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Effect of high temperature stress on *Hordeum vulgare* L. growth

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Abstract. Barley (*Hordeum vulgare* L.) is a vital cereal crop that is highly susceptible to a range of abiotic stresses, including low temperatures, drought, salinity, and particularly heat stress, which can significantly impair its growth and productivity. This study aimed to assess the impact of elevated temperature on the germination and physiological responses of the Astana 2000 barley cultivar. Seeds were germinated under controlled growth room conditions at an optimal temperature of 25°C (control) and a high temperature of 40°C to simulate heat stress. We evaluated several physiological and biochemical parameters, including chlorophyll content, malondialdehyde (MDA), and proline levels. Heat stress led to a noticeable decline in photosynthetic pigments, indicating reduced photosynthetic efficiency. In contrast, MDA and proline concentrations increased, reflecting enhanced lipid peroxidation and osmotic stress, respectively. Additionally, the activities of antioxidant enzymes such as aldehyde oxidase and catalase were significantly elevated under high temperature, suggesting an adaptive defense mechanism to counteract oxidative damage by detoxifying reactive oxygen species.

Keywords: *Hordeum vulgar*e, antioxidant enzymes, chlorophyll content, malondialdehyde (MDA), proline accumulation, oxidative stress, heat tolerance

Introduction

Abiotic stresses such as drought, salinity, heavy metal toxicity, and high temperature negatively affect crop productivity, leading to significant global yield losses [1]. Combined stress conditions are more detrimental to plants than individual stresses, as demonstrated by experiments involving barley, maize, and sorghum [2–4]. However, there is still insufficient data explaining the mechanisms of plant adaptation to stress conditions and how plants respond to different types of stress [5].

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Recent studies have reported that plants respond differently to various stress conditions, and the responses to one stress cannot be generalized to others [6,7]. Barley is one of the most widely cultivated crop species globally and is known for its superior adaptation to abiotic stresses [8]. This adaptation is attributed to its morphological flexibility, such as changes in root and shoot biomass and length, as well as the development of reproductive organs [9].

High temperature stress particularly affects the reproductive organs of barley and photosynthesis-related parameters [10]. Under heat stress, plants activate internal cooling mechanisms to lower tissue temperature, which helps maintain relative water content (RWC) [11]. Another damaging consequence of heat stress is the accumulation of reactive oxygen species (ROS), which results from an imbalance in ROS metabolism. The predominant ROS, hydrogen peroxide and superoxide can disrupt essential cellular processes in plants [12].

Oxidative stress also leads to a reduction in chlorophyll content and damage to Photosystem II (PSII) [13]. Additionally, ROS molecules interact with lipid double bonds, forming lipid hydroperoxides (LOOH). This accumulation of ROS disrupts membrane integrity and is indicated by stress markers such as malondialdehyde (MDA), acrolein, and 4-hydroxy-2-nonenal (HNE) [14,15]. Lipid peroxidation and increased MDA levels also affect amino acids such as arginine (Arg), lysine (Lys), proline (Pro), threonine (Thr), and tryptophan (Trp), leading to protein degradation [14].

In response to abiotic stress, plants activate an antioxidant defense system that participates in ROS scavenging [16]. The antioxidant system is divided into two groups. The first includes non-enzymatic antioxidants composed of low molecular weight molecules such as ascorbate (AsA), glutathione (GSH), non-protein amino acids, phenolic compounds, α-tocopherol, and various alkaloids. The second group consists of enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), peroxidases (POX), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione peroxidase (GPX), and glutathione S-transferase (GST) [17].

Catalase is a unique antioxidant enzyme capable of converting up to 26 million hydrogen peroxide molecules per minute per enzyme molecule [18]. Most studies on antioxidant enzyme activity in barley have examined moderate heat conditions (30–36°C), while less is known about enzyme activity at more extreme temperatures. Additionally, catalase activity has been detected in peroxisomes, mitochondria, and the cytosol [19]. The activity of antioxidant enzymes, including catalase and aldehyde oxidase, in plant tissues under heat stress remains underexplored in crops such as Hordeum vulgare L. In this study, we investigated the activity of these enzymes in barley under high-temperature stress.

Materials and research methods

Growth conditions and experimental procedures

For the research work, uniform seeds of the barley variety "Astana-2000" (*H. vulgare)* were used. Before sowing, the seeds were sterilized with a solution of hydrogen peroxide (H_2O2) for 10 minutes. The seeds were washed three times with purified water and dried. 150 g of sterilized soil and 10 g of vermiculite were placed in the pots, and 40 ml of purified water was

poured on top. 20 seeds were sown in each plastic pot. The soil pH was in the range of 6.0-6.5, and the main nutrients contained: nitrogen ($NH_4^+ + NO_3^-$) – 150 mg/l, phosphorus (P_2O_5) – 270 mg/l, and potassium (K_2O) – 300 mg/l. The plants were grown for 3 days at a temperature of +25°C (day and night), a photoperiod of 16 hours of light and 8 hours of darkness, and a relative humidity of 20–22%. 2700 K and 6400 K spectral lamps were used to light the growth chamber. Plants grown at a suitable temperature were divided into 2 groups after 3 days. For observation in a suitable environment, they were placed in chambers at a temperature of +25°C and a stress environment (high temperature) at +40°C.

Relative Water Content (RWC)

Relative Water Content (RWC) is a method for estimating the water content in plant tissues. Fresh weight (FW) was cut from leaf discs. The data was weighed and placed in a tube with water in a refrigerator at + 10°C for 24 hours to obtain the turgid weight (TW). After 24 hours, the fresh weight (FW) was dried on filter paper and weighed. To obtain the dry weight (DW), the samples were dried in an oven at + 80°C for 3 days [12]. RWC was calculated according to the standard formula:

$$\mathrm{RWC}(\%) = \frac{(\mathrm{FW} - \mathrm{DW})}{(\mathrm{TW} - \mathrm{DW})} \times 100\%$$

Determination of proline content

70 mg of leaf sample was mixed with 5 ml of 3% aqueous sulfosalicylic acid and ground in a mortar. The mixture was then centrifuged at 3000 rpm for 10 minutes. To 2 ml of this filtrate was added 2 ml each of glacial acetic acid and acid ninhydrin. The mixture was heated in a water bath at 100°C for 1 hour and cooled to room temperature. The toluene-containing chromophore was aspirated by removing the reaction mixture with 5 ml of toluene. The absorbance was recorded at 520 nm using a toluene buffer, and the proline concentration was measured using 0-50 mg/ml proline standards [20].

Determination of malondialdehyde (MDA) content

The MDA level in leaves was measured according to the method of Cakmak and Horst (1991), with minor modifications [14]. First, 100 mg of fresh leaves were ground in a mortar in 1 ml of 0.1% w/v trichloroacetic acid. The mixture was then centrifuged at 2000 rpm for 10 minutes, and the supernatant was added with 1 ml of 0.5% thiobarbituric acid prepared in 20% TCA and incubated in a water bath (95°C) for 45 minutes. After that, the solutions in the test tubes were cooled on ice and centrifuged again at 12000 rpm for 10 minutes. The supernatants were then selected for spectrophotometric analysis. To determine the amount of MDA, the optical density (OD) was measured at wavelengths of 532 and 600 nm.

Determination of chlorophyll content

Total chlorophyll content was measured according to the method of Arnon [15]. 100 g of plant leaves were homogenized with 25 ml of acetone (80%), and the homogenate was filtered. It was centrifuged at 6000 rpm for 15 minutes. Chlorophyll a, b, and carotenoids were calculated by

recording the absorbance at 645, 663, and 480 nm according to the recommendation of Arnon (1949) enzymes.

Protein extraction and fractionation for in gel activities

The preparation of samples for native PAGE was carried out. In ice-cold extraction buffers containing 250 mM Tris–HCl (pH 7.5), 250 mM sucrose, 1 mM ethylenediaminetetraacetic acid (EDTA), 4 mM 1,4-dithiothreitol (DTT), 5 mM l-cysteine, 0.001 mM aprotinin, 0.1 mM phenylene diamine tetraacetic fluoride (PMSF) and 0.001 mM pepstatin, fresh tissues were homogenized. The ratio of extraction buffer and tissue was 1:2 for leaves and 1:3 for roots. The plant tissue extracts were then centrifuged for 20 min at 10,000 rpm (+ 4 °C), then the supernatants were transferred to new tubes and carried out at 4 °C until 7.5% polyacrylamide gel electrophoresis in the absence of SDS Bradford M (1976) et.al [21]. The amount of soluble protein in the samples was calculated by Bradford assay, with BSA as a standard. All samples had been recalculated with the aim of loading 20 μg of soluble protein per line.

Determination of catalase (CAT) in gel activity

CAT activity was performed following the method of Aebi H (1984) et al [22]. The reaction mixture contained 10 μl of sample supernatant, 50 mM potassium phosphate buffer (pH 6.9), and 0.03% H_2O_2, mixed thoroughly for 15 min. After that, for visualization of catalase isozymes, the gel was incubated in 0.003% hydrogen peroxide solution for 10 min. Then, specific staining for catalase activity was performed in a solution containing 1% potassium hexacyanoferrate (III) and 1% iron (III) chloride.

Determination of aldehyde oxidase (AO) in gel activity

AO activity was determined following the method described by Sagi (1998) et.al [23] with slight changes. After electrophoresis, the gels were washed with distilled water and immersed in a staining solution that contained 1 mM indole-3-carboxaldehyde as substrate, 1 mM MTT (3-(4,5-dimethylthiazol-2-yl)-2,5-diphenyltetrazolium bromide) as indicator, 0.1 mM phenazine methosulfate as electron carrier in 0.1 M TRIS–HCl, pH 7.4, at + 37 °C for 40 min.

Results and discussions

Measurement of morphological traits of barley during high temperature stress

Like other abiotic stresses, high temperature stress negatively affects the growth and development of the entire plant organism, which plays a critical role in both the environment and agriculture. Increasing temperatures lead to reductions in morphological parameters such as root and shoot weight and length. As shown in our experiment, barley plants also exhibited a decreasing trend in shoot and root growth under heat stress (Figure 1). According to our results, shoot curling and rigidity appeared after 3 days at 40°C, in comparison with control plants grown at 25°C. Similar results were reported by Rollins et al., where shoot growth parameters declined under high temperature stress, and the lower leaves of barley cultivars were more severely damaged than the upper leaves [21]. Additionally, heat stress was found to delay shoot elongation in barley.

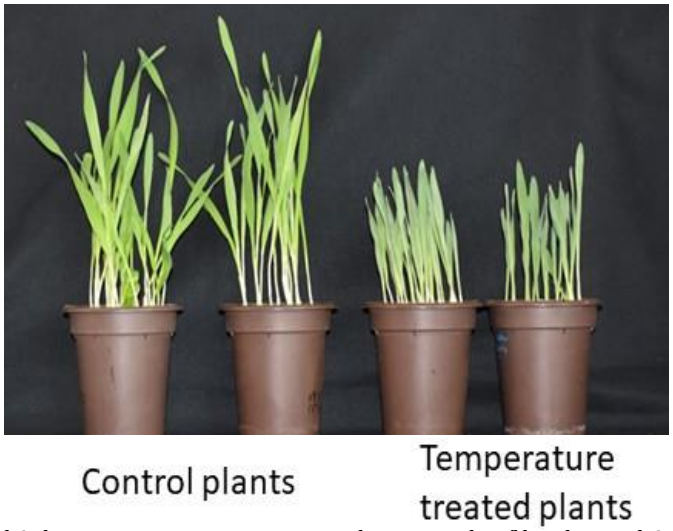
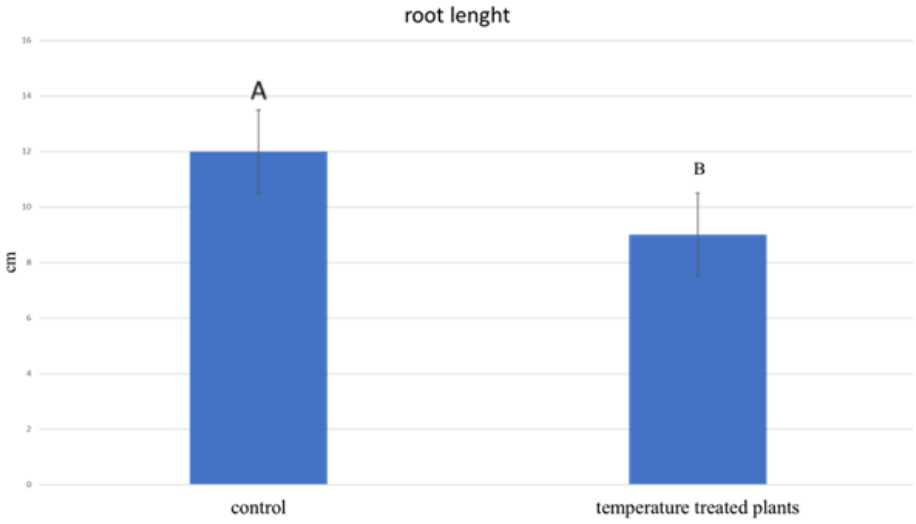


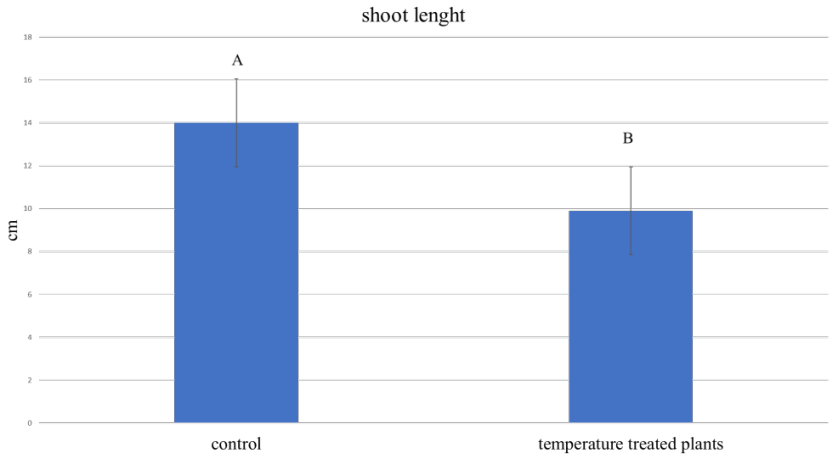
Figure 1. Effect of high temperature stress on the growth of barley cultivars in comparison with control plants within 3 days

As an above-ground part of plants, root growth also decreased under heat stress conditions in comparison with control plants. The length of roots declined and hardened at high temperature stress. Root length of heat-treated barley plants reached about 8-9 cm on average, whereas the control plants' roots varied from 12 to 15cm. These data are supported by other research results, which described a lessening trend of root parameters such as length, dry weight, and fresh weight (Figure 2,3) [24]. Additionally, root parameters decreased were detected in *Mimosa sepiaria* Benth. *(Fabaceae, Mimosoideae),* and *Ormosia glaberrima* Y. C. Wu *(Fabaceae, Papilionoideae*) [25].



Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, $P < 0.05$ (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature and control plants.

Figure 2. The root and shoot changes of barley plants exposed to heat stress for 3 days

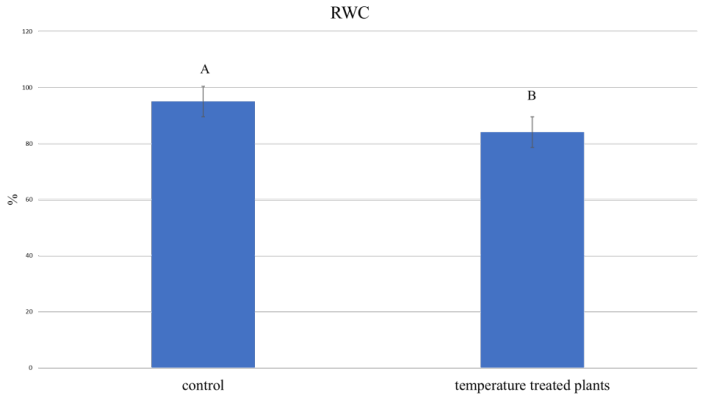


Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, P < 0.05 (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature and control plants.

Figure 3. The shoot changes of barley plants exposed to heat stress for 3 days

Effect of High Temperature on Relative Water Content (RWC) in Barley Plants

A reduction in morphological parameters as a consequence of heat stress leads to a decline in the relative water content (RWC) of plants. In our study, a noticeable decrease in RWC was observed in barley plants exposed to 40°C after three days. Furthermore, similar trends have been reported in other studies involving barley, tomato, and maize [21,26,27]. However, tall fescue plants exhibited a higher relative water content (RWC), which may be attributed to the unique physiological characteristics of tall fescue, particularly its ability to rapidly absorb water (Figure 4) [28].



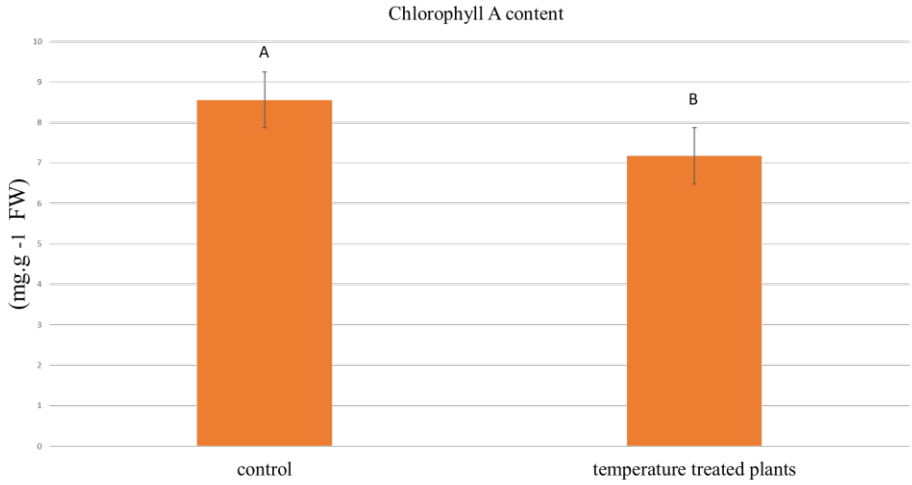
Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, P < 0.05 (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature control plants. Asterisks indicate significant differences between temperature stress and control.

Figure 4. The relative water content (RWC) changes of barley plants in response to heat stress (changes are shown as a percentage)

Under elevated temperatures, markers related to photosynthetic activity were significantly diminished. One of the primary factors contributing to the reduced growth rate is the decline in chlorophyll content [29,30]. In line with our findings, the barley cultivar also demonstrated a decrease in chlorophyll levels in heat-treated plants compared to the control group. Moreover, chlorophyll a (chlA) (Figure 5) content exceeded chlorophyll b (chlB) (Figure 6) content under both conditions; however, the chlA/chlB ratio declined in stressed plants, whereas control plants exhibited a significantly higher ratio (Figures 5, 6).

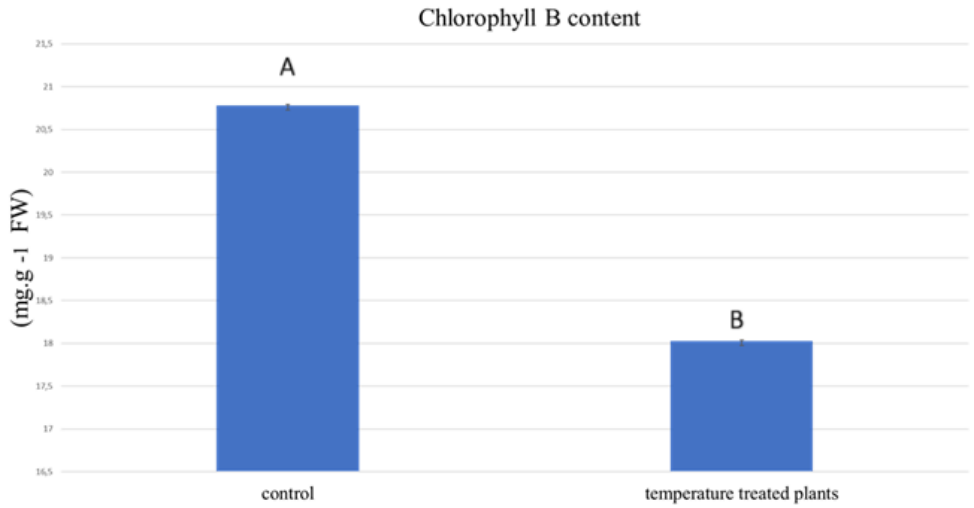
A reduction in chlorophyll content has also been observed in other barley cultivars, suggesting a suppression of stomatal aperture, which enhances resistance by limiting carbon dioxide uptake and minimizing water loss [31]. Additionally, during heat stress, the structure of enzymes is disrupted by reactive oxygen species (ROS), leading to a decline in chlorophyll biosynthesis [32,32,33]. A decrease in chlorophyll biosynthesis, particularly chlorophyll a (chlA) (Figure 5), has been documented in both soybean and barley [31].

Under stress conditions, ROS are generated within plastids and are highly toxic to the photosynthetic machinery. As a result, the thylakoid membranes become a primary target for oxidative damage caused by aldehydes [34]. As previously mentioned, ROS accumulation is a common response in plants subjected to abiotic stress, including elevated temperatures. Excessive ROS production triggers the activation of the plant's antioxidant defense systems, which comprise both enzymatic and non-enzymatic components [35].



Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, $P < 0.05$ (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature and control plants

Figure 5. The photosynthetic pigments changes of barley plants, such as chlorophyll a, in response to heat stress



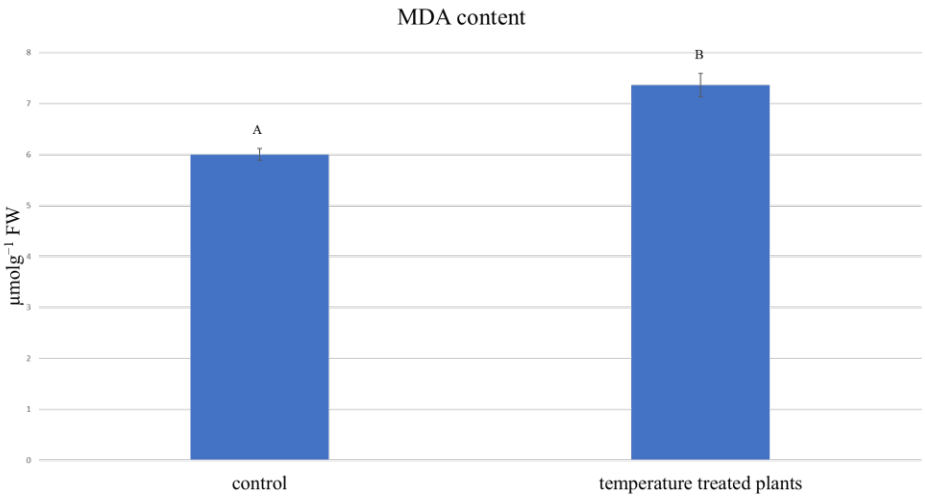
Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, $P < 0.05$ (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature and control plants

Figure 6. The photosynthetic pigments changes of barley plants, such as chlorophyll b, in response to heat stress

Detection of Enzymatic and Non-Enzymatic Antioxidant Activity in Barley Plants

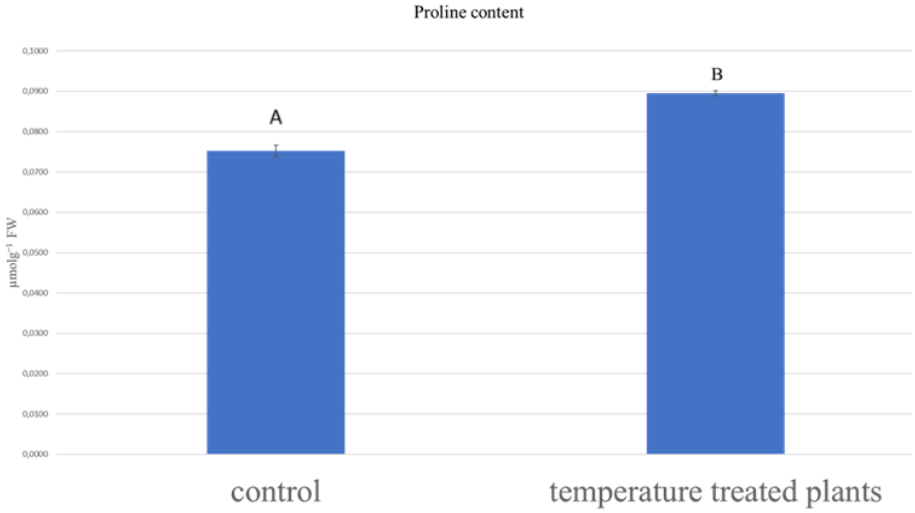
It is well established that thylakoid membranes contain a high proportion of polyunsaturated fatty acids, which serve as precursors to various aldehydes, including malondialdehyde (MDA) [36,37]. When barley plants are exposed to heat stress, MDA levels increase sharply. Elevated MDA content indicates significant disruption of membrane integrity. Similar patterns have been reported in barley, rice, and maize cultivars under high-temperature stress conditions (Figure 7) [29,38]. MDA accumulation within plant tissues can activate defense mechanisms known as the non-enzymatic antioxidant system.

One of the key molecules of non-enzymatic antioxidant systems is proline. Proline accumulation during the heat stress condition is associated with its function acting as a ROS scavenging molecule [31]. In our experiments, was detected higher accumulation of proline molecules was detected in temperature-treated plants in comparison with control plants (Figure 8).



Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, P < 0.05 (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature and control plants.

Figure 7. Malonaldehyde (MDA) changes of barley plants in response to heat stress



Note: Values denoted with different letters are significantly different according to the Tukey–Kramer HSD and T test analyses, P < 0.05 (JMP 15.1.0) software, http://www.jmp.com/). Different uppercase letters indicate significant differences between temperature control plants.

Figure 8. Proline changes of barley plants in response to heat stress

Excessive proline accumulation may be associated with the plant's adaptive response to heat stress (Figure 8). Proline contributes to enhancing the water potential of plant tissues by improving osmotic balance, thereby reducing oxidative stress-induced damage [38,39]. Furthermore, increased proline levels facilitate greater water uptake under stress conditions, which in turn positively influences stomatal aperture regulation [40].

Aldehyde Oxidase (AO) and Catalase (CAT) Activity in Barley Plants Under High Temperature Stress

Aldehyde oxidase (AO) belongs to a multigene family of enzymes characterized by broad substrate specificity. AO plays a key role in the biosynthesis of abscisic acid (ABA) by catalyzing the conversion of abscisic aldehyde into abscisic acid. Additionally, it contributes to the biosynthesis of indole-3-acetic acid (IAA) by converting indole-3-acetaldehyde into IAA [41–43]. AO activity has been reported to increase under stress conditions in both maize and barley [44,45]. Consistent with these findings, our results also demonstrated a significant rise in AO activity when barley plants were exposed to 40 °C for three days (Figure 9A). This suggests an upregulation of abscisic acid biosynthesis during heat stress, with elevated AO activity serving as a biochemical indicator of this process.

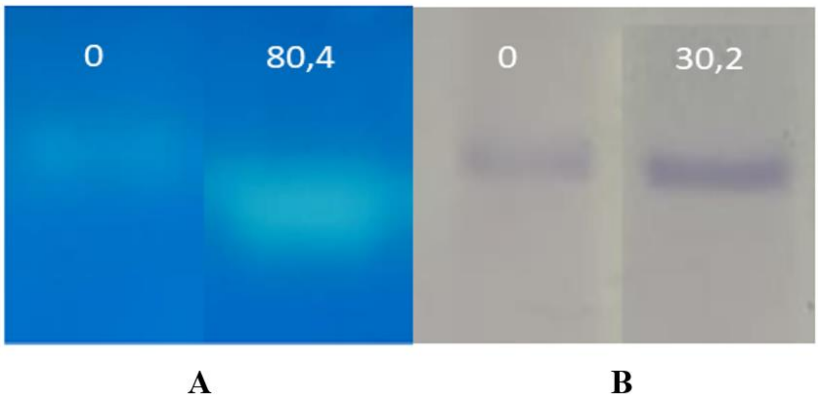


Figure 9. (A) Catalase activity (B) aldehyde oxidase activity in barley plants during the high temperature stress

When plants are exposed to high-temperature stress, their antioxidant defense systems are activated in response to oxidative stress (Figure 9B). The enzymatic antioxidant defense system functions by converting toxic reactive oxygen species (ROS) into less harmful molecules. Key enzymes involved in this process include superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). Catalase plays a vital role in plant responses to temperature fluctuations - both increases and decreases - as demonstrated in experiments with maize plants [46].

Similarly, barley plants exhibited increased catalase activity under elevated temperature conditions compared to control plants. This enhanced activity is associated with rising ROS levels during heat stress, where catalase contributes to mitigating oxidative damage by decomposing

hydrogen peroxide into water. However, chronic exposure to elevated temperatures may not always induce significant oxidative stress, which can result in a non-significant increase in catalase activity. Nevertheless, such prolonged stress can impair plant growth and development [47].

Conclusion

High-temperature stress is a critical environmental factor that can hinder plant growth and development. Growth retardation is typically observed through shortened shoots, hardened roots, and leaf curling. As reported in previous studies, ROS accumulation occurs primarily in the plastids and mitochondria under high-temperature conditions. The presence of excessive ROS leads to membrane damage, as lipid components within the membranes undergo oxidation. This oxidative damage is evidenced by an increase in malondialdehyde (MDA), a byproduct of lipid peroxidation.

Furthermore, oxidative stress can suppress photosynthetic performance, resulting in a reduction of chlorophyll content, as observed in barley plants compared to control groups. To counteract such stress, plants activate antioxidant defense mechanisms comprising both enzymatic and non-enzymatic components, including proline, catalase, and aldehyde oxidase (AO). Catalase functions as a ROS scavenger, alleviating oxidative damage, while AO contributes to the biosynthesis of abscisic acid (ABA), a key hormone involved in stress signaling pathways.

As demonstrated in our research, barley plants exhibited elevated antioxidant defense responses under heat stress; however, growth and developmental processes were still adversely affected. These findings underscore the necessity for further investigations into stress-related signaling cascades, ABA biosynthesis, and its alternative pathways. Such research is crucial for the development of heat-tolerant crop hybrids.

Authors contributions

A.S., B.B., and **A.K. –** conceptualization; **B.B.** and **A.S.** – data curation; **B.B.**, **A.S.**, and **A.K.** – formal analysis; **B.B.**, **A.S.** and **A.K.** – writing – original draft; **B.B.**, **A.S.**, **A.K.**, **A.S.**, **M.B., K.Zh., M.M.**, **Zh.M.**, and **A.K.** – writing – review & editing; **A.K.** and **Zh.M.** – supervision. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Compliance with ethical standards

This article does not contain a description of studies performed by the authors involving people or using animals as objects.

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Жоғары температура стрессінің Hordeum vulgare L. өсуіне әсері

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Аңдатпа. Арпа (*Hordeum vulgare* L.) – абиотикалық күйзелістерге, соның ішінде төмен температураға, құрғақшылыққа, тұздылыққа, әсіресе оның өсуі мен өнімділігін айтарлықтай нашарлататын ыстық күйзелістерге өте сезімтал өмірлік маңызды дәнді дақыл. Бұл зерттеу жоғары температураның Астана 2000 арпа сортының өнуіне және физиологиялық реакцияларына әсерін бағалауға бағытталған. Тұқымдар жылу кернеуін модельдеу үшін 25°C

(бақылау) оңтайлы температурада және 40°C жоғары температурада бақыланатын өсу бөлмесі жағдайында өніп шықты. Біз бірнеше физиологиялық және биохимиялық параметрлерді, соның ішінде хлорофилл мазмұнын, малондиальдегидті (МДА) және пролин деңгейін бағаладық. Жылулық стресс фотосинтетикалық пигменттердің айтарлықтай төмендеуіне әкелді, бұл фотосинтетикалық тиімділіктің төмендеуін көрсетеді. Керісінше, МДА және пролин концентрациясы жоғарылады, бұл сәйкесінше липидтердің асқын тотығуының және осмостық стресстің жоғарылауын көрсетеді. Сонымен қатар, альдегидоксидаза және каталаза сияқты антиоксиданттық ферменттердің белсенділігі жоғары температурада айтарлықтай жоғарылады, бұл реактивті оттегі түрлерін детоксикациялау арқылы тотығу зақымдануына қарсы тұру үшін бейімделген қорғаныс механизмін ұсынады.

Түйін сөздер: *Hordeum vulgare*, антиоксидантты ферменттер, хлорофилл мазмұны, малондиальдегид (МДА), пролиннің жинақталуы, тотығу стрессі, жылуға төзімділік

Влияние высокотемпературного стресса на рост Hordeum vulgare L

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Аннотация. Ячмень (*Hordeum vulgare* L.) является жизненно важной зерновой культурой, которая очень восприимчива к ряду абиотических стрессов, включая низкие температуры, засуху, засоление и особенно тепловой стресс, которые могут значительно ухудшить его рост и урожайность. Целью данного исследования была оценка влияния повышенной температуры на прорастание и физиологические реакции сорта ячменя Астана 2000. Семена проращивали в контролируемых условиях вегетационной комнаты при оптимальной температуре 25 °C (контроль) и высокой температуре 40 °C для имитации теплового стресса. Мы оценили несколько физиологических и биохимических параметров, включая содержание хлорофилла, малоновый диальдегид (МДА) и уровни пролина. Тепловой стресс привел к заметному снижению фотосинтетических пигментов, что указывает на снижение эффективности фотосинтеза. Напротив, концентрации МДА и пролина увеличились, отражая усиление перекисного окисления липидов и осмотического стресса соответственно. Кроме того, активность антиоксидантных ферментов, таких, как альдегидоксидаза и каталаза, значительно возросла при высокой температуре, что предполагает адаптивный защитный механизм для противодействия окислительному повреждению путем детоксикации активных форм кислорода.

Ключевые слова: *Hordeum vulgare*, антиоксидантные ферменты, содержание хлорофилла, малондиальдегид (МДА), накопление пролина, окислительный стресс, устойчивость к теплу

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