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EFFECT OF GIBBERELLIC ACID ON TOTAL ANTIOXIDANT ACTIVITY DURING *CHENOPODIUM RUBRUM* L. ONTOGENESIS IN VITRO

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Abstract — Total antioxidant activity (TAA) represents the combined ability of diverse antioxidants present in a sample of plant material to scavenge free radicals. *Chenopodium rubrum* L. sel. 184 is a qualitatively short-day plant; as an early-flowering species, it is a suitable object for studying ontogenesis in vitro. We investigated the effect of GA3 (5 mg/l) on TAA during *C. rubrum* ontogenesis under two different inductive photoperiodic regimes in vitro. Total antioxidant activity does not change in different phases of *C. rubrum* ontogenesis under the same photoperiodic treatment. Exposure to continuous irradiation caused an increase of TAA in both *C. rubrum* plants and collected matured seeds. Gibberellic acid stimulated stem elongation, but did not affect leaf development or the number of matured seeds per plant, regardless of photoperiodic treatment; it induced a decrease of TAA in *C. rubrum* plants regardless of photoperiodic treatment or the phase of development, while it had no effect on TAA of matured seeds.

Key words: *Chenopodium rubrum*, gibberellic acid, growth, flowering, seed maturation, total antioxidant activity

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INTRODUCTION

Generation of reactive oxygen species (ROS), the superoxide radical ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2), and the hydroxyl radical ($OH^{\cdot-}$) in plant cells is a consequence of normal metabolism, linked with a signaling role in plant developmental processes (Elstner, 1982). The antioxidative system, composed of both enzymatic and nonenzymatic constituents, functions as a singlet or triplet oxygen quencher, free radical scavenger, peroxide decomposer, enzyme inhibitor, and synergist (Larson, 1988). As for the antioxidative enzymes catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD), they are known to be engaged in regulation of plant growth and development processes: seed germination and seedling growth (Dučić et al., 2003-2004; Bailly, 2004; Prodanović et al., 2007); root growth (Gaspar et al., 1992; Kukavica et al., 2007); plant growth and development (Bailey and McHargue, 1943; Fielding and Hall, 1978; Mitrović and Bogdanović, 2008); senescence (Procházková and Wilhelmová, 2004); fruit ripening (Mondal et al., 2004); and protection against pathogens or abiotic stress (Khan and Panada, 2002).

Total antioxidant activity comprises the contribution of different small molecules with antioxidant capacity (ascorbate, glutathione, phenolics, sugars…). Changes in levels of some nonenzymatic antioxidants, mainly ascorbate and glutathione, have also been linked with different physiological proceses in plants: seed aging (Mitrović et al., 2005); seed germination (Tommasi et al., 2001; Dučić et al., 2003-2004; Bailly, 2004); senescence (Procházková and Wilhelmová, 2004); fruit ripening (Mondal et al., 2004); and plant aging (Jaleel et al., 2006). Phenolics are diverse secondary metabolites abundant in plant tissues. Phenolic compounds take part in protection, regeneration, and degradation processes caused by toxic pollutants (Rice-Evans et al., 1997). Soluble phenolics have significant antioxidant effects and are considered to be stress-related (Wild and Schmitt, 1995). Sugars as signaling compounds have a profound effect in all stages of the plant's life cycle, from germination and vegetative growth to reproductive development and seed formation (Smeekens, 2000). Sugars such as glucose and fructose are important for intermediary and respiratory metabolism and are

the substrate for synthesis of complex carbohydrates such as starch and cellulose. Using the ABTS test, we recently showed that glucose, fructose, fructose 6-phosphate, and fructose 1, 6-bisphosphate have radical-scavenging capacity (Bogdanović et al., 2008). In the same paper we demonstrated the direct antioxidant role of soluble sugars.

Total antioxidant activity (TAA) reflects the ability of a sample of plant material to scavenge free radicals. It is not related to a particular kind of antioxidants, but rather represents the combined activity of diverse antioxidants. Knowledge of all potential antioxidant compounds of a plant sample does not necessarily indicate its TAA. Cooperative action between different antioxidants of the sample may influence its TAA (Arnao et al., 1999).

It has been shown that TAA varies considerably in different stages of maturity of berry crops and in different plant parts (Wang and Lin, 2000). In *Quercus ilex* leaves (Omari et al., 2003) and broccoli inflorescences (Leja et al., 2002), the highest TAA activity was found in spring due to high irradiance. Studies of extracts of different medicinal and aromatic plants showed a wide variation in TAA (Mantle et al., 2000; Miliauskas et al., 2004).

Chenopodium rubrum L. sel. 184 is a qualitatively short-day plant, with a defined critical night length of 8 h (Tsuchiya and Ishiguri, 1981). It is sensitive to photoperiodic stimulation of flowering as early as at the cotyledon stage (Seidlová and Opatrná, 1978). Six inductive photoperiodic cycles are sufficient for flowering induction, and plants *in vitro* flower 9 days later (Živanović et al., 1995). Seed maturation occurs 10 weeks after germination, regardless of the day length during flowering induction (Mitrović et al., 2007) or the plant age when flowering induction was received (Mitrović and Bogdanović, 2008). *Chenopodium rubrum* plants modify their growth and development in accordance with the photoperiod they are exposed to (Cook, 1975; Mitrović et al., 2007).

Gibberellins play an important role in many aspects of plant growth. In *C. rubrum* plants, GA_3 stimulated both stem elongation and flowering (Živanović et al., 1995). It had no effect on germination percentage, but induced an increase of CAT and SOD activity prior to radicle protrusion and lowered ascorbate and dehydroascorbate concentrations (Dučić et al., 2003-2004). Gibberellic acid also lowered the difference in growth and flowering between plants derived from seeds differing in age (Mitrović et al., 2005).

By exposing one group of plants to a photoperiod inductive for flowering at the cotyledon stage and another group 17 days later, we tried to separate (on a time scale) vegetative growth, flowering, and seed development in plants of the same age. We showed earlier (Mitrović and Bogdanović, 2008) that activities of antioxidative enzymes (CAT, SOD, and POD) change during *C. rubrum* vegetative and reproductive development. The aim of this study was to determine the effect of GA_3 (5 mg/l) on TAA during *C. rubrum* ontogenesis under conditions of two different inductive photoperiods *in vitro.*

MATERIAL AND METHODS

Plants *in vitro*. The experiments were carried out with intact *C. rubrum* plants derived from seeds sown *in vitro*. Seeds (1-year-old) were collected from plants grown *in vitro* on MS medium under 16 h/8 h photoperiods at 25°C. They were surface-sterilized with 4% Na-hypochlorite for 2 min, washed with sterile distilled water and aseptically sown on moistened filter paper in Petri dishes. Germination was attained by subjecting the seeds to appropriate temperature and dark/light cycles (24 h of darkness at 32°C, 24 h of darkness at 10°C, and 48 h of white light at 32°C). Four-day-old seedlings were transferred to glass jars containing 100 ml of MS (Murashige and Skoog, 1962) mineral solution supplemented with sucrose (5%) and/or GA_3 (5 mg/l) and gelled with agar (0.7%). Seedlings were exposed to two different photoperiodic treatments: 65 days of a 14 h/10 h photoperiod or 17 days of continuous light followed by 43 days of 14 h/10 h. Irradiance was about 70 μmol m^{-2} s^{-1}. Temperature in the growth chambers was 25 ± 2°C.

Plant parameters (height, number of leaves, percentage of flowering, number of matured seeds)

were measured after 17, 37, and 65 days of culturing *in vitro*. Stems with leaves and collected matured seeds were frozen in liquid nitrogen prior to extraction. Samples (four replicates of 0.2 g for each experimental point) were powdered in liquid nitrogen, and 0.2 g of plant powder was homogenized for 10 min in 1 ml of 80% methanol and centrifuged at 12000g for 5 min. The supernatant was used for TAA measurements.

ABTS test. Total antioxidant activity was measured using the ABTS/HRP end-point method according to Arnao et al. (2000). The reaction mixture contained 2 mM ABTS, 15 μM hydrogen peroxide, 0.25 μM HRP, and 20 μl of 80% methanol extract of powdered plant matter in 50 mM phosphate buffer (pH 7.5) in a total volume 2 ml. The assay temperature was 25°C. The reaction was monitored at 730 nm using a Shimadzu UV-160 spectrophotometer until stable absorbance, due to ABTS radical formation, was obtained. Total antioxidant activity was expressed as micromoles of ascorbic acid equivalents (standard) per gram of plant fresh weight.

RESULTS AND DISCUSSION

Effect of photoperiodic treatment and GA_3 on growth, flowering, and seed maturation. On the 17th day, plants grown under an inductive 14 h/10

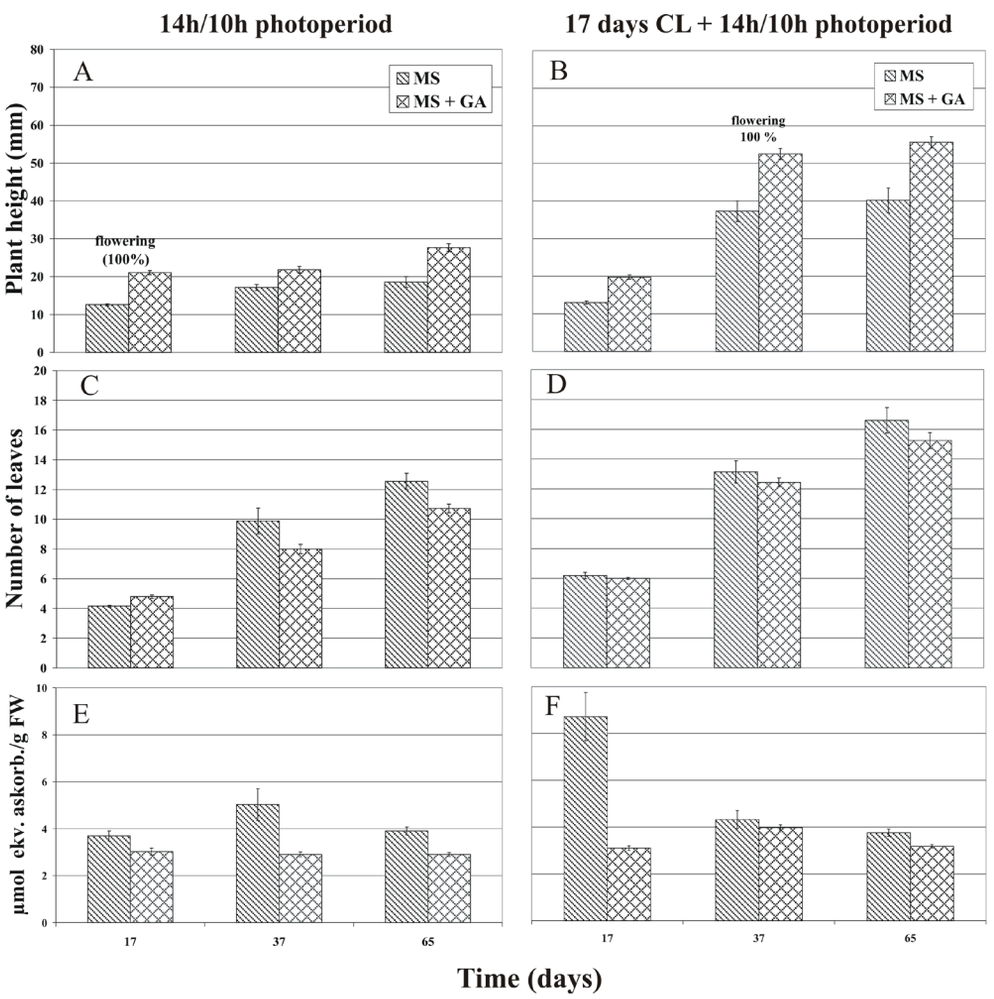

Fig. 1. Effect of GA3 (5 mg/l) and different photoperiodic conditions (65 d of 14 h/10 h photoperiod or 17 d of CL followed by 48 d of 14 h/10 h photoperiod) on *C. rubrum* development in vitro and TAA: A) plant height, B) number of leaves, C) total antioxidant activity of samples of stems with leaves; means ± SE, n = 48; CL – continuous light, d – days..

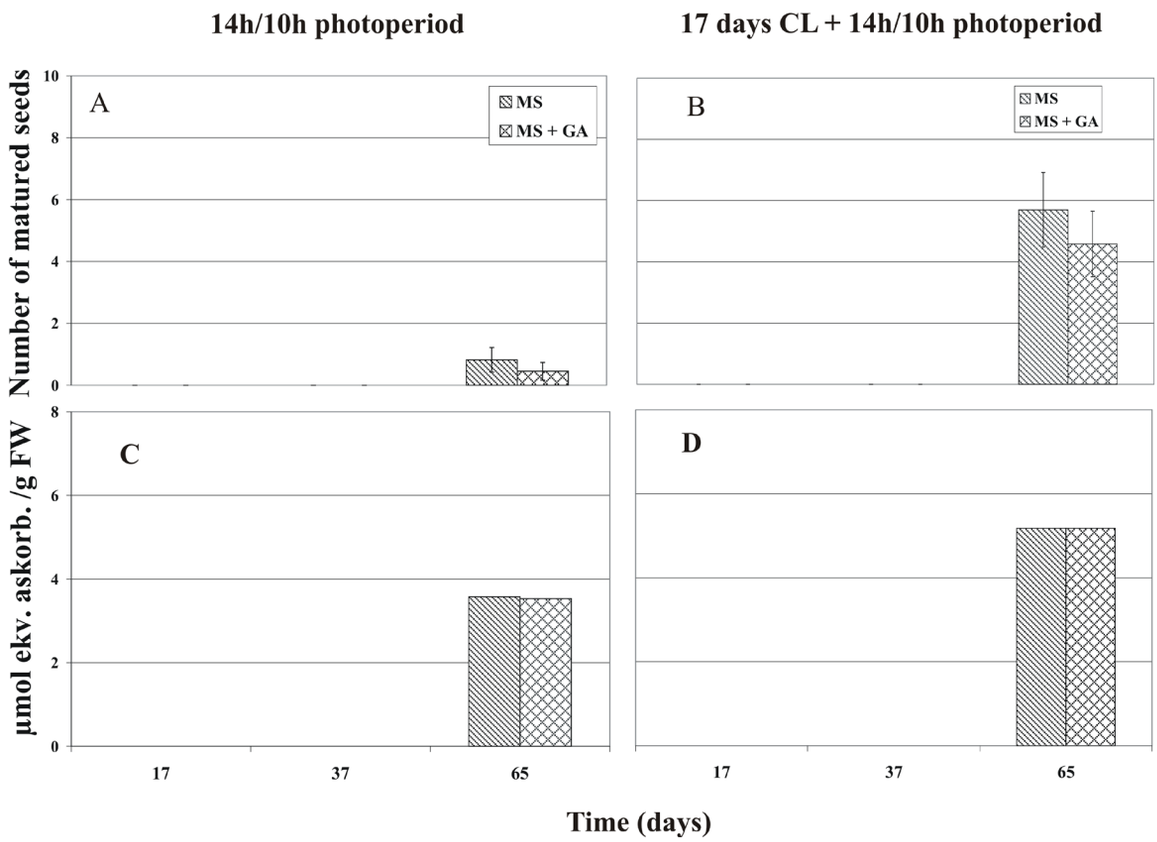

Fig. 2. Effect of GA3 (5 mg/l) and different photoperiodic conditions (65 d of 14 h/10 h photoperiod or 17 d of CL followed by 48 d of 14 h/10 h photoperiod) on *C. rubrum* seed maturation and TAA of matured seeds. A) number of matured seeds, B) TAA in seed samples; means ± SE, n = 48; CL – continuous light, d – days.

h photoperiod flowered 100%, while plants grown under noninductive CL stayed vegetative. No difference in growth was visible (Fig. 1A, B), but leaf development was stimulated by CL (Fig. 1C, D).

On the 37th day, plants whose flowering was delayed by 17 days of continuous light flowered 100% and immature seeds were barely visible to the naked eye on the lower nodes, while plants grown continuously under an inductive photoperiod were in the phase of seed development. Plants grown for the first 17 days under noninductive CL were about twice as high as ones grown continuously under an inductive 14 h/10 h photoperiod (Fig. 1A, B). We showed earlier (Mitrović et al., 2007) that the vegetative and reproductive development of *C. rubrum* is determined by the photoperiod the seedlings experience during a precise short early period of its life cycle, and that plant height and the number of leaves increase with increase of day length.

On the 65th day, both groups of plants were in the phase of seed maturation. About five times more seeds were collected from plants in which flowering induction was delayed by 17 days of CL compared to those grown continuously under an inductive 14 h/10 h photoperiod (Fig. 2A, B). It has been shown that besides day length during induction and evocation of flowering (Cook, 1975; Mitrović et al., 2007), day length before flowering induction is also significant for seed development and maturation (Mitrović and Bogdanović, 2008). Seed maturation *in vitro* in *C. rubrum* occurs in 10 weeks regardless of day length (Mitrović et al., 2007) or the plant's age when reproductive development begins (Mitrović and Bogdanović, 2008).

Gibberellic acid (5 mg/l) stimulated stem elongation (Fig. 1A, B), but had no effect on leaf development (Fig. 1A, B) or the number of matured seeds per plant (Fig. 2A, B), regardless of photoperiodic treatment and/or the phase of plant development. Stimulation of stem elongation and flowering by exogenously applied GA_3 was previously reported for both *C. rubrum* (Živanović et al., 1995; Seidlová, 1989) and *C. murale* (Mitrović et al., 2000). It was shown that GAs play a primary role in the process of seed development (Rudrapal et al., 1992; Nakayama et al., 2002), and Groot et al. (1987) reported that exogenous GAs increase seed weight and delay seed dehydration.

Effect of photoperiodic treatment and GA_3 on TAA. Total antioxidant activity did not change significantly during *C. rubrum* ontogenesis under conditions of an inductive 14 h/10 h photoperiod (Fig. 1E). The highest TAA was registered in *C. rubrum* plants after 17 days of CL (Fig. 1F); after transfer of this group of plants to the same 14 h/10 h photoperiod, TAA showed values similar those recorded in plants grown continuously under that photoperiod. This suggests that TAA is linked with photoperiodic treatment, but does not vary as a function of different phases of *C. rubrum* development. It is likely that individual components of the nonenzymatic antioxidant system change during *C. rubrum* ontogenesis, but TAA remains on the same level under unchanged surrounding conditions. This is in agreement with published data: the highest TAA values in *Quercus ilex* leaf extracts were measured during spring in connection with high irradiance, high temperature, and high metabolic activities, all of which increase ROS generation and photoprotective mechanisms (Omari et al., 2003); and TAA values of broccoli inflorescences were much higher during spring than during autumn (Leja et al., 2002), which was also linked to higher insolation during spring. Asada (2006) showed that exposure to CL brings about an increase of ROS production, and exposure of *Phaseolus vulgaris* cotyledons to CL increased the content of all nonenzymatic antioxidants, while it lowered antioxidative enzyme production (Procházková and Wilhelmová, 2004). Production of antioxidative enzymes (CAT, POD, and SOD) was also lowered in *C. rubrum* plants exposed to 17 days of CL (Mitrović and Bogdanović, 2008).

Gibberellic acid (5 mg/l) lowered TAA in *C. rubrum* plants and kept it on about the same level regardless of photoperiodic treatment or the phase of development (Fig. 1E, F). This is in agreement with the data of Abdel-Kadar (2001), who found that GA_3 treatment alleviated water stress responses in lettuce. Bethke et al. (2001) hypothesized that GA treatment prevents aleurone cells from effectively metabolizing ROS by reducing the activities of ROS-metabolizing enzymes.

Seeds collected from plants grown continuously under a 14 h/10 h photoperiod showed significantly lower TAA compared to seeds collected from plants in which flowering induction was delayed by 17 days of CL (Fig. 2C, D). It can be supposed that seed TAA is affected by the photoperiod the maternal plants were exposed to, since a maternal effect of photoperiod is discernible in different amounts of small molecules, components of the nonenzymatic antioxidant system, in matured *C. rubrum* seeds. It was previously demonstrated that maternal photoperiod affects seed weight (Cook, 1975; Bertero et al., 1999); germination (Gutterman, 2002; Galloway, 2005); and plant growth and flowering (Mitrović et al., 2002).

Treatment of *C. rubrum* plants with GA_3 (5 mg/l) had no effect on TAA of collected matured seeds (Fig. 2C, D).

CONCLUSIONS

Our data indicate that TAA remains on the same level during *C. rubrum* ontogenesis under unchanging surrounding conditions. Exposure to continuous irradiation causes an increase of TAA in *C. rubrum* plants. Gibberellic acid treatment causes a decrease of TAA, regardless of photoperiodic treatment or the phase of development.

The difference of TAA in matured seeds collected from *C. rubrum* maternal plants grown under different photoperiodic conditions suggests that small molecules, components of nonenzymatic anti-

oxidant system, participate in the mechanism governing the maternal effect of photoperiod.

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ЕФЕКАТ ГИБЕРЕЛИНА НА УКУПНУ АНТИОКСИДАТИВНУ АКТИВНОСТ У РАЗЛИЧИТИМ ФАЗАМА ОНТОГЕНЕЗЕ *CHENOPODIUM RUBRUM* L. *IN VITRO*

АЛЕКСАНДРА МИТРОВИЋ и ЈЕЛЕНА БОГДАНОВИЋ

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Укупна антиоксидативна активност (UAA) представља укупан капацитет различитих антиоксиданата, присутних у узорку биљног материјала за уклањање слободних радикала. *Chenopodium rubrum* L. sel. 184 је квалитативно краткодневна биљка, која је као рано цветајућа врста погодан објекат за проучавање онтогенезе *in vitro*. Испитиван је ефекат GA_3 (5mg/l) на UAA *C. rubrum* у различитим фазама онтогенезе гајених на два различита фотопериодска режима. UAA се не мења у различитим фазама онтогенезе под истим фотопериодским режимом. Излагање континуалној светлости утиче на пораст UAA, како у узорцима стабла са листова, тако и у сакупљеним сазрелим семенима. GA_3 стимулира издуживање стабла, не утиче на развиће листова, као ни на број сазрелих семена по биљци, независно од фотопериодског третмана; утиче на пад UAA у стаблу и листовима независно од фотопериодског третмана или фазе развића, док нема ефекта на UAA сазрелих семена.