, therefore *T*c is a sensitive indicator for thermotolerance (Mitchell *et al*. 2025) in connection with the integrity of thylakoid lamellae (Nauš *et al*. 1992, Lazár and Ilík 1997, Hill *et al*. 2009). Shu *et al*. (2015) have described an increase in the saturated fatty acid content of photosynthetic membranes under severe ion toxicity caused by sodium chloride. The higher ratios of saturated fatty acids to unsaturated ones may be beneficial even at high temperatures due to the reduced membrane fluidity (Raison *et al.* 1982, Guo *et al*. 2019, Vineeth *et al*. 2023). In parallel with the significant increase in phenotypic plasticity (Fig. 2), the temperature dependence of F_v/F_m (Fig. 3) was also improved by salt stress. Thus, these changes in membrane composition may be partly responsible for the increase in thermal stability of PSII under salt stress in the examined lines. In this context, it is also well known that high-temperature tolerance of PSII is greatly influenced by the thermal sensitivity of oxygen-evolving complex (OEC; Nash *et al.* 1985, Tóth *et al*. 2007, 2009; Wang *et al*. 2010, Shanker *et al*. 2022) and the salt treatment enhances not only the membrane rigidity but also OEC or PSII thermal stability in some ways (Chen *et al*. 2004, Wen *et al.* 2005, Yan *et al.* 2012). Since reduced oxygen-evolving ability is also associated with the detachment of chloride ions under high-temperature conditions (Nash *et al.* 1985), it is possible that the higher chloride ion concentration under salt stress may increase the stability of OEC and result in more thermostable PSII. Thus, these changes may trigger the formation of higher thermal stability even in dark-adapted state for the salt-stressed wheat (Mathur *et al*. 2013). In this regard, Lazár *et al*. (1997) demonstrated the appearance of a K peak (T_k) in the chlorophyll fluorescence induction curve concerning the possible destruction of OEC in heat-treated plants. As was found, T_k showed a strong correlation with the *T*c values of the FTC measurements (Lazár and Ilík 1997), which also confirms the above-mentioned results.

The effect of water deficit on thermostability is known (Havaux 1992), but according to some observations (Dulai *et al*. 2005, 2006) and our results, it possibly occurs only to a limited extent under dark-adapted conditions. As a result, the NaCl-induced decrease in temperature sensitivity in a dark-adapted state can probably only be a minor consequence of the osmotic effect of salt stress. This may be true even if we take into account the fact that the increase in thermostability appears relatively quickly after 150 mM NaCl treatment, already at the stage where the osmotic effect of salt is considered important (Munns 2002, dos Santos *et al*. 2022). In our case, the salt treatments we applied only had osmotic potentials of –0.67 and –1.35 MPa and the decrease in RWC values was also very similar in the case of 15% PEG and 150 mM salt treatments (Table 1). Therefore, if the decrease in dark-temperature sensitivity was exclusively caused by the osmotic effect, then it should occur both during moderate (–0.72 MPa) and severe (–1.8 MPa) osmotic treatment. All this makes it clear that the salt-induced increase in thermostability (Yan *et al*. 2012, Szopkó and Dulai 2018, Touchette *et al*. 2020), at least in the examined varieties, can be interpreted largely as an ionic effect of salt treatment. This is also supported by the fact that by the end of the seven-day relaxation period, this salt treatment-induced increase in thermotolerance remained in the lines that survived the treatment, while this disappeared in the case of osmotic stress (Fig. 1*A*,*D*). If we compare the temperature tolerance of the individual lines, we can conclude that there is no significant difference between them under either osmotic or salt treatments in their thermal stability (Figs. 1, 2).

Under natural conditions, plants are exposed to the effects of high-temperature stress in the presence of light. A positive correlation between the thermal stability of PSII and light intensity has been found by Molnár *et al.* (1998), therefore energized thylakoids could play a considerable role in the thermostability of the photosynthetic apparatus even in different ways (Dulai *et al.* 2006, Sun *et al*. 2022). Accordingly, in the presence of light, better high-temperature stability was observed already in the case of well-watered plants (Fig. 1*B*,*C*,*E*,*F*) by comparison with dark-adapted samples (Fig. 1*A*,*D*). Furthermore, some studies demonstrated that water deficit before heating could increase the thermal stability of PSII, which was also reflected by the higher values of critical temperatures (Tc_{200}, Tc_{1000}) for F_sTCs and lower temperature sensitivity of effective quantum yield of PSII (Figs. 1, 4) in the PEG-treated wheat cultivars (Dulai *et al*. 2005, 2006; Ribeiro *et al*. 2008, Szopkó and Dulai 2018). This is also confirmed by the heat-induced changes in phenotypic plasticity (Fig. 2). In this context, Mitchell *et al*. (2025) have also shown a relationship between water scarcity and higher temperature tolerance of the photosynthetic apparatus in species from natural biomes. In addition, salt stress increased the thermal stability of PSII even more significantly compared to PEG treatment. This was also manifested by the shift of the *T*c values of the F_sTCs and phenotypic plasticity towards higher temperatures and the much better temperature dependence for Φ_{PSII} (Figs. 1, 2, 4). In parallel, the threshold values for the increase in quantum yield of nonregulated energy dissipation (Φ_{NO}) also shifted upward significantly (Fig. 6), indicating that thermal damage to PSII also occurred at higher temperatures compared to the untreated plants. All of this demonstrates the temperature-sensitivity-reducing effect of salt treatment (Touchette *et al*. 2020). In this regard, some studies observed enhanced thermal tolerance of the main targets of high temperatures such as the oxygen-evolving complex and PSII reaction centre (Chen *et al*. 2004, Wen *et al.* 2005, Yan *et al*. 2012, Mathur *et al*. 2013, Touchette *et al*. 2020) as a result of salt adaptation. In this case, since PEG treatment also moderately increased high-temperature

tolerance, it cannot be ruled out that the osmotic effect of salt treatment, in a light-adapted state, may be partially responsible for the decreased temperature sensitivity.

The nonradiative dissipation of excitation energy depends on both the trans thylakoid pH gradient and the activity of the xanthophyll cycle (Demmig-Adams 1990). Zeaxanthin, besides its direct photoprotective role, enhances the development of nonphotochemical quenching (NPQ; Kiss *et al.* 2008, Demmig-Adams *et al.* 2020, Ramakers *et al.* 2025) and maintains the stability of the thylakoid membranes (Havaux *et al.* 1996, Lavaud and Kroth 2006, Hemker *et al.* 2024), thus it possibly increases the thermal tolerance of PSII (Havaux and Tardy 1996, Molnár *et al.* 1998). The induction of the high-energy component (q_E) of NPQ requires a conformational change in the antenna system of PSII also associated with zeaxanthin accumulation (Jahns and Holzwarth 2012), leading to LHCII aggregation (Horton *et al.* 1991) which also represents a protective mechanism to high temperature (Khristin *et al.* 2021), through the dissipation of excess excitation energy (Tang *et al.* 2007). The values of the quantum yield of regulated energy dissipation (Φ_{NPQ}) in the osmotic/salt-treated plants significantly surpassed the control already at normal temperatures (*see* data in the legend to Fig. 5) and Φ_{NPQ} maxima were close to the Tc_{200} breakpoints of F_sTCs at the applied light intensity (Fig. 5). Thus, it can be seen, that the secondary effects of low lumen pH (Müller *et al.* 2001) may also play an important role in the protection against both the high temperature and the osmotic/salt stress (Dulai *et al.* 2005, Tang *et al.* 2007, Khristin *et al.* 2021). All this is also supported by the fact that significant shifts in *T*c values could be generated by the presence of light already in nonstressed plants in comparison with the Tc_{dark} values measured in a dark-adapted state (Fig. 1). Furthermore, the PEG and NaCl treatments applied in the light-adapted state resulted more significant increase in "absolute" phenotypic plasticity to high temperature and better thermal tolerance (Fig. 2). In addition, this Φ_{NPQ} upward shift, and the parallel higher thermal stability, partly persisted at the 2nd and 7th days of the relaxation period in salt-treated plants. Since the elevated excitation energy, and higher preillumination (actinic light) before and under heating, in osmotic and salt-treated plants did not further enhance the thermostability of PSII (Fig. 1*B–F*), it seems likely that light only modulates, *i.e.*, it does not directly influence, the extent of the rapid temperature tolerance change. However, this short-term improvement in thermal tolerance of photosynthesis requires energized thylakoids contrary to the ionic effect of salt treatment mentioned above which also occurs in a dark-adapted state.

As reported, net CO_2 assimilation may show stronger sensitivity to water deficit and salinity than the operation of the electron transport around PSII (Dulai *et al.* 2014, Darkó *et al.* 2015, Szopkó *et al.* 2017, Wang *et al.* 2024). During salt stress, high concentrations of Na^+ are undoubtedly toxic to various cellular functions, including photosynthesis, while K^+ is essential. The initial effect of salt treatment is osmotic stress, which causes stomatal closure, while the stronger ionic effect also damages other key processes of photosynthesis (Lu *et al.* 2023, Vineeth *et al.* 2023, Zahra *et al.* 2023, Wang *et al.* 2024). Osmotic stress tolerance and the exclusion of Na^+ and Cl^- therefore play an important role in protecting against the effects of salt stress. Thus, maintaining the Na^+/K^+ ratio low during salt stress is crucial to avoid severe damage (Munns and Tester 2008) in photosynthetic apparatus. As can be seen in Table 1S, the 300 mM salt treatment affected the Na^+/K^+ ratio of the shoots and roots to different degrees. Where this value was very high (Mv9kr1, Semito, GTA), P_N also decreased strongly, and in fact, the Semito and GTA varieties did not survive the salt treatment. In those cultivars, where this value decreased by the end of the relaxation period, the recovery of both P_N and P_{Nmax} was more adequate (Fig. 7).

In light-saturated C_3 plants with a well water supply, P_N does not reach the maximum level which would otherwise be measurable at saturating CO_2 concentration (P_{Nmax}; Lawlor and Cornic 2002). When stomatal closure is the main limiting factor during the osmotic/salt stress for CO_2 fixation, P_{Nmax} can be obtained by the application of saturating CO_2 concentration (Molnár *et al.* 2004, Dulai *et al.* 2014, Szopkó *et al.* 2017, Yang *et al.* 2021). As can be seen in Fig. 7, P_{Nmax} was practically fully restored during the osmotic stress in MvBéres, GTA, and Ancomarsio varieties indicating that the regulation of P_N was affected by stomatal limitation even at 21% PEG treatment. Furthermore, P_N and P_{Nmax} were fully recovered in all varieties during the relaxation period except GTA. The sensitivity of Mv9kr1, MvNádor, and Semito to osmotic stress was indicated by the fact that the saturation CO_2 concentration had a partial influence only, at stronger PEG treatment. Moderate salt stress (150 mM NaCl) had a similar effect to PEG treatment in most of the lines indicating the primary role of stomatal limitation (Szopkó *et al.* 2017). The extent of P_{Nmax} decreased in parallel with the severity of salt treatment for the wheat lines, confirming the importance of nonstomatal processes, such as biochemical (metabolic) and diffusional factors in the background of the limitation of CO_2 fixation (Lawlor and Cornic 2002, Flexas *et al.* 2004, Chaves *et al.* 2009, Yang *et al.* 2021). This decrease in P_{Nmax} was more pronounced in those lines where the shoot and root Na^+/K^+ ratio was higher, which can be related to the inhibitory effects of ionic stress on the photosynthetic apparatus (Lu *et al.* 2023, Wang *et al.* 2024).

The high temperature-induced decrease in the capacity of photosynthesis may be manifested in the limitation of CO_2 assimilation and alterations of photosynthetic electron transport and photophosphorylation (Berry and Björkman 1980, Sharkey 2005, Zahra *et al.* 2023, Wang *et al.* 2024). Although moderately high temperatures (below 40°C) do not damage PSII (Sharkey 2005), it is likely, that the less activity of photosynthetic electron transport causes a decrease in P_N indirectly due to stronger high-temperature stress (Berry and Björkman 1980). As shown in Fig. 7, the 45°C temperature treatment dramatically reduced both P_N and P_{Nmax}, and these parameters did not recover even after cooling back to 25°C in well-watered plants. This is consistent with the fact that *T*c values were mostly between 44 and 45°C at both AL intensities of 200 and

1,000 µmol(photon) m^{-2} s^{-1}. *T*c can be used as an indicator of the thermotolerance of the photosynthetic apparatus (Mitchell *et al*. 2025) in connection with the integrity of photosynthetic membranes (Hill *et al*. 2009). In addition, *T*c may also indicate the critical temperature where the quantum efficiency of net CO_2 fixation is impaired by heat treatment (Schreiber and Bilger 1987, Szopkó and Dulai 2018). Although P_N remained negative at 45°C during the osmotic treatments, P_{Nmax} took positive values, indicating a moderately improved thermal stability of photosynthesis in parallel with the higher *T*c values (Lu and Zhang 1999, Ladjal *et al*. 2000, Dulai *et al*. 2005). Thus, increasing the supply of CO_2 to Rubisco by high ambient CO_2 concentration slightly restores fixation even at such high temperatures in osmotically stressed plants. However, the increase in P_{Nmax} is definite but small, so photosynthetic CO_2 fixation is probably under nonstomatal control at such high temperatures. One of the nonstomatal factors affecting CO_2 fixation under stress conditions is the inhibition of photochemical and electron transport processes (Kalaji *et al.* 2011, Dulai *et al*. 2014, Szopkó *et al.* 2017). F_v/F_m, Φ_{PSII}, and the quantum yield of nonregulated energy dissipation (Φ_{NO}), which represents the energy fraction that is passively dissipated mainly from the closed PSII reaction centres, were strongly affected by temperature treatment at or above 45°C (Fig. 3, 5, 6). Thus, the inhibition of CO_2 fixation may be a consequence of downregulation of electron transport and at least partly of PSII damage (Berry and Björkman 1980, Dulai *et al*. 1998, Pshybytko *et al*. 2008, Jat *et al*. 2024, Moloi *et al*. 2025). After osmotic treatment, by the end of the relaxation period, this temporary improvement of thermal stability for P_{Nmax} subsided, similarly to the *T*c values, indicating the restoration of original thermal tolerance.

Salt stress had a much more pronounced effect on the temperature stability of CO_2 fixation: P_N showed slightly positive values after cooling back to 25°C from the 45°C temperature treatment, and the temperature stability of P_{Nmax} measured at 45°C was higher compared to the osmotic treatments (Fig. 7). All this was also reflected in the temperature dependence of the maximum and effective quantum yields, which were improved significantly. In addition, the threshold temperature for the increase in Φ_{NO} values was also shifted upward. In our experiments, F_v/F_m and Φ_{NO} were practically unaffected by 45°C temperature treatment. These results suggest that high temperature (45°C) under high salinity had no noticeable effect on the capacity of primary charge separation, and no high temperature-induced PSII damage was observed (Szopkó and Dulai 2018) even at such high temperatures. The extent of P_{Nmax} at 45°C was lower in parallel with temperature treatment for wheat lines than in a well-watered state at 25°C, indicating the primary role of nonstomatal factors. However, P_{Nmax} was partially restored even at a high temperature under salt stress which shows that the role of stomatal limitation cannot be neglected either. All the facts mentioned above clearly show the salt treatment enhances the thermal tolerance of photosynthesis (Chen *et al*. 2004, Yan *et al*. 2012, Szopkó and Dulai 2018, Touchette *et al*. 2020) much better than osmotic stress in the examined wheat varieties.

Comparing the wheat lines, Mv9kr1, MvNádor, and Semito were more sensitive to osmotic stress than the other examined varieties, but P_N was also recovered in these varieties after rewatering. GTA, MvBéres, and Ancomarsio were able to maintain the P_N measured in the control level even in the case of 21% PEG treatment, and for the latter two, this was not changed during the regeneration period. As the decrease in RWC for MvBéres was a sight (around 4% only), this suggests that an efficient osmoregulation mechanism may exist in this line, allowing maintenance of water uptake and thus serving as a promising ability to preserve photosynthesis during osmotic stress (Clifford *et al*. 1998, Dulai *et al*. 2014). And Ancomarzio, despite the moderate but measurable water loss, was also able to maintain its photosynthetic activity at a promising level. These do not mean that their photosynthetic parameters would not be sensitive to decreased cell water content, in any case, this could be an advantageous strategy for overcoming dry periods of a given duration while maintaining adequate photosynthesis and so dry matter production (Dulai *et al*. 2014). On the other hand, earliness is an important factor for wheat, because of its ability to escape from drought, salt and high-temperature stress (Mondal *et al*. 2013). In this regard, Semito matured and developed spikes by the end of the relaxation period for both the osmotic and salt stress. Salt treatment had a stronger effect on the photosynthesis of the lines than osmotic stress and recovery after rewatering was complete in only two varieties (MvNádor, MvBéres). In addition, GTA, similarly to osmotic treatment, dried out by the end of the experimental cycle, and necrotic symptoms appeared at 300 mM NaCl treatment in this variety indicating more pronounced salt susceptibility. However, salt increased the temperature stability of the photosynthetic apparatus much more strongly than the osmotic treatment. Interestingly, there was no significant difference between the wheat lines in either the osmotic or salt stress-induced increase in thermostability.

In conclusion, the individual wheat lines examined are sensitive to osmotic and salt stress to different degrees, but this possibly cannot be directly related to the climatic conditions of the cultivating areas. This may be true even if the fields of Central Europe are becoming increasingly drier and warmer. Both osmotic and salt stress stimulate the temperature stability of the photosynthetic apparatus in the light-adapted state, but only salt treatment has such an effect in the dark which can be interpreted largely as an ionic effect of salt treatment. Thus, it seems likely that the osmotic stress-induced thermal stability increase of PSII happens only in energized photosynthetic membranes, but salt stress can also affect thermal stability in other ways as well. In addition, salt stress induced thermal stability improvement of PSII even more significantly compared to PEG treatment in the preilluminated plants, which is also shown by the broader "absolute" phenotypic plasticity. This change in thermal tolerance plays a significant role in preventing the effects of daily changes in ecological factors. The secondary effects of low lumen pH may be important in protection against the effects of excess light and water/salt stress, *i.e.*, it is possible that the protection

against the effects of light, high temperature, water deficit, and salt stress partly reveals common characteristics. The facts mentioned above confirm that the rapid acclimation/acclimatization processes which protect against the simultaneous effects of environmental factors (light, osmotic/salt stress) have a pronounced agroecological role in the toleration of the unfavourable factors of growing areas for the examined wheat cultivars.

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