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The phenylurea cytokinin 4PU-30 protects maize plants against glyphosate action

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Abstract

The effects of the phenylurea cytokinin 4PU-30 and the herbicide glyphosate, applied alone and in combination on young maize plants were investigated. The influence of the compounds on the changes of growth, chlorophyll content, levels of hydrogen peroxide, and some stress markers, the activities of peroxidase, catalase, and glutathione-*S*-transferase, as well as glutathione amount were measured 3, 6, and 10 days after the treatment. The application of glyphosate increased the levels of lipid peroxidation, glutathione, and free proline content, ion fluxes, and the activity of catalase, guaiacol peroxidase, and glutathione-*S*-transferase, i.e., along with the inhibition of its target enzyme the herbicide induced also an oxidative stress. We found that the phenylurea cytokinin 4PU-30 alleviated in some extent the detrimental effects due to the glyphosate action. Moreover, we speculated that the cytokinin renders its protective action by induction of "hardiness" in the antioxidant defense systems in maize plants similarly to the effects observed after the application of some herbicide safeners.

Keywords: Phenylurea cytokinins; 4PU-30; Herbicide safeners; Glyphosate; Maize; Oxidative stress; Glutathione; Hydrogen peroxide

1. Introduction

Glyphosate [(*N*-phosphonomethyl)glycine] is a highly effective broad-spectrum, non-selective, post-emergence herbicide which is used extensively worldwide. The target site of glyphosate action is the enzyme 5-enoylpyruvylshikimate-3-phosphate synthase [1,2]. The inhibition of this enzyme causes an accumulation of shikimic acid and a consecutive diminish in the biosynthesis of aromatic amino acids, auxins, vitamins, as well as a number of key metabolites produced via the shikimate pathway, all this leads to a suspended plant growth, and in turn to plant death [3]. The glyphosate degradation appears to be very slow or is not taking place in higher plants [4]. Several classes of pesticides (including sim.-triazine and dichloroacetamide herbicides) are metabolized in plants into glutathione conjugates by the action of the enzyme glutathione-*S*-transferase (GST) [5]. Presently, the role of glutathione in glyphosate detoxification (conjugation) has not been exactly elucidated. However, increased levels of non-protein thiols, especially glutathione, as well as glutathione-*S*-transferase activity due to glyphosate action in several plant species were recently reported [6–8]. These observations give a ground for a search of factors which could enhance the plant tolerance to the unfavorable consequences due to the glyphosate action and thus to alleviate the herbicide toxicity.

Cytokinins are the class of plant hormones which were first identified as factors promoting cell division and have been implicated in many aspects of plant growth and development. Proper application of hormone-containing products can not only enhance the plant growth but also can improve the stress tolerance [9]. For example, the treatment with kinetin protects creeping bentgrass subjected to drought [10], and use of zeatin riboside alleviates heat stress injury [11]. Phenylurea cytokinins are compounds evoking growth response comparable to or higher than the adenine derivatives [12,13]. It was found that the application of

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BRIEF COMMUNICATION

Influence of cytokinins and novel cytokinin antagonists on the senescence of detached leaves of *Arabidopsis thaliana*

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Abstract

Cytokinins N^6-benzyladenine (BA) and 1-(2-chloropyridin-4-yl)-3-phenylurea (4PU-30) delayed the senescence of detached leaves (3rd to 7th leaf node) of wild and ethylene insensitive *eti5* mutant of *Arabidopsis thaliana*. The novel anticytokinins, structural analogues of purine and phenylurea cytokinins also affected the senescence of detached rosette leaves of *A. thaliana*. They diminished to a significant extent the cytokinin-induced delay of chlorophyll destruction, but without a considerable difference in their action against both types of cytokinins. These results correlated with changes observed in ribonuclease (RNase) activity.

Additional key words: anticytokinins, chlorophyll, ethylene insensitive mutant, leaf node, RNase.

Senescence (natural or induced by various artificial factors) is accompanied by destruction of photosynthetic pigments and leaf yellowing is one of the first visible symptoms of this process (Thomas and Stoddart 1980, Zacarias and Reid 1990, Sergiev *et al*. 2003, Todorov *et al*. 2003a,b, Alexieva *et al*. 2004). The leaf isolation is a key event leading to commencement of the senescence mechanisms. The growth promoting as well as senescence-delaying properties of cytokinins and their action as anti-senescence agents are wide studied (Van Staden *et al*. 1988, Zacarias and Reid 1990, Stoynova-Bakalova *et al*. 2001, Wilhelmová *et al*. 2004). On the other side, the application of cytokinin antagonists eliminates the cytokinin-induced hindrance of senescence in excised leaves and other model systems (Karanov *et al*. 1993, Alexieva *et al*. 1994, Sergiev 1999). The destruction of RNA and induction of RNase activity are characteristic for the senescence in higher plants (Dangl *et al*. 2000). To our knowledge, the effects of cytokinin antagonists in relation to senescence-induced changes in RNase activity are not studied.

Arabidopsis mutants have been used increasingly in physiological and biochemical studies (Kieber 1997). We used plants of *Arabidopsis thaliana* (L.) Heynh. wild type (WT), and the ethylene insensitive mutant *eti5*. This mutant (Harpham *et al*. 1991) possesses characteristics of delayed senescence accompanied with higher amount of leaf pigments and soluble proteins (Sergiev *et al*. 2003, Todorov *et al*. 2003a,b). In the present work we investigated the effect of synthetic purine and phenylurea cytokinins and their novel structural analogues with anticytokinin properties on chlorophyll (Chl) content and RNase activity in detached rosette leaves.

The plants were grown in plastic pots, filled with soil/*Perlite* mixture (3:1) in a growth chamber (16-h photoperiod, 70 µmol m^{-2} s^{-1} photon flux density, 24/20 °C day/night temperature, 60 % air humidity). The plants were daily irrigated. In order to characterize the senescence of detached rosette leaves in presence of purine and phenylurea cytokinins, their antagonists

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Abbreviations: BA - N^6-benzyladenine; 2PU-3 - 1-(4-chlorophenyl)-3-(pyridin-2ylmethyl)urea; 4PU-30 - 1-(2-chloropyridin-4-yl)-3-phenylurea; RNase - ribonuclease; TP-5 - 3-benzyl-7-(4-methylpiperazin-1-yl)-3*H*-[1,2,3]triazolo[4,5-*d*]pyrimidine.
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ORIGINAL PAPER

Polyamine content in *Arabidopsis thaliana* (L.) Heynh during recovery after low and high temperature treatments

Dessislava Todorova · Iskren Sergiev · Vera Alexieva · Emanuil Karanov · Aileen Smith · Michael Hall

Received: 26 January 2006 / Accepted: 18 October 2006 / Published online: 1 February 2007

Abstract Comparative studies on the effect of temperature treatment on the endogenous polyamine content in wild type and the ethylene insensitive mutant *eti5* of *Arabidopsis thaliana* (L.) Heynh were performed. The levels of free and conjugated putrescine, spermidine and spermine were measured in rosette leaves of 38-day-old plants subjected to low and high temperature for 24 h in darkness. Data for fractions measured in treated wild type plants during recovery suggest that alterations in polyamine levels may be a consequence of the conversion of the supernatant-bound into free form and *vice versa*, while in treated *eti5* plants *de novo* synthesis of spermidine and spermine could not be excluded. It was found that high temperature provoked more significant changes in polyamine levels than low temperature. The results suggest that the *eti5* mutant showed a better ability to recover after the temperature treatments than wild type partly as a consequence of changes in polyamine content.

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Keywords *Arabidopsis thaliana* (L.) Heynh · Ethylene insensitive mutant (*eti5*) · High temperature · Low temperature · Polyamines · Putrescine · Spermidine · Spermine

Abbreviations

HT	High temperature (38°C)
LT	Low temperature (4°C)
PA	Polyamine
Put	Putrescine
Spd	Spermidine
Spm	Spermine
TCA	Trichloroacetic acid
Wt	Wild type

Introduction

Polyamines (PAs) are organic molecules, widely distributed in both higher and lower plants. The PAs common for all plant species are putrescine (Put), spermidine (Spd) and spermine (Spm). They occur as free molecules, but can also be conjugated with small molecules such as phenolic acids or macromolecules like nucleic acids and proteins (Bouchereau et al. 1999). Like plant hormones, PAs may promote growth and provoke

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HYDROGEN PEROXIDE PRETREATMENT ALLEVIATES PARAQUAT INJURIES IN PEA (*PISUM SATIVUM* L.)

Irina Moskova, Dessislava Todorova, Vera Alexieva, Iskren Sergiev

(*Submitted by Academician V. Golemansky on June 20, 2007*)

Abstract

Hydrogen peroxide is a molecule natively generated in plants during the normal physiological processes. However, under stress conditions it can be massively produced and can become toxic for the cells. Recently other authors reported that the exogenous application of hydrogen peroxide in low concentrations renders protection of plants against different stress factors. In this investigation we report the protective role of preliminary treatment with H_2O_2 against the toxic action of the herbicide paraquat in pea plants. The changes in some physiological parameters, such as plant survival, content of malondialdehyde, leaf pigments and photosynthetic rate were determined in relation to the paraquat toxicity in H_2O_2-treated plants.

Key words: CO_2 assimilation, hydrogen peroxide, leaf pigment, MDA, paraquat, *Pisum sativum*

Abbreviations: H_2O_2 – hydrogen peroxide, MDA – malondialdehyde, PQ – paraquat

Introduction. Hydrogen peroxide is a native metabolite in all living organisms. It is generated enzymatically (by superoxide dismutase, glycolate oxydase, NADPH peroxidase, etc.) or nonenzymatically in plant cells. In photosynthetic tissues H_2O_2 is produced mainly in chloroplasts. However, in high concentrations H_2O_2 is a toxic metabolite. On the other hand, exogenous application of H_2O_2 in low concentrations is announced to stimulate the activity of some antioxidant enzymes in plants which can increase their protective capacity against some stress factors. For example, the application of H_2O_2 increased the resistance of maize seedlings [1], mung been [2] and potato nodal explants [3] to low temperature. The preliminary treatment with H_2O_2 of Arabidopsis or tobacco protects the plants from oxidative damages due to high light intensity [13,14].

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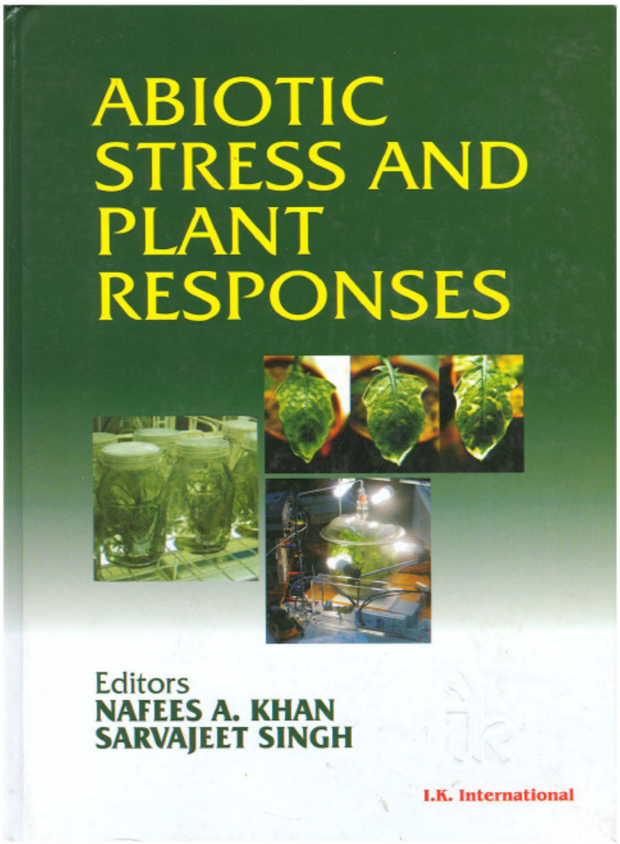

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Changes in Endogenous Polyamines and Some Stress Markers Content Induced by Drought, 4PU-30 and Abscisic Acid in Wheat Plants

D. Todorova[1], I. Moskova[1], I. Sergiev[1], V. Alexieva[1]* and S. Mapelli[2]

ABSTRACT

Aerial parts of 7-day old wheat (*Triticum aestivum* L.) seedlings were sprayed with a water solution of the phenylurea cytokinin 4PU-30 or ABA. Twenty-four hours later, part of them was subjected to moderate (– 0.2MPa) or strong (–1.0MPa) water stress. It was found that both stresses induced an accumulation of free, SN-bound and pellet-bound Put in shoots and roots of wheat plants. Free Spd and Spm fractions were little affected by drought in both organ tissues. SN-bound and pellet-bound fractions of Spd and Spm were enhanced in shoots, but in roots strong water deficit provoked a decrease in these fractions. The application of ABA and 4PU-30 caused a slight rise in polyamine levels. In combination with water deficit they increased almost all polyamine levels, but the effect on the free Put in shoots was most substantial. Water shortage also provoked membrane integrity deterioration, mainly due to the lipid peroxidation. Both plant growth regulators significantly reduced the malondialdehyde levels and free proline content of drought-treated wheat seedlings. The results obtained present additional information about the physiological role of growth regulators in relation to water stress.

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ORIGINAL PAPER

Effect of exogenous hydrogen peroxide on enzymatic and nonenzymatic antioxidants in leaves of young pea plants treated with paraquat

Irina Moskova · Dessislava Todorova · Vera Alexieva · Sergei Ivanov · Iskren Sergiev

Received: 14 August 2007 / Accepted: 28 September 2008 / Published online: 18 October 2008

Abstract The effects of exogenously applied hydrogen peroxide on the antioxidant system of pea plants were investigated. Ten-day-old pea seedlings were sprayed with 2.5 mM H_2O_2 and 24 h later with 0.2 mM PQ. Samples were taken 0, 2 and 5 h after the start of illumination. The protective effect of H_2O_2 was evaluated by monitoring of parameters related to the damage caused by PQ. The treatment with PQ led to a severe leakage of electrolytes from leaf tissues. Malondialdehyde level increased in PQ treated plants, but remained unchanged in H_2O_2 pre-treated ones after 5 h of illumination. Increased catalase and glutathione-S-transferase activity was observed in pea plants treated with H_2O_2 and PQ. Ascorbate peroxidase activity decreased significantly after paraquat application, but pre-treatment with H_2O_2 prevented ascorbate peroxidase inhibition to some extent. Increased guaiacol peroxidase activity was detected after H_2O_2 application. PQ application caused a drastic decline in the levels of thiol-group bearing compounds, reduced glutathione and ascorbate, while the quantity of oxidized glutathione and dehydroascorbate were increased. The results presented on changes in enzymatic and nonenzymatic antioxidants suggest that preliminary H_2O_2 application to pea plants treated with PQ, alleviates the toxic effects of the herbicide.

Keywords Antioxidants · Hydrogen peroxide · Paraquat · *Pisum sativum* · Stress markers

Abbreviations

APX	Ascorbate peroxidase
AsA	Ascorbic acid
DHA	Dehydroascorbic acid
GSH	Reduced glutathione
GSSG	Oxidized glutathione
GST	Glutathione-S-transferase
H_2O_2	Hydrogen peroxide
MDA	Malondialdehyde
PQ	Paraquat
ROS	Reactive oxygen species
SOD	Superoxide dismutase

Introduction

Oxidative stress emerges as a result of unfavorable environmental conditions leading to generation of reactive oxygen species (ROS), such as superoxide radicals (O_2^-), hydroxyl radicals (HO), and hydrogen peroxide (H_2O_2), which are highly detrimental to the cells. Similarly, oxidative stress occurs in response to pathogen attack and during the natural processes of senescence. It is a widespread phenomenon and leads

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BIOLOGIE

Physiologie des plantes

LEAF MORPHOLOGY AND HISTOLOGY CHANGES OF PEA PLANTS TREATED WITH HYDROGEN PEROXIDE AND PARAQUAT

Irina Moskova, Dessislava Todorova, Vera Alexieva, Iskren Sergiev

(*Submitted by Academician A. Atanassov on July 18, 2011*)

Abstract

The effects of herbicide paraquat and hydrogen peroxide, applied alone and in combination, on pea leaf morphohistology were analysed. A single treatment with H_2O_2 provoked histological, but not evident morphological changes of pea leaves. Paraquat disturbed the histology organization significantly decreasing the intercellular spaces and cell sizes in all leaf tissues. Additionally paraquat caused a distinct leaf wilting. The results clearly demonstrate the leaf damages provoked by paraquat. The herbicide did not induce these effects when applied to preliminary treated with H_2O_2 leaves. The data demonstrate that hydrogen peroxide rendered some protective action against the herbicide injuries.

Key words: hydrogen peroxide, paraquat, *Pisum sativum*

Introduction. Paraquat is a bipyridilium contact herbicide which is diverting electrons from Photosystem I, and thus forming bipyridilium radicals which by reaction with oxygen are producing superoxide radicals. Paraquat is inhibiting CO_2 fixation in plants, but its rapid herbicide action is attributed mainly to the generation of reactive oxygen species [1]. The double-bonds of the biomembrane's unsaturated fatty acids are primary targets for the active oxygen species which initiate chain reactions of lipid peroxidation followed by destruction and disorder in the normal membrane permeability [2–4]. In our previous investigations concerning alterations in enzymatic and nonenzymatic antioxidants [5], and photosynthetic pigments and gas exchange rate [6], we have established that the pretreatment of young pea plants with low concentration of hydrogen peroxide decreased the damages caused by paraquat. The objectives of the present study

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Oxidative stress in biological systems

OXIDATIVE STRESS PROVOKED BY LOW AND HIGH TEMPERATURES IN WILD TYPE AND ETHYLENE-INSENSITIVE MUTANT *ETI5* OF *Arabidopsis thaliana* (L.) H e y n h

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ABSTRACT

Arabidopsis thaliana (L.) H e y n h wild type (*wt*) and ethylene-insensitive (*eti5*) type plants were used in this study. The plants were grown in growth chamber and 38 days after sowing the plants were subjected to low temperature (LT) 4°C or high temperature (HT) 38°C for 24 h in darkness. The content of stress markers and enzyme activities were measured at 0, 24, 48 and 120 h after the temperature treatment. The aim of our investigation was to compare the effect of low and high temperature on hydrogen peroxide (H_2O_2), malondialdehyde (MDA), free proline and carbonyl group content, ascorbate/dehydroascorbate content as well as catalase, guaiacol peroxidase (POD), and superoxide dismutase (SOD) activities in both types of *Arabidopsis*. Data obtained showed higher levels of the stress-markers MDA and carbonyl groups as well as decreased catalase activity (detoxifying H_2O_2) and increased SOD activity (producing H_2O_2) at the end of the measuring period (120 h) in the *wt* than in the mutant, which indicates that the *wt* is more sensitive to temperature stress than the mutant. On the other hand, the observed higher levels of stress markers (carbonyl groups, MDA) in both genotypes at 0 h after HT treatment as compared to LT is indicative that *Arabidopsis* is more sensitive to HT stress probably due to the fact that this plant species is cold-tolerant.

Keywords: *Arabidopsis thaliana* (L.) H e y n h, ethylene-insensitive mutant (*eti5*), temperature stress, stress markers.

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* For correspondence.

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APPLICATION OF NATURAL AND SYNTHETIC POLYAMINES AS GROWTH REGULATORS TO IMPROVE THE FREEZING TOLERANCE OF WINTER WHEAT (*Triticum aestivum* L.)

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Wheat cultivars were grown as soil culture under normal growth conditions. Two-week-old seedlings were exposed to 4°C for 6 h and then transferred to –12°C for 24 h in the dark. Twenty-four hours before freezing stress, some of the plants were sprayed with aqueous solutions of spermine, spermidine, putrescine, 1,3-diaminopropane (1,3-DAP) and diethylenetriamine (DETA). The data showed that freezing stress caused a decrease in the fresh weight, chlorophyll content and plant survival rate, accompanied by a simultaneous accumulation of free proline and the enhanced leakage of electrolytes. Preliminary treatment with polyamines caused a decline in electrolyte leakage and a considerable augmentation in proline quantity, indicating that the compounds are capable of preventing frost injury. Additionally, the foliar application of polyamines retarded the destruction of chlorophyll, and lessened fresh weight losses due to freezing stress. The synthetic triamine DETA was the most effective, having the most pronounced action in all the experiments, followed by the tetraamine spermine. The application of polyamines to wheat crops could be a promising approach for improving plant growth under unfavourable growth conditions, including freezing temperatures. The results demonstrate that treatment with polyamines could protect winter wheat by reducing the stress injuries caused by subzero temperatures.

Key words: freezing temperature, stress, growth regulators, survival, electrolyte leakage

Introduction

Plants are able to acquire tolerance to various environmental stresses including cold. The development of cold tolerance involves many physiological, genetic and metabolic processes (Thomashow, 1990; Săulescu and Braun, 2001; Yadav, 2010). Additionally, cold tolerance can be increased not only by cold hardening at low temperatures, but also by the preliminary application of plant growth regulating substances, such as abscisic acid (Gusta et al., 2005, and references therein), cytokinins (Jeon et al., 2010), salicylic acid, (Wang et al.,

Parvaiz Ahmad • M.M. Azooz • M.N.V. Prasad
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Ecophysiology and Responses of Plants under Salt Stress

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Chapter 13
Role of Polyamines in Alleviating Salt Stress

Dessislava Todorova, Zornitsa Katerova, Iskren Sergiev, and Vera Alexieva

13.1 Introduction

Abiotic and biotic stresses cause alterations in the normal physiological processes of all plants, including the economically important crops. Plant damage and decrease in their productivity take place most often due to naturally occurring unfavorable factors of the environment (natural stress factors). These include extreme temperatures; water deficit or abundance; increased soil salinity; high solar irradiance; early autumn or late spring ground frosts; pathogens, etc. Along with these factors, plants are imposed to a large scale of new stressors related to human activity (anthropogenic stress factors) including, toxic pollutants such as pesticides, noxious gasses (SO_2, NO, NO_2, NO_x, O_3 and photochemical smog); photooxidants; soil acidification and mineral deficit due to acid rains; overdoses of fertilizers; heavy metals; intensified UV-B irradiation, etc. (Fig. 13.1). All these stresses cause an increased production of reactive oxygen species (ROS) in plants that alter their normal physiological functions, decrease the biosynthetic capacity of plant organisms, and cause damages which may lead to plant death (Mittler 2002; Ahmad et al. 2008; Gill and Tuteja 2010b; Potters et al. 2010).

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ORIGINAL ARTICLE

Long-term impact of sublethal atrazine perturbs the redox homeostasis in pea (*Pisum sativum* L.) plants

Sergei Ivanov · Elena Shopova · Pavel Kerchev · Iskren Sergiev · Lyuba Miteva · Djovani Polizoev · Vera Alexieva

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Abstract Atrazine frequently contaminates soil, groundwater, rivers, and ponds. It is well know that acute doses (1–5 mM) of atrazine induce massive generation of singlet oxygen by blocking photosystem II. The sublethal concentrations of this herbicide, similar to those found in the environment, also reduce growth and disrupt photosynthesis in a long-term aspect, but exact mechanisms remain much uncertain. In this study the effects of environmentally relevant atrazine levels, ranging from 0.1 to 10 μM, on pea plants were characterized for up to 20 days. The plants exposed to continuous influence of atrazine exhibited perturbed redox homeostasis with increases of the lipid peroxides, the total and oxidized glutathione pools and elevated guaiacol peroxidase and glutathione-*S*-transferase activities. In contrast, the long-term atrazine impact did not affect superoxide dismutase activity whereas the catalase was inhibited. The perturbations of the redox status and the recruitment of the antioxidant machinery imply that the sublethal atrazine concentrations alter the poise between production and scavenging of reactive oxygen species. Taken together these results show that the long-term impact of sublethal atrazine has hallmarks of oxidative stress most probably triggered by generation of singlet oxygen.

Keywords Atrazine · Antioxidant enzymes · Singlet oxygen · Glutathione · Hydrogen peroxide · Lipid peroxidation

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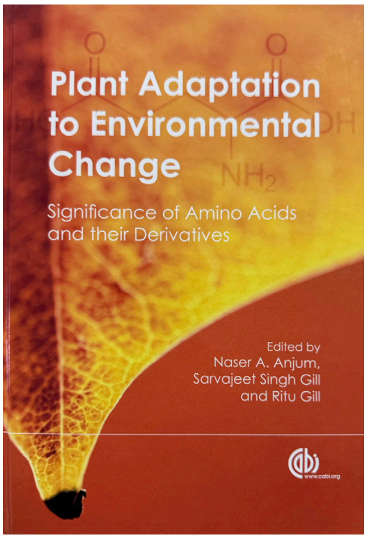
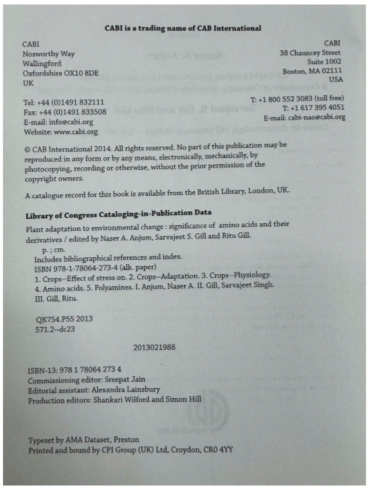
Introduction

Atrazine [6-chloro-N-ethyl-(1-methylethyl)-1,3,5-triazine-2,4-diamine], and other *s*-triazines, have been widely used as herbicides in USA (according to the US Environmental Protection Agency) and probably throughout the world for the last 50 years. It is primarily used on maize, sorghum, and sugarcane. The triazines belong to the herbicides that degrade most slowly in soils and water. Under field conditions, less than 5% of the atrazine and 1% of simazine in soil is degraded for 1 month (Taylor 1995). Atrazine frequently contaminates soil, groundwater, rivers, and ponds. Concentrations were as high as 120 μg/liter in agricultural basins, 14 μg/l in urban basins, and 22 μg/l in river basins (Cox 2001). The highest measured residual amounts of simazine in agricultural surface soils reach 1,000 μg/l (Braun and Hawkins 1991). Typical environmental contaminations in agricultural lands vary in diapason 1–100 μg/l or kg soil (Van Maanen et al. 2001; Vitanov et al. 2003). Water quality monitoring data show that in England and Wales, more than 10% of the surface and groundwater samples investigated from, the amounts of *s*-triazines (including atrazine) exceeded European standard (0.1 μg/l) for quality of drinking water

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11 Polyamines – Involvement in Plant Stress Tolerance and Adaptation

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11.1 Polyamines – Occurrence, Chemistry and Metabolism

The triamine spermidine (Spd), tetraamine spermine (Spm) and their precursor the diamine putrescine (Put) are the major polyamines (PAs) widespread in all plant species. Polyamines are organic compounds with low-molecular weight and a straight-chain C_3-C_{15} aliphatic structure that includes at least two primary amino groups and one or more internal imino groups (Edreva, 1996; Groppa and Benavides, 2008; Gill and Tuteja, 2010a). Besides Put, Spd and Spd, which are common for all plant species, there are also unusual PAs occurring only in distinct plant species (i.e. diamines cadaverine and 1,3-diaminopropane, and PAs homospermine, thermospermine and canavalmine), or synthesized under certain conditions, i.e. norspermine and norspermidine (Table 11.1).

Polyamine biosynthesis in plants can be outlined as a two-stage process (Fig. 11.1) – the first phase is the biosynthesis of diamines, and the second phase is Spd and Spm biosynthesis. The Put is synthesized through decarboxylation of L-arginine to agmatine by arginine decarboxylase (ADC), followed by hydrolysis and deamination of agmatine by agmatine iminohydrolase and formation of N-carbamoylputrescine. Further, N-carbamoylputrescine is subjected to hydrolysis, deamination and decarboxylation by N-carbamoylputrescine amidohydrolase to outcome the final product Put. An alternative pathway for Put synthesis is the direct decarboxylation of L-ornithine, catalysed by ornithine decarboxylase (ODC). Spermidine and Spm are synthesized by incorporation of an aminopropyl residue from decarboxylated S-adenosylmethionine to Put or Spd – this step is catalysed by the enzymes spermidine synthase (SPDS) or spermine synthase (SPMS) respectively. The essential for PAs biosynthesis, decarboxylated S-adenosylmethionine, is formed by decarboxylation (S-adenosylmethionine decarboxylase, SAMDC) of S-adenosylmethionine, which is a common precursor of PAs and ethylene (Slocum, 1991).

The PA degradation (Fig. 11.2) is realized through oxidative deamination catalysed by aminooxidases. They are copper-containing diamine oxidases (DAO) and flavoprotein-containing polyamine oxidases (PAO). DAO oxidize the primary amino groups of PAs. The oxidative deamination of Put produces Δ^1-pyrroline, H_2O_2 and NH_3. PAO oxidize the secondary amino groups of PAs and the final products of the process are Δ^1-pyrroline (from Spd oxidation) or

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Effects of auxin analogues and heat stress on garden pea

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Abstract

The biochemical responses of high temperature (HT) stressed garden pea (*Pisum sativum* L.) pre-treated with the auxins 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethyla minoethoxicarbonylmethyl]naphthalene chlormethylate (TA-14) were studied. The HT stress caused an increase in lipid peroxidation in leaves indicating the occurrence of oxidative stress. The concentration of free proline and hydrogen peroxide (H_2O_2) decreased, while the total phenolics, free thiols and the activity of catalase (CAT), superoxide dismutase (SOD) and guaiacol peroxidase (POX) were increased in the high temperature stressed plants. The pre-treatment with auxins mitigated the oxidative stress provoked by HT treatment. The favourable effect of these auxin-like compounds was interpreted in relation to their ability to counteract the oxidative stress caused by high temperature in pea plants. The auxin analogues maintained the concentrations of non-enzymatic antioxidants and the activities of defence enzymes scavenging reactive oxygen species to equal or near to normal physiological level. Based on the obtained data, we suggest that exogenous application of TA-12 and TA-14 alleviates the harmful effect of high temperature in pea.

Key words: antioxidant enzymes, auxin type compounds, high temperature stress, *Pisum sativum*, stress markers.

Introduction

The elevated air temperature is among the abiotic stress factors associated with climate change (Sita et al., 2017). Higher than the optimal air temperatures disturb the plant growth and these environmental conditions are regarded as high temperature (HT) stress (Kaushal et al., 2016; Bhandari et al., 2017; Sita et al., 2017). Extremely high temperatures induce accumulation of reactive oxygen species (ROS) which injure protein and nucleic acids structures and have deleterious effect on plant cell biomembranes (Awasthi et al., 2015; Kaushal et al., 2016). Therefore HT stress affects the overall plant growth and productivity through its negative influence on principal physiological and biochemical processes (Wahid et al., 2007; Hasanuzzaman et al., 2013; Kaushal et al., 2016; Bhandari et al., 2017; Fahad et al., 2017; Sita et al., 2017). Plant organisms have developed non-enzymatic and enzymatic defence systems (Kaushal et al., 2016; Szymańska et al., 2017; Czarnocka, Karpinski, 2018) to counteract the negative consequences of stresses including high temperature (Bhandari et al., 2017; Fahad et al., 2017). Plants react to unfavourable environmental factors through activation of some or all elements of the antioxidant defence system (Wahid et al., 2007; Bhandari et al., 2017).

Application of growth regulating substances can increase plant tolerance by influencing positively the plant defence system (Hasanuzzaman et al., 2013; Kaushal et al., 2016; Bhandari et al., 2017; Fahad et al., 2017). Auxins along with the other major classes of phytohormones involved in the control of diverse developmental processes play essential role in plant adaptive responses to a number of abiotic and biotic stresses (Kazan, 2013; Ahammed et al., 2016). The HT stress was reported to provoke an increase of endogenous auxin levels in different plant species like tobacco and cotton (Dobra et al., 2010; Min et al., 2014). In legumes and some other model crops, suppressed auxin biosynthesis and signalling in developing anthers were observed, resulting in pollen abnormalities (Ozga et al., 2017). The auxin physiological analogues 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA 12) and 1-[2-dimethylaminoethoxicarbonylmeth yl]naphthalene chlormethylate (TA-14) were reported to improve the cold acclimation and overwintering of oilseed rape (Velička et al., 2005; Anisimovienė et al.,

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Exogenous auxin type compounds amend PEG-induced physiological responses of pea plants

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ABSTRACT

Drought is among the abiotic stresses, which considerably decrease the agricultural production worldwide. The effects of exogenous auxin-type compounds 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethylaminoethoxicarbonylmethyl]naphthalene chlormethylate (TA-14) on drought stress responses induced by polyethylene glycol-6000 (PEG) in garden pea (*Pisum sativum* L.) plants were investigated. Preliminary application of TA compounds partially restored the normal growth of PEG-treated plants, led to less accumulation of proline, phenolic compounds and low-molecular thiols and did not provoke malondialdehyde buildup. The pea plants pretreated with auxin-type compounds displayed reduction in hydrogen peroxide content and consequently lower oxidative stress levels. This was confirmed by a decrease of the activity of the antioxidant enzymes superoxide dismutase, catalase, and guaiacol peroxidase. Taken together these results showed that the preliminary application of TA-12 and TA-14 reduced the negative effects of drought stress in pea plants.

1. Introduction

Drought is an important environmental factor that limits significantly the growth of many plant species and decreases crop production quantity and quality. Physiological drought stress in plants can occur due to environmental conditions such as soil water shortage, soil salinity, and high air temperature (Hasanuzzaman et al., 2018). Plants subjected to water shortage undergo an overproduction of reactive oxygen species (ROS), and the accumulation of ROS leads to loss of membrane integrity and damage to nucleic acids and proteins in plant cells (Gill and Tuteja, 2010; Li et al., 2015). Thus, water scarcity causes changes in key physiological and biochemical processes and reflects the plant growth and productivity (Griesser et al., 2015; Mutava et al., 2015; Yin et al., 2015; Zhang et al., 2017; Fahad et al., 2017). Plants have developed protective systems to cope with harmful effects of the unfavourable environmental conditions, particularly drought, which include a complex of non-enzymatic and enzymatic antioxidants (Gill and Tuteja, 2010; Talbi et al., 2015). In addition, plants accumulate huge amounts of compatible solutes such as free amino acids, proline and glycinebetaine (Diaz et al., 2014). In agricultural practice considerable efforts are focused on enhancing drought tolerance by exogenous application of different plant growth-regulating substances that can modulate antioxidant capacity of plant organisms to overcome the negative oxidative stress consequences (Habibi, 2012; Fayez and Bazaid, 2014; Li et al., 2015; Todorova et al., 2016; Fahad et al., 2017; Gou et al., 2017). Auxins are major class of phytohormones that primarily control cell division and growth of roots, stems, and fruits, but also participate in plant responses to different unfavourable environmental factors, including drought (Kazan, 2013). Under water stress conditions, the endogenous levels of auxins in different crops and model plants most often increased in order to facilitate plants to cope with drought (Llanes et al., 2016; Naser and Shani, 2016). Exogenous application of auxins enhanced the plant drought tolerance by increasing endogenous auxin levels (Llanes et al., 2016). Under water depletion NAA application could maintain seed yield and yield components in chickpea (Aslam et al., 2010) and improved the physiological adaptation capability and drought tolerance in soybean (Liang et al., 2011; Xing et al., 2016).

1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethylaminoethoxicarbonylmethyl] naphthalene chlormethylate (TA-14) are structural analogues of synthetic auxin naphthyl acetic acid (NAA). Exogenous application of these

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BIOLOGY
Plant physiology

PROTECTIVE EFFECT OF PLANT GROWTH REGULATORS MEIA AND 4PU-30 AGAINST *TOMATO SPOTTED WILT VIRUS* (TSWV) ON TWO TOMATO GENOTYPES

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(*Submitted by Academician A. Atanassov on August 23, 2018*)

Abstract

The effects of β-monomethyl ester of itaconic acid (MEIA) and phenylurea cytokinin 4PU-30 on two genotypes of tomato ("Keti" and VK1) infected with *Tomato spotted wilt virus* (TSWV) were investigated. The stress markers malondialdehyde and free proline as well as the viral concentration, expressed by the extinction values of TSWV as indicators of the level of oxidative stress and rate of virus replication were measured. The β-monomethyl ester of itaconic acid (MEIA) rendered inhibiting effect on TSWV infection in both lines of tomato while the phenylurea cytokinin 4PU-30 (N^1-(2-chloro-4-pyridyl)-N^2-phenylurea) was effective only in line "Keti". It was found that line "Keti" was more susceptible to TSWV infection than line VK1.

Key words: *Tomato spotted wilt virus* (TSWV), β-monomethyl ester of itaconic acid (MEIA), phenylurea cytokinin (4PU-30), tomato, oxidative stress

Introduction. Tomato spotted wilt virus, *Bunyaviridae* family, *Tospovirus* genus is a reason for considerable yield and quality reduction of field and greenhouse grown tomatoes. The use of plant growth regulators is a promising approach to achieve control of economically important virus diseases such as tomato spotted wilt and tomato mosaic. This is valid especially for greenhouse production

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ORIGINAL ARTICLE

Assessment of synthetic auxin type compounds as potential modulators of herbicide action in *Pisum sativum* L.

Iskren Sergiev[1] · Dessislava Todorova[1] · Elena Shopova[1] · Liliana Brankova[1] · Jurga Jankauskienė[2] · Sigita Jurkonienė[2] · Virgilija Gavelienė[2] · Rima Mockevičiūtė[2]

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Abstract

The physiological effects of the synthetic auxins 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethylaminoethoxicarbonylmethyl]naphthalene chlormethylate (TA-14) on herbicide-induced responses in pea (*Pisum sativum* L.) seedlings were studied. Two different herbicides inhibiting amino acid biosynthesis namely Glyphosate and Glean-75 were used in this study. The herbicide treatments provoked metabolic disruption and consequently led to inhibition of plant growth. Pretreatment with the synthetic auxins partially improved the growth of herbicide-treated plants. This was accompanied by a decrease of non-enzymatic antioxidants (free proline, low-molecular thiols, and total phenolics), malondialdehyde, hydrogen peroxide and superoxide dismutase activity. Glutathione reductase activity was increased by the herbicide treatments, but was not altered by the TAs. The pretreatment with the auxin compounds modulated the activities of catalase, guaiacol peroxidase, and glutathione-S-transferase in specific manner and the plants were able to cope with the negative consequences of the herbicides and to sustain their growth.

Keywords Antioxidants · Herbicides · Pea plants · Stress markers · Synthetic auxins

Introduction

Herbicides are the most widely used chemicals among the different types of products applied in the modern agriculture. This determines the need to study their effects on the target organisms, namely weeds, as well as on non-target plant species (crops). The herbicidal active compounds belong to 36 chemical groups (classification according to their chemical structure: http://www.hclrss.demon.co.uk/class_herbicides.html) but according to their mechanism of action they are classified as photosynthesis blockers, auxin type herbicides, inhibitors of amino acid biosynthesis, inhibitors of lipid and fatty acid biosynthesis, etc. (Cobb 1992). The herbicides can also be classified as selective (which affect certain plant species) and total (strike all plant species).

Glyphosate (N-(phosphonomethyl) glycine) is a total herbicide that has a toxic effect on all plant species (Cobb 1992; Gomes et al. 2014; de Freitas-Silva et al. 2017; Ferreira et al. 2017). It is used to destroy undesirable plants in both agricultural and non-agricultural areas. It is often used to prepare the field for crops when it is necessary to destroy all weeds there. By its mechanism of herbicidal action Glyphosate falls within the so-called aromatic amino acid synthesis inhibitors (phenylalanine, tryptophan, tyrosine) which block the enzyme 3-enolpyruvylshikimate-5-phosphate synthase - the basic unit in the shikimate biosynthetic pathway (Cobb 1992; Gomes et al. 2014; de Freitas-Silva et al. 2017). A number of articles documented that Glyphosate substantially altered germination and physiological responses of pea (Miteva et al. 2003, 2005, 2010; Mondal et al. 2017).

The herbicide Glean-75 (DuPont) is used to control the dicotyledonous weeds in wheat. It is sulfonylurea herbicide with the active substance chlorsulfuron - 1-(2-chlorophenyl)sulfonyl-3-(4-methoxy-6-methyl-1,3,5-triazin-2-yl)urea (Cobb 1992; Zhou et al. 2007). Its mechanism of action is based on inhibition of the biosynthesis of branched-

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PHYSIOLOGICAL RESPONSES OF PEA PLANTS TO TREATMENT WITH SYNTHETIC AUXINS AND AUXIN-TYPE HERBICIDE

Dessislava Todorova[1], Iskren Sergiev*[1], Elena Shopova[1], Liliana Brankova[1], Jurga Jankauskienė[2], Sigita Jurkonienė[2], Virgilija Gavelienė[2], Rima Mockevičiūtė[2]

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Abstract

Todorova D., Sergiev I., Shopova E., Brankova L., Jankauskienė J., Jurkonienė S., Gavelienė V., Mockevičiūtė R., 2021: Physiological responses of pea plants to treatment with synthetic auxins and auxin-type herbicide. – Botanica, 27(2): 125–133.

The effect of exogenously applied 2,4-D (2,4-dichlorophenoxyacetic acid) on growth and antioxidant defence of pea plants, preliminary treated with two synthetic auxin compounds 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethylaminoethoxycarbonylmethyl]naphthalene chlormethylate (TA-14) was examined. All chemicals were applied by foliar spraying. Applied alone, TA-12 and TA-14 had no significant effects, but they modulated the 2,4-D induced changes on most investigated biochemical parameters. The shoot fresh weight reduction caused by 2,4-D was partially overcome by the use of TAs. The use of TAs partially overcame the shoot fresh weight reduction induced by 2,4-D. Apart from this, no significant changes were observed in the other biometric parameters. Treatment with 2,4-D did not enhance lipid peroxidation, and hydrogen peroxide content was slightly increased. These data indicate that treatment with 2,4-D did not cause severe oxidative stress, which is also confirmed by the results of the antioxidant defence system. The application of 2,4-D provoked mild accumulation of thiol-containing compounds, free proline and phenolic compounds and increased the antioxidant enzyme activities (GST, SOD, CAT, POD and GR) to a moderate degree. Pretreatment with TAs noticeably decreased the non-enzymatic antioxidants (free proline, total phenolics and total low-molecular thiols) compared to plants treated with 2,4-D only. Except for GR, TAs pretreatment returned the enzyme activities to levels close to the controls. Based on the results obtained, we suggest that the application of both synthetic auxins could modulate 2,4-D herbicide effects.

Keywords: antioxidants, growth, *Pisum sativum* (L.), stress markers, 2,4-D.

INTRODUCTION

The chemicals possessing herbicidal activity are more than 1500 compounds and are the most used farming products applied against weeds in agriculture worldwide (Pesticide Properties Database, 2021). The herbicides which affect all plant species are classified as total, and those which affect certain plant species are classified as selective. Regarding their mechanism of action, herbicides can be merged into four main groups: blockers of photosynthesis, inhibitors of amino acid biosynthesis, inhibitors of lipid and fatty acid biosynthesis, and auxin type herbicides.

The highly effective selective herbicide of the auxin type 2,4-dichlorophenoxyacetic acid (hereafter, 2,4-D) is applied against dicotyledonous weeds in monocotyledonous crops (Cobb, 1992; Peterson et al., 2016). Formulations containing 2,4-D are manufactured in the form of more than 20 different preparations alone and in combination with other herbicides (Peterson et al., 2016). It is mainly foliar ap-

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Plant breeding

EFFECTS OF TRIACONTANOL ON PEPPER PLANTS INFECTED WITH *TOMATO SPOTTED WILT VIRUS* (TSWV)

Irina Moskova, Iskren Sergiev#, Elisaveta Kirova, Bistra Dikova*

(*Submitted by Academician A. Atanassov on November 16, 2020*)

Abstract

The *Tomato spotted wilt virus* (TSWV) induces disease in tomato, pepper, tobacco, and a number of other crop and wild plant species.

The effects of plant growth regulator triacontanol on young pepper plants infected with TSWV were studied. Triacontanol was applied before or after infection with the virus. The rate of TSWV infection was quantified by Enzyme-linked immunosorbent assay, Double antibody sandwich (DAS-ELISA). In relation to the symptoms of leaf disease, the optical density of TSWV and the relative water content were measured. To assess the level of oxidative stress, the contents of free proline and malondialdehyde in the leaves were determined.

It was found that triacontanol decreased the optical density of TSWV and its effect was better expressed when the plant growth regulator was applied before the infection. In regard to cell water loss and the stress markers proline and malondialdehyde, both treatments were effective in equal degree, with values in TSWV infected and triacontanol treated plants close to the control levels.

Key words: triacontanol (TRIA), *Tomato spotted wilt virus* (TSWV), pepper plants, oxidative stress

Introduction. *Tomato spotted wilt virus* (family *Bunyaviridae*, genus *Tospovirus*) causes reduction in the yield and production quality of many economically important field and greenhouse grown plants [1].

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Communication

The Physiological Responses of Wheat and Maize Seedlings Grown under Water Deficit Are Modulated by Pre-Application of Auxin-Type Plant Growth Regulators

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Abstract: The physiological responses of wheat and maize seedlings to exogenous auxin-type compounds 1-[2-chloroethoxycarbonyl-methyl]-4-naphthalenesulfonic acid calcium salt (TA-12) and 1-[2-dimethylaminoethoxicarbonylmethyl]naphthalene chlormethylate (TA-14) application prior to polyethyleneglycol-6000 (PEG) treatment were studied. PEG treatment inhibited seedlings growth and caused alterations in their antioxidant defence which was crop-specific. PEG increased the non-enzymatic antioxidants along with inhibition of enzymatic antioxidant activity in wheat, while in maize the opposite effects were found. The TA-12 and TA-14 applied alone increased most of the growth parameters measured in both crops, as well as the catalase activity and protein content of wheat. The growth of PEG-treated wheat and maize plants was improved by foliar spray with TA-compounds (TAs). Application of TAs before PEG treatment maintained low-molecular weight thiol-containing compounds and protein contents, and catalase and peroxidase activities close to the control levels. This was better expressed in maize than in wheat seedlings. The results showed that the preliminary application of TA-12 and TA-14 can reduce the adverse effects of moderate water deficit by crop-specific adjustment of the antioxidant defence to counteract stress.

Keywords: antioxidants; auxin-type compounds; PEG-6000; *Triticum aestivum* (L.); *Zea mays* (L.)

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1. Introduction

Drought negatively impacts agricultural production on a worldwide scale and is one of the most widespread abiotic stress factors due to global warming and the sequential climate changes. It might be induced by water deficiency, by high temperatures and/or evaporation, and by a combination of these factors [1,2]. Drought affects all aspects of plant physiology, including a reduction of photosynthesis rate and overproduction of reactive oxygen species (ROS), resulting in retarded plant growth and significant crop losses [2,3]. Plants have developed antioxidant defence system that consists of enzymatic (superoxide dismutase, SOD; catalase, CAT; guaiacol peroxidase, POX, etc.) and non-enzymatic (ascorbate, glutathione, phenolics, proline, etc.) components [3,4], which change significantly in response to different stresses, including drought.

The positive physiological defense responses induced by different compounds and causing adaptive cellular response to subsequent exposure to stressor is known as chemical priming [5,6]. The induced resistance to a given stressor after priming could be manifested by induction of various phytohormone-signaling pathways, secondary metabolites, defense proteins, elevation of ROS as signaling molecules, activation of antioxidant defense systems, etc. Alagna et al. [5] emphasized the necessity to expand the knowledge of the factors

Lithuania. Twenty-four hours after the foliar treatment, part of the seedlings were subjected to water solution of polyethylene glycol 6000 (10% (−0.2 MPa)) imitating moderate drought stress in the nutrient solution [50,51].

Measurements of growth parameters (fresh weight and length of shoots and roots) were performed 72 h after PEG application using a ruler and electronic balance (Precision Standard TS4000, Ohaus®, Parsippany, NJ, USA). Samples for the biochemical analyses were collected from the aboveground part of plants and after weighing were immediately frozen in liquid nitrogen. Approximately 250 mg of leaf material was homogenized in 4 mL 1% trichloroacetic acid and then centrifuged (15,000× *g* for 30 min at 4 °C). The resulting supernatant was used for measuring the content of free proline, free low-molecular weight thiols, and total phenolics. The content of free proline was measured after acid derivatization with ninhydrin reagent on a water bath for 1 h [52]. The reaction was terminated by placing the samples in ice. The optical density was measured at 520 nm. The free low-molecular weight thiols were measured using aliquot of supernatant supplemented with Ellman's reactive and after incubation at room temperature, the absorbance was measured at 412 nm [53]. The total phenolics content was measured according to Swain and Goldstein [54]. The supernatant was incubated with Folin–Ciocalteu reagent for 3 h at room temperature. The optical density was read at 725 nm. Gallic acid was used as a standard. For determination of the total protein content and the activities of catalase and guaiacol peroxidase, approximately 250 mg of leaf material was ground in cold isolating buffer (100 mM K_2HPO_4/KH_2PO_4, pH 7.0, with 1 mM EDTA) containing 1% polyvinylpyrolidone and centrifuged for 30 min at 15,000× *g* at 4 °C. The total soluble protein content was measured according to Bradford [55]. As a standard, bovine serum albumin was used. The activity of catalase (EC 1.11.1.6) was measured by monitoring the degradation of hydrogen peroxide at 240 nm [56]. The guaiacol peroxidase (EC 1.11.1.7) activity was determined by following the change of the absorbance at 470 nm according to the method of Dias and Costa [57]. As a donor of electrons, 1% guaiacol was used. The supernatants were obtained on a refrigerated Sigma 2-16K centrifuge (SciQuip, Wem, UK), and the spectrophotometric measurements were done on a Multiskan Spectrum spectrophotometer with microplate reader (Thermo Electron Corporation, Vantaa, Finland) and on Shimadzu UV-1601 spectrophotometer (Shimadzu, Kyoto, Japan).

The experiments were repeated three times in three replicates of each treatment. The data presented are mean values with ±SE. The significance of the different treatments was analyzed by one-way ANOVA with post-hoc Duncan's multiple range test ($p < 0.05$).

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Photosynthesis Alterations in Wheat Plants Induced by Herbicide, Soil Drought or Flooding

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Abstract: The wheat plants were pretreated with the selective herbicide Serrate® (Syngenta) and subsequently subjected to drought or flooding stress for 7 days. The gas exchange parameters, chlorophyll *a* fluorescence and leaf pigment content were measured. The measurements were performed during the stress period and after 4 days of plants recovery. Herbicide pretreatment did not cause significant alterations in photosynthesis and fluorescence parameters in alone- or combined-treated seedlings. A significant reduction in gas exchange parameters (net photosynthesis rate, stomatal conductance, transpiration rate, and water use efficiency), F_v/F_m and F_v/F_0 values during drought or flooding was observed. The disruption of photosynthesis together with reduction in the pigment content was stronger in droughted than flooded plants. When the normal irrigation was restored, the gas exchange and fluorescence parameters tended to increase. The comparative analysis of recovery and resilience indices of photosynthetic traits indicate that the plants subjected to drought recovered better than those subjected to flooding stress.

Keywords: selective herbicide; chlorophyll *a* fluorescence; flooding; *Triticum aestivum* L.; drought; gas exchange parameters

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1. Introduction

The extensive agriculture employs different strategies to satisfy the Earth's population growing needs for food. One of these strategies is the chemical control of weeds, which compete the crops for nutrients. [1] Herbicides, by selectively killing weeds, ensure crop's growth and yield. Serrate® is a selective herbicide for wheat, rye, and triticale. It is developed by Syngenta (Bazel, Switzerland) and consists of two active ingredients: clodinafop-propargyl (prop-2-ynyl(R)-2-(4-(5-chloro-3-fluoro-2-pyridyloxy) phenoxy) propionate)—inhibitor of acetyl co-enzyme A carboxylase, involved into the fatty acids biosynthesis; and pyroxsulam ((N-(5,7-dimethoxy (1,2,4)triazolo (1,5-a) pyrimidin-2-yl)-2-methoxy-4-(trifluoromethyl)pyridine-3-sulfonamide))—inhibitor of acetolactate synthase enzyme, involved into the biosynthesis of branched-chain amino acids [2].

During their lifespan, crops are exposed to a number of unfavorable environmental conditions of biotic and abiotic origin which cause considerable yield losses. Water deficit and water excess are abiotic stresses directly linked to global climate change. Both factors can disturb normal plant metabolism and disrupt key physiological processes such as photosynthesis [3,4]. Soil drought causes water deficit in plant tissues, leading to a significant decrease in the photosynthesis rate [5]. Under conditions of water deficit, the electron transport through PS II is inhibited [6]. Several in vivo studies demonstrated that drought stress caused damages to the oxygen-evolving complex of PSII [7], and to dissociation of the light-harvesting complexes from photosynthetic reaction centers of PSII [6]. The plants react to water deficit through a rapid stomata closure to avoid further water losses [3,4,8].

photosynthetic electron transport is the donor part of PSII, and especially the Q_B^- site on D1 protein in the reaction center of PSII, which prevents Q_A^- from reducing Q_B [32]. Our data of chlorophyll *a* fluorescence (Figures 4–6) are in line with the photosynthesis parameters (Figure 3) and indicated that during the stress period drought caused much more severe alterations in the physiological responses than the flooding stress. During the recovery period, the chlorophyll *a* fluorescence indices (Figure 7) tended to recover to controls state in drought stressed seedlings but not in those exposed to flood.

In relation to the second question of our study—whether plants subjected to multi-factorial treatments can recover important physiological processes after the termination of stress—we estimated the recovery and resilience indices of photosynthesis traits (Table 1). Recovery and resilience are terms usually used in ecology to assess ecosystems functioning under disturbance of ecological conditions. Most studies have estimated the ecosystem stability and response to perturbation, such as drought [33]. Recovery is the ability of the plant community to compensate biomass losses or reproductive outputs due to the perturbation, while resilience is the ability of the plant community to return to its original state following perturbation [34]. Recently, Qi et al. [4] introduced recovery and resilience in use for the assessment of photosynthesis traits of maize crop subjected to drought stress and re-watering. We used recovery and resilience indices to assess the ability of wheat plants to recover after drought and flooding stress. In the current study, full and over-compensatory upturn of photosynthetic traits A_n, g_s, E, and WUE was observed in terms of both recovery and resilience indices of drought and herbicide + drought treated plants. These data correspond to the results of Pinheriro et al. [35], who found that upon re-watering, the rapid growth of new tissues and organs might accelerate plant growth of *Lupinus albus* and potentially enhance CO_2 assimilation. Contrastively, an under-compensatory recovery (i.e., a negative percentage of the recovery and resilience) of photosynthetic traits A_n, g_s, E, and WUE was observed in flooded and herbicide + flooding treated plants. Positive values of the resilience index of drought and herbicide + drought treated plants as compared to flooding treated plants implies a greater ability to recover, which is also evident from Figure 1. The values of the recovery index were higher in combined-treated wheat as compared to drought-only treated wheat. This fact allows us to suggest that the application of Serrate® did not worsen photosynthesis-related parameters of drought-treated wheat, and they recovered successfully after re-watering.

5. Conclusions

Our study demonstrates for the first time that the herbicide Serrate® caused insignificant changes in photosynthesis-related parameters of wheat plants when applied alone or in combination with drought or flooding. The reported considerable alterations in photosynthetic traits could be attributed to the negative consequences of the abiotic stress and depend on the particular tolerance/susceptibility of wheat to drought or flooding. Drought and flooding hampered growth and decreased the photosynthetic capacity of plants to a different extent during the course of stress. The alterations in leaf gas exchange parameters correlated with the changes in chlorophyll *a* fluorescence indices with the most significant variations after 7 days of stress. During the recovery, the photosynthetic functions of droughted plants almost completely recovered, while in flooded plants, the impaired photosynthesis continued to worsen, which is evidenced also by the recovery and resilience indices.

Author Contributions: I.S. and D.T. conceptualized and coordinated the research; D.T. grew and treated the plants; S.A., V.A., D.T. and I.S. performed the analyses, collected and interpreted the data; I.S. and V.A. prepared figures and photos; D.T. prepared original draft of manuscript; I.S. and D.T. reviewed and edited the manuscript; D.T., project administration and funding acquisition. All authors have read and agreed to the published version of the manuscript.

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Comparative Study of Photosynthesis Performance of Herbicide-Treated Young Triticale Plants during Drought and Waterlogging Stress

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Abstract: Owing to global climate changes, periods of soil drought or waterlogging occur. Each of these factors causes negative effects on plant physiological processes and growth. Weeds are another factor that limits plant productivity. The main task of this study is to investigate the physiological reactions of triticale to herbicide treatment and subsequent drought or waterlogging. Young triticale plants were treated with Serrate® (selective herbicide produced by Syngenta) and exposed for 7 days to drought or waterlogging. Plant growth, chlorophyll and carotenoids content, the net photosynthesis rate and chlorophyll *a* fluorescence were measured during the stress period and after 4 days of plant recovery. Herbicide by itself did not induce considerable changes in the abovementioned parameters during the stress period. Serrate® did not affect strongly the efficiency of the photosynthetic machinery under harsh conditions. A significant reduction in fresh weight (85%), water content (93%), net photosynthesis rate, chlorophyll *a* fluorescence indices F_v/F_m and F_v/F_0, and leaf pigments (58% for chlorophyll *a*, 53% for chlorophyll *b*, and 45% for carotenoids) was found because of drought. Waterlogging also influenced negatively these parameters but to a smaller extent. After resuming the normal irrigation, the photosynthesis and chlorophyll *a* fluorescence tended to increase and showed signs of recovery. The comparative analysis of growth and photosynthetic parameters demonstrated that triticale plants subjected to waterlogging could recover to a higher degree than those exposed to drought.

Keywords: herbicide; chlorophyll *a* fluorescence; waterlogging; *Triticosecale*; drought; gas exchange parameters

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1. Introduction

Crops grown in field conditions are often exposed to variety of unfavorable factors that disrupt plant physiological processes and limit growth and yield. Moreover, under the natural environment, not only individuals but also multiple environmental factors of biotic or abiotic origin can influence the plant's metabolism.

In the extensive agriculture, the use of herbicides is still an essential strategy for chemical weed control [1]. The preparation Serrate®, developed by Syngenta (Bazel, Switzerland), is a selective herbicide suitable for the effective control of annual grassy and broad-leaf weeds in the field areas sown with wheat, rye, and triticale. Its effectiveness results from its specific double-component formulation: Serrate consists of clodinafop-propargyl, an inhibitor of acetyl co-enzyme A carboxylase (enzyme of the fatty acids biosynthetic pathway), and pyroxsulam, which inhibits acetolactate synthase (a key enzyme of the branched-chain amino acids biosynthesis pathway) [2]. According to the producer's recommendations, Serrate® should be applied on healthy cereals, which have not faced preliminary environmental unfavorable issues. However, occasionally, stress threats can decreased PI_{total} (Figure 5A). However, all these were fully recuperated in a short time, as it was noticed on 7th day of stress (Figures 4 and 5B).

Most of the growth, biochemical and biophysical parameters tended to reach the control levels after cessation of the stress (Figures 1–4). After restoration of the normal irrigation, an increase in all gas exchange indices A_n, E, g_s, and WUE, along with the chlorophyll *a* fluorescence parameters F_0, F_v, F_m, F_v/F_m and F_v/F_0, indicated reparation in the electron transport chains and higher CO_2 assimilation. This is suggesting that the photosynthetic functions in the treated plants were nearly recovered. Our findings are in line with the observations of other researchers regarding photosynthesis performance of drought-treated and/or waterlogged crops during the recovery period [4,5,15,16,34–36]. In addition, the high values of φR_o and δR_o of drought and herbicide + drought-treated triticale (Figure 5C) mean that more electrons have reached PSI to reduce final electron acceptors at the PSI acceptor side, which could signify an over-compensatory effect on quantum yields and efficiency at the PSI acceptor side [37].

The indices of recovery and resilience of the biometric parameters (Table 1) showed that although triticale was capable of recovering FW and WC after the termination of drought stress, their DW remained stunted; i.e., plants needed more time to accumulate newly developed biomass. On the other hand, the recovery and resilience indices in waterlogged triticale indicated that its growth continued even during the stress period, and after the recovery, plants tended to reach their control growth level more rapidly. Similarly, the recovery and resilience indices, calculated for photosynthesis-related parameters (Table 2), indicated that although the drought-treated triticale recovered transpiration and stomatal conductance at highest degree, A_n still was negative, which probably indicates that plants needed more time to recover successfully their deprived photosynthesis rate. The recovery indices of waterlogged triticale had positive values, and resilience indices had minimal negative values, which confirmed again that the plants almost reached their initial physiological state (Table 2) and recovered better than those exposed to drought. The indices of recovery and resilience had positive values in triticale treated with Serrate® only (Tables 1 and 2), except for WC, which indicates that this herbicide could be used as a reliable implement even under unfavorable environment conditions such as water stress.

5. Conclusions

Our study confirms that the application of the selective herbicide Serrate® did not cause considerable variations in the growth and photosynthesis performance of triticale when applied alone or in combination with subsequent exposure of plants to drought or waterlogging. Drought and waterlogging decreased the efficiency of photosynthesis of triticale to a different extent during the stress period. We also found that waterlogging did not worsen significantly most of the biometric, chlorophyll *a* fluorescence, and photosynthesis-related parameters in both waterlogged and herbicide + waterlogging-treated plants. After the period of recovery, the photosynthesis of waterlogged plants was almost completely recovered, while drought-treated plants needed more time to repair the photosynthetic functions and to continue to grow. These findings are also supported by the indices of recovery and resilience of triticale growth and photosynthesis parameters. Our study provides new facts about the photosynthesis performance and chlorophyll *a* fluorescence responses of triticale associated to the application of Serrate® under unfavorable growth conditions, which extends the information in this particular topic to encourage upcoming exploration in the same area.

Author Contributions: I.S. and D.T. conceptualized and coordinated the research; D.T. grew and treated the plants; S.A., V.A., D.T. and I.S. performed the analyses, collected and interpreted the data; I.S. and V.A. prepared figures and photos; D.T. prepared the original draft of the manuscript; I.S. and D.T. reviewed and edited the manuscript; D.T. provided project administration and funding acquisition. All authors have read and agreed to the published version of the manuscript.