

Research Article

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Evaluation of Heat Shock-Induced Stress Tolerance to Some Abiotic Factors in Barley Seedlings by the Chlorophyll a Fluorescence Technique

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Abstract

In this study, the effect of heat shock pretreatment on the occurrence of cross tolerance to heat, salinity, drought, and UV-B stress in three barley (*Hordeum vulgare* L.) cultivars (Bülbül-89, Tarm-92, and Tokak 157/37) was investigated through the chlorophyll a fluorescence technique. Heat stress increased F_o (minimum fluorescence) significantly when compared to the controls of these barley cultivars, but heat shock pretreatment led to lower F_o values in all cultivars. F_m (maximum fluorescence), F_v/F_m (maximum quantum efficiency of photosystem II) and PI (performance index) were significantly decreased in all barley cultivars subjected to heat stress. In Tarm-92, heat shock pretreatment caused higher F_m , F_v/F_m and PI values than heat stress alone. On the other hand, heat shock pretreatment decreased F_m , F_v/F_m and PI more drastically in Bülbül-89 and Tokak 157/37. As a consequence, changes in F_o , F_m , F_v/F_m and PI may be attributed to thermotolerance development in Tarm-92 as a result of heat shock pretreatment.

Keywords: Barley, chlorophyll fluorescence, drought, heat shock, thermotolerance, UV-B

Arpa Fidelerinde Bazı Abiyotik Faktörlere Karşı Isı Şoku ile İndüklenen Stres Toleransının Klorofil a Floresansı Tekniği ile Değerlendirilmesi

Öz

Bu çalışmada üç farklı arpa (*Hordeum vulgare* L.) genotipinde (Bülbül-89, Tarm-92 ve Tokak 157/37) ısı şoku ön uygulamasının yüksek sıcaklık, tuz, kuraklık ve UV-B streslerine karşı çapraz tolerans oluşumu üzerindeki etkisi klorofil a floresansı tekniği ile araştırılmıştır. Yüksek sıcaklık stresi tüm genotiplerde F_o (minimum floresans) değerini kontrollere göre önemli derecede artırmış ancak ısı şoku ön uygulaması F_o değerini azaltmıştır. Yüksek sıcaklık stresine maruz bırakılan tüm arpa genotiplerinde F_m (maksimum floresans), F_v/F_m (fotosistem II'nin maksimum kuantum etkinliği) ve PI (performans indeksi) parametrelerinin kontrollere göre önemli oranda azaltmıştır. Tarm-92'de ısı şoku uygulaması, yüksek sıcaklık stresi uygulaması ile karşılaştırıldığında daha yüksek F_m , F_v/F_m and PI değerlerine neden olmuştur. Bülbül-89 ve Tokak 157/37'de ise ısı şoku ön uygulaması F_m , F_v/F_m ve PI parametrelerini daha belirgin şekilde azaltmıştır. Sonuç olarak F_o , F_m , F_v/F_m ve PI parametrelerindeki değişimlerin, Tarm-92'de ısı şoku ön uygulamalarının termotolerans gelişimine neden olduğu söylenebilir.

Anahtar kelimeler: Arpa, klorofil floresansı, kuraklık, ısı şoku, termotolerans, UV-B

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Introduction

An increasing body of evidence indicates that global climate change will have important effects on biological processes over the next decades. The expected climate changes include an increase in average temperature, an increase in atmospheric CO₂ concentrations and an alteration in rainfall regimes. Combustion of fossil fuels and widespread deforestation have caused atmospheric concentration of CO₂ to increase by 25% since the Industrial Revolution [1]. Concentration of other gases, including methane, nitrous oxide and chlorofluorocarbons, have also risen significantly due to human activities. Because of being radiatively active, these greenhouse gases absorb thermal radiation emitted from the Earth's surface and reradiate it back to Earth. There has been a consensus between environmental scientists that thermal energy circulation between greenhouse gases in the atmosphere and the Earth's surface is responsible for accelerated global warming. It has been reported that global mean surface air temperature has increased about 0.74°C during the last 100 year and will rise about 1.1-6.4°C by the end of this century [2]. However, a predicted 2°C increase in air temperature might lead to a 20-40% decrease in cereal yield, especially in Asia and Africa [3]. On the other hand, an

average annual increase in grain production of 44 million metric tons is required to meet food demands of the world by 2050 [4]. Another important process which is accompanied by global warming is increases in solar ultraviolet-B radiation due to continuous depletion of stratospheric ozone. Researchers have also proposed a linkage between ozone depletion and global warming due to some atmospheric gases such as CO₂ and CH₄ because of stratospheric cooling which favors ozone depletion reactions [5, 6]. Additionally, it has been known that any increases in evaporation due to warmer conditions would result in drought and salt accumulation in soil [7, 8]. As a result, we may conclude that plants must experience global warming-derived stress factors in natural environments either at the same time or in sequence. Observed changes in phenotypic traits of several plant species indicate that natural populations are responding to global warming [9]. For example, photosynthesis and respiration have been proposed as the main physiological reactions affected by high temperature and CO₂ increases [10]. Exposure of plants to elevated temperatures for short time (heat shock) induced different metabolic pathways, thereby enhancing thermotolerance and improving cellular survival to subsequent heat stress [11, 12].

Furthermore, heat-shock treatment improves not only plants' thermotolerance, but also increases their tolerance to chilling, salinity, drought and metal ion stress [13, 14, 15, 16]. This so-called cross tolerance, exposure of plants to a moderate stress induces resistance to other stresses, has been shown for different kind of stress combination [17, 18, 19, 20, 21].

In this preliminary study, we aimed to investigate whether a heat-shock pretreatment could simultaneously induce cross tolerance of barley seedlings to heat, salt, drought and UV-B stress thorough chlorophyll a fluorescence technique.

Material-Method

Plant Material and Growth Conditions

In the present work, three commercial cultivars of barley (*Hordeum vulgare* L. cv. Blbl-89, Tarm-92 and Tokak 157/37) were used. After sterilization in 5% sodium hypochlorite for 10 min, the seeds of these commercial cultivars of barley were pre-soaked for imbibition in distilled water for 4 h. The soaked seeds were sowed in plastic pots containing perlite and then put in a controlled growth chamber at $25/20 \pm 0.2^\circ\text{C}$ day/night temperature, with 16 h photoperiod under $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD and a relative humidity of $40 \pm 5\%$. The

plants were grown until they reached at four leaf stage.

Heat Shock Pretreatment and Stress Application

The plants at four leaf stage were transferred to 40°C for 4 h for heat shock. After this heat shock pretreatment, the plants were cultured under the same conditions as control plants 4 h for recovery. Immediately afterwards, the plants with and without heat shock were transferred to different stress treatments (50°C , 300 mM NaCl, dry perlite or UV-B irradiation) to test their cross tolerance to heat, salt, drought and UV-B stress. For heat stress, the plants were treated at 50°C for 12 h. For salt stress, the plants were irrigated with 300 mM NaCl solution for 2 days. For drought stress, the plants were transferred to other pots containing dry perlite for 2 days. For UV-B stress, the plants were irradiated with narrow band UV-B (312 nm) fluorescent tubes 1 h for 2 consecutive days from 30 cm distance. In all cases, temperature, humidity, photoperiod and light intensity values were the same as control plants except heat stress application. At the end of these stress treatments, plants were transferred to control conditions for 2 days for recovery and chlorophyll a fluorescence measurements were done in fully expanded 4th leaves. All measurements were replicated four times.

Chlorophyll a Fluorescence Measurements

Chlorophyll fluorescence measurement was made at room temperature with a Handy-PEA fluorometer (Hansatech Instruments Ltd, Kings Lynn, UK) after dark adaptation in growth chamber for 30 min. After measuring minimum (F_o) and maximum (F_m) fluorescence, the photochemical efficiency of PSII open centers was calculated from $[F_v/F_m = (F_m - F_o)/F_m]$ and expressed as the ratio of variable fluorescence (F_v) to maximum fluorescence, F_v/F_m . Performance index on an absorption basis (PI_{abs}) was calculated using the polyphasic rise of chlorophyll fluorescence transients provided from the JIP test [22].

Statistical analysis

The experimental design was a complete randomised block with four independent replicates. The replicated block consisted of five pots of five seedlings. The significance of difference from controls (mean values) was determined by one-way analysis of variance at 95% confidence level by using SPSS 11.0 statistical program.

Results

The changes of photosynthetic activity in barley leaves were evaluated on the basis of chl fluorescence measurement. F_o was not affected in all barley cultivars exposed to

heat shock (40°C for 4 h), salinity (300 mM for 2 d), drought (2 d) and UV-B (1 h for 2 consecutive days) stress alone. Also, heat shock pretreatment (40°C for 4 h) before salinity, drought and UV-B stress did not change F_o . Heat stress (50 °C for 12 h) caused significant increases in F_o in all barley cultivars. Heat shock pretreatment, on the other hand, decreased F_o significantly and alleviated the adverse effect of heat stress (Fig. 1). In Bülbül-89 and Tokak 157/37, heat shock, drought, heat stress and UV-B stress lowered F_m values significantly when compared to that of their controls. In these cultivars, however, F_m values were nearly as high as controls in drought and UV-B stressed seedlings as a result of heat shock pretreatment. In Tarm-92, heat shock pretreatment did not affect F_m significantly and as a result of heat shock pretreatment higher F_m value was obtained when compared to seedlings under heat stress alone. In Bülbül-89 and Tokak 157/37 subjected to heat stress, however, heat shock pretreatment caused lower F_m values (Fig. 2). The photochemical efficiency of PSII, assessed as F_v/F_m , were close to the upper theoretical value of 0.83 in all barley cultivars exposed to heat shock, salinity, drought, and UV-B stress irrespective of heat shock treatment.

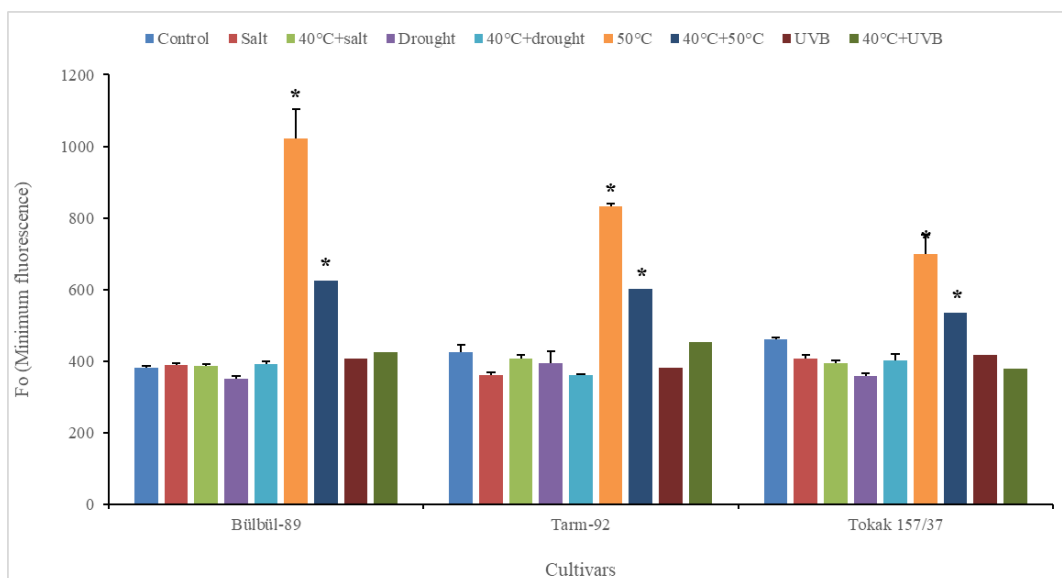


Figure 1. Effects of salinity, drought, heat and UV-B stress on F_o (minimum fluorescence) in heat shock pretreated and non-treated barley cultivars. Values are means \pm SE of four replicates in three independent experiments, and stars indicate significant difference from controls at the level of 0.05 ($P < 0.05$).

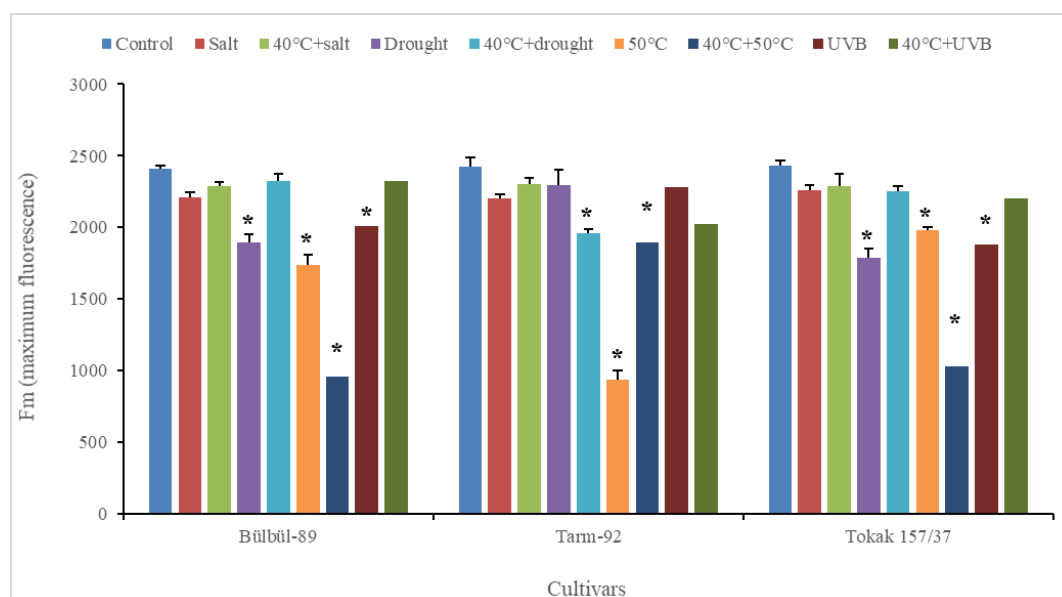


Figure 2. Effects of salinity, drought, heat and UV-B stress on F_m (maximum fluorescence) in heat shock pretreated and non-treated barley cultivars. Values are means \pm SE of four replicates in three independent experiments, and stars indicate significant difference from controls at the level of 0.05 ($P < 0.05$).

Heat shock pretreatment caused lower F_v/F_m ratio in Bülbül-89 and Tokak 157/37 exposed to heat stress alone while heat

shock pretreatment led to higher F_v/F_m ratio in heat stressed seedlings in Tarm-92 (Fig. 3).

PI was significantly lower than controls for heat shock pretreated and non-treated seedlings in all cultivars. In Bülbül-89 and Tokak 157/37, heat shock pretreatment increased PI when compared to seedlings under salinity, drought and UV-B stress alone and decreased PI in heat stressed seedlings. In Tarm-92, on the other hand, the negative effect of salinity,

drought, and UV-B stress was aggravated by heat shock pretreatment, as indicated by lower PI values. Nonetheless, PI was found to be higher in heat stressed seedlings pretreated with heat shock than non-pretreated ones in Tarm-92 (Fig. 4).

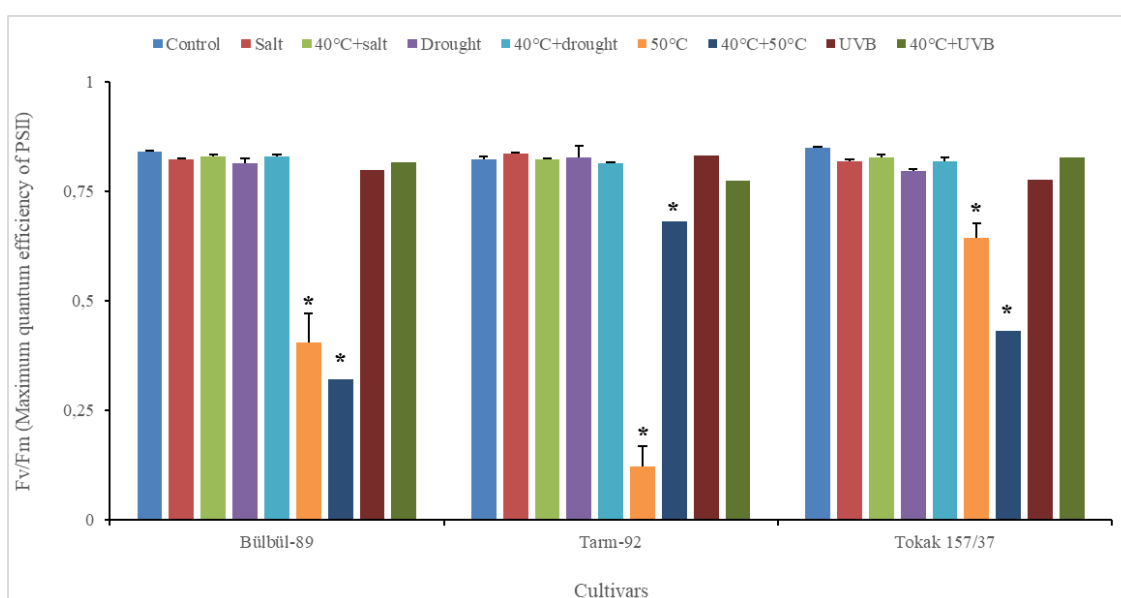


Figure 3. Effects of salinity, drought, heat and UV-B stress on F_v/F_m (maximum quantum efficiency of PSII) in heat shock pretreated and non-treated barley cultivars. Values are means \pm SE of four replicates in three independent experiments, and stars indicate significant difference from controls at the level of 0.05 ($P < 0.05$).

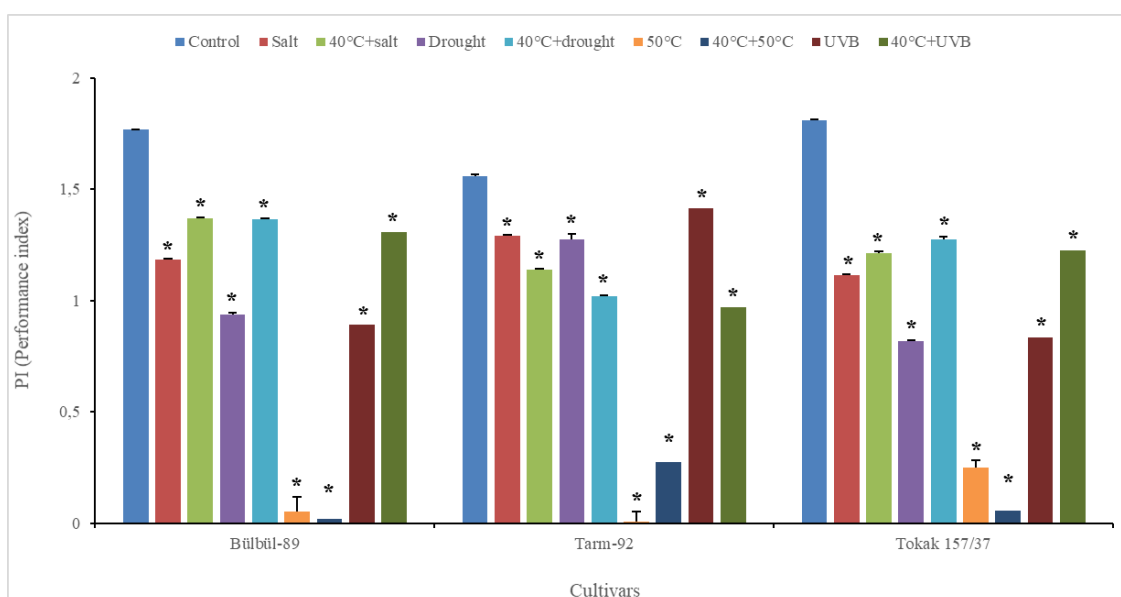


Figure 4. Effects of salinity, drought, heat and UV-B stress on PI (performance index) in heat shock pretreated and non-treated barley cultivars. Values are means \pm SE of four replicates in three independent experiments, and stars indicate significant difference from controls at the level of 0.05 ($P < 0.05$).

Discussion

All environmental stresses bring about perturbation in the cellular energy homeostasis in plants. Photosynthesis, as an energy-producing process, is considered as the physiological process most sensitive to environmental stress factors and plays an important role in modulating energy signaling and balance of the whole organism [23]. Consequently, it is essential to measure photosynthetic activity of plants under stress. For decades, chlorophyll a fluorescence technique has been recognized as an efficient method to screen plants for stress tolerance. This technique can give valuable information about the extent of damage which is caused by stress factors on

photosynthetic apparatus and about the ability of plants to tolerate any environmental stress [24]. It has been reported that chlorophyll a fluorescence technique can extensively be used in assessing plant responses to environmental stress [25]. According to Georgieva and Yordanov [26], increase in F_0 under stress could be interpreted as a decrease in the absorption efficiency of photons by chlorophyll a in the LHC (light harvesting complex) and of the reaction centre of PSII (photosystem II). It has been reported that high temperature treatments could promote dissociation between the LHC and PSII reaction centre, causing an increase of F_0 [27], while some authors considered that

increases of F_o may also be related to changes in the redox state of plastoquinone A (Q_A) [28]. F_o was not affected by salinity, drought, and UV-B stress in both heat pretreated and non-treated barley cultivars suggesting that the flux of energy from the LHC to the reaction centre of PSII is not affected. However, F_o values were significantly higher than controls in seedlings under heat stress but lower F_o values were measured as a result of heat shock pretreatment. Therefore, it may be interpreted that the damage and photoinactivation of the reaction centre of PSII units in heat stressed plants are alleviated by heat shock pretreatment. It is possible that heat shock pretreatment increased the effectiveness of excitation energy capture in PSII. It has been reported that all traps become closed and chlorophyll fluorescence rises to a maximal level (F_m) under stress conditions [25]. Maxwell and Johnson [24] stated that higher F_m values indicate that the fluorescence yield reaches a value equivalent to that which would be attained in the absence of any photochemical quenching. Georgieva and Lichtenthaler [29] suggested that changes in F_m values reflect the reduction degree of PSII acceptor side. Our results indicated that heat shock pretreatment led to higher F_m values in heat stressed seedlings in

Tarm-92 while lower F_m values were measured in Bülbül-89 and Tokak 157/37 seedlings subjected to heat stress alone. Therefore, it may be concluded that adverse effect of heat stress on the electron transport from the Q_A to the electron transfer chain was partly eliminated by heat shock pretreatment in Tarm-92. In Bülbül-89 and Tokak 157/37, as indicated by lower F_m values, the acceptor side of PSII was more reduced due probably to cumulative inhibitory effect of both heat shock and heat stress. The F_v/F_m ratio represents the efficiency of energy capture by open PSII centres. This value has been reported to be highly conserved at about 0.83 for non-stressed plants. A reduction in this value, referred to quantum yield of photosynthesis, indicates photoinhibition and damage to PSII due to environmental factors [30]. According to our results, there was no apparent photoinhibition in heat shock pretreated and non-pretreated seedlings as a result of salt, drought and UV-B stress although relatively lower but insignificant F_v/F_m values were measured than controls in all cultivars. Heat stress, on the other hand, decreased F_v/F_m significantly, which is regarded as an indicator of inactivation of PSII reaction centres because of the damage to thylakoid membrane [31]. But in the case of heat shock pretreatment, F_v/F_m value

was increased in Tarm-92 while it was decreased in Blbl-89 and Tokak 157/37. Several authors have reported that PSII is known to be the most heat-sensitive component of photosynthesis [32, 33, 34]. These results may be explained by the ameliorative effect of heat shock pretreatment on the physiochemical properties of the cellular membrane systems of foliar tissue in Tarm-92 seedlings, as demonstrated by electrolyte leakage measurement [35]. In Blbl-89 and Tokak 157/37, however, it appears that heat shock pretreatment caused more chronic photoinhibition. It has been reported that most chlorophyll a fluorescence parameters can offer detailed information on the structure and function of plant photosynthetic apparatus, mainly PSII [36]. Performance index (PI) is defined as a fluorescence parameter that could characterize plant vitality [37]. In our present study, significantly lower PI values than controls in all cultivars exposed to heat stress may indicate the interference of high temperature on the whole photosynthetic electron transport reactions. Straser et al. [38] reported that PI reflects the functionality of both PSI and PSII and gives us quantitative information on the current state of plant performance under stress conditions. On the basis of PI, these results

demonstrated that photosynthetic performance was seriously inhibited in Blbl-89 and Tokak 157/37 seedlings pretreated with heat shock before heat stress, but it was ameliorated in Tarm-92.

Conclusions

In conclusion, our results clearly showed significant indications for cross tolerance between heat shock and heat stress or thermotolerance development in Tarm-92 when evaluating the changes in chlorophyll a fluorescence parameters such as F_o , F_m , F_v/F_m and PI (Fig. 1). The changes in all chlorophyll fluorescence parameters were well correlated with thermotolerance development in Tarm-92. These chlorophyll fluorescence parameters has been reported to be routinely used for estimating thermotolerance in plants [39-41]. Similarly, Gamon and Pearcy [42] has stated that a sustained decrease in F_v/F_m and increase in F_o indicate the occurrence of photoinhibitory damage in response to high temperature, in accordance with our results. As a result, our chlorophyll fluorescence measurements confirmed that PSII activity in Tarm-92 could acclimate to heat stress and acquire thermotolerance probably via reprogramming cellular activity induced by heat shock pretreatment. Our results are in accordance with the findings of Law and Crafts-Brandner [43] for cotton and wheat.

Thermotolerance is a cellular phenomenon and results from prior exposure to a conditioning pretreatment, which can be a short but sublethal high temperature [44]. In addition to photosynthetic electron transport reactions, various physiological changes occur in plant cells for acquiring thermotolerance [44]. It is necessary to clarify the mechanism of thermotolerance development as a result of heat shock pretreatment in these barley cultivars. Hence, our investigations is still continuing to uncover physiological and biochemical responses for thermotolerance development.

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