Ultraviolet-B Radiation Damage on Kentucky Bluegrass II: Hormone Supplement Effects

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Abstract. High ultraviolet-B (UV-B; 290–320 nm wavelength) radiation may significantly contribute to the quality decline and death of kentucky bluegrass (*Poa pratensis* L.) sod during summer transplanting. Antioxidants and protective pigments may be involved in plant defense against oxidative stress caused by UV-B. Selected exogenous hormones may alleviate UV-B damage by upregulating plant defense systems. The objectives of this study were to determine if exogenous hormone or hormone-like substances could alleviate UV-B damage to ‘Georgetown’ kentucky bluegrass (*Poa pratensis* L.) under greenhouse conditions. The hormone salicylic acid at 150 mg·m⁻² and the hormone-containing substances, humic acid (HA) at 150 mg·m⁻² and seaweed extract (SWE) at 50 mg·m⁻², were applied to plugs of kentucky bluegrass and then subjected to UV-B radiation (70 µmol·m⁻²·s⁻¹). The UV-B irradiation stress reduced turf quality by 51% to 66% and photochemical efficiency by 63% to 68% when measured 10 or 12 days after initiation of UV-B. Endogenous alpha-tocopherol (AT) and antioxidant enzymes (superoxide dismutase (SOD) and catalase) were reduced by UV-B stress. Anthocyanin content was increased from day 1 to 5 and then decreased from day 5 to 10 of continuous UV-B irradiation. Application of SA and HA + SWE enhanced photochemical efficiency by 86% and 82%, respectively, when measured 10 or 12 days after UV-B initiation. In addition, application of the hormonal supplements increased AT concentration, SOD, catalase activity, and anthocyanin content when compared to the control at 10 days after UV-B initiation. Bluegrass with greater AT concentration and SOD and catalase activity exhibited better visual quality under UV-B stress. The results of this study suggest that foliar application of SA and HA + SWE may alleviate decline of photochemical efficiency and turf quality associated with increased UV-B light levels during summer.

The vagaries of the turfgrass and landscaping industry often dictate that kentucky bluegrass sod be harvested, transported, and transplanted during the summer. Frequently, increased respiratory heating during storage, transport, and subsequent exposure to high UV-B during transplanting can cause shock (Giese et al., 1997). The shock often results in bleached, inactive turfgrass leaves. Plants better adapted to resist UV-B induced photo-bleaching usually contain more robust screening (pigment) and scavenging (antioxidant) protection systems (Mackerness, 2000). Resistance to UV-B damage most likely involves both avoidance and tolerance mechanisms.

Day et al. (1992) noted conifers are efficient avoiders of UV-B damage due to higher needle levels of flavonoid and related phenolic pigments (anthocyanins) that strongly absorb UV and transmit nondamaging longer wavelengths. Most herbaceous species do not

appear to have such robust screening systems. However, it has been established that exposure of herbaceous plants to UV radiation will up-regulate the formation of flavonoids (Salisbury and Ross, 1991). Additionally, application of a green-pigmented colorant that strongly absorbs in the UV range (250 to 400 nm) has been shown to improve avoidance of UV-B damage in kentucky bluegrass (Ervin et al., 2004) and creeping bentgrass (*Agrostis stolonifera* L.; Schmidt and Zhang, 2001). Further, by exogenously applying ascorbic acid and alpha-tocopherol, endogenous alpha-tocopherol and antioxidant enzyme activities increased and directly correlated with greater tolerance of UV-B by kentucky bluegrass (Ervin et al., 2004).

Greater tolerance to oxidative stress caused by high UV-B may involve hormonal signals to up-regulate antioxidant enzyme activity. One of the implicated hormones is the phenolic compound, salicylic acid (SA). Numerous studies have shown that SA is a key signaling compound involved in the activation of certain plant defense mechanisms including induction of pathogenesis-related genes and antioxidant enzymes (Mackerness, 2000; Jordan, 1996). Recently, Clarke et al. (2002) noted that SA reduced heat-induced oxidative damage and increased catalase, glutathione reductase and peroxidase activity in *Phaseolus vulgaris*. Sanjay et al. (2001) indicated SA increased

peroxidase activity and phenolic content in *Pisum sativum*. Exogenous application of SA reduced visual injury and loss of photochemical efficiency of kentucky bluegrass and creeping bentgrass under UV-B stress (Schmidt and Zhang, 2001).

It has been documented that application of alkaline extracts of the seaweed *Ascophyllum nodosum* Jol. (SWE), in combination with acid extracts of the humic acid (HA) component of Leonardite enhanced antioxidant activity (Zhang and Schmidt, 1999), photochemical efficiency (Zhang et al., 2003), and improved resistance to UV-B induced damage in kentucky bluegrass (Schmidt and Zhang, 2001). This SWE source contains ≈70 mg·kg⁻¹ of the cytokinin, zeatin riboside (Zhang and Ervin, 2004). Higher cytokinin levels in tissues undergoing abiotic stress have been associated with greater antioxidant enzyme activities resulting in less photosynthetic damage (Liu and Huang, 2002). Numerous HA sources have been shown to contain indole acetic acid (IAA) and exhibit auxin-like activity (Canellas et al., 2002; Muscolo et al., 1998; O'Donnell, 1973). Increased endogenous amounts of cytokinins and auxins have been associated with membrane stabilization leading to protection of photosynthetic activity during osmotic and temperature stress (Nooden and Leopold, 1988; Aldesuquy, 2000).

Given this evidence, our hypothesis was that application of SA or HA + SWE, before UV-B exposure, would up-regulate plant defense mechanisms resulting in greater tolerance of kentucky bluegrass to UV-B. Our objectives were to determine if these substances would improve endogenous antioxidant concentrations and antioxidant activities in kentucky bluegrass and be associated with greater UV-B tolerance as determined by photochemical efficiency, visual quality, and pigment content responses.

Materials and Methods

The detailed experimental procedures, including field growth conditions of harvested plant material, subsequent greenhouse growing conditions, UV-B treatments, data collection, measurement, and statistical protocols were described in a companion paper (Ervin et al., 2004).

Experiment 1. Treatments for this study were 1) SA at 150 mg·m⁻², 2) HA at 150 mg·m⁻² + SWE at 50 mg·m⁻², and 3) control. Three replications were arranged in randomized complete blocks on the greenhouse bench. Salicylic acid (Research Organics; Cleveland, Ohio), seaweed extract (Acadian Seaplants Limited, Dartmouth, Nova Scotia, Canada) and HA (Plant Wise Biostimulants, Inc. Louisville, Ky.) are each available as dry powders. Solutions were made by mixing the products with water. Salicylic acid solution required addition of a surfactant (Aqua-Gro, Aquatrols Corporation, Cherry Hill, N.J.) at 0.05% to encourage uniform coverage.

Light absorbance of the two treatment solutions was measured across the UV spectral range (250 to 400 nm) and results are presented as percent absorbance at each wavelength (Fig. 1). The SA-treatment solution had 20%

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Fig. 1. Ultraviolet (250 to 400 nm) absorbance characteristics of the supplements used in this study.

to 30% absorbance across the UV-B spectra, while maximum absorbance of 20% occurred at 290 to 300 nm for the HA + SWE solution. The treatments were sprayed onto kentucky bluegrass foliage using 60-mL syringes with needles on 15 Mar. 2001. The treated turfgrass was not irrigated for 24 h.

Twenty-four hours after treatment the plugs were placed under artificial UV-B radiation ($70 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) provided by three 40-W UV-B fluorescent lamps (UVB-313, Cleveland, Ohio). The plugs were spaced evenly (2.5 cm), kept 0.5 m below the UV-B source, and grown under continuous UV-B in a greenhouse maintained at $22 \pm 2^\circ\text{C}$. Daylength averaged 11 h. Plugs were subjected to UV-B from 16 to 26 Mar. and irrigated three times a week to prevent moisture stress. On 27 Mar., the plugs were removed from UV-B treatment and placed under a mist system for recovery. Photochemical efficiency and turf quality (based on a visual scale of 1 to 9, with 9 indicating the best quality) scores (as an indication of the degree of visual injury or lack thereof) were determined as in previous trials.

Experiment 2. Treatments remained the same as in Expt. 1. The plugs were treated on 31 May and then placed under continuous UV-B irradiation from 1 through 12 June 2001. On 13 June, UV-B treatment ceased and the plugs were set under a mist system for recovery. Photochemical efficiency and turf quality scores were determined as in previous trials.

Experiment 3. Treatments remained the same as those in Expts. 1 and 2. However, there were four replications instead of three. The plugs were treated on 24 Jan. 2002 and placed under continuous UV-B from 25 Jan. through 4 Feb. 2002. On 5 Feb., UV-B irradiation stress was discontinued and the plugs were placed under a mist system for recovery.

Photochemical efficiency and turf quality scores were determined as in previous trials. Antioxidant concentration and activity (AT, SOD, catalase, and ascorbate peroxidase) were measured by leaf samples which were taken from each experimental unit at 1, 5, and 10 d after UV-B initiation, immediately frozen with liquid N_2 , and stored at -80°C until laboratory analyses could be performed as detailed in the companion paper (Ervin et al., 2004). Anthocyanin content was determined following the procedure of Rabino and Mancinelli (1986). Briefly, anthocyanin was extracted from leaf samples (100 mg FW) by periodically shaking samples over a 48 h period at 4°C in acidic (1% HCL) methanol. The absorbance of the extract, clarified by filtration, was measured at 530 and 657 nm using a spectrophotometer (BioMate 3, Thermo Spectronic, Rochester, N.Y.). The formula $A^{530} - (0.25 \times A^{657})$ was used to calculate anthocyanin content.

Statistical analyses. Measured variables were subjected to a two-factor ANOVA using the general linear models procedure in the Statistical Analysis System (SAS Institute, 1990).

Factor one included three levels of supplement treatments and factor two included three levels of experimental time periods (i.e., Expts. 1, 2, and 3). Supplement $\times$ experiment interactions were nonsignificant for three of four sampling dates, therefore, quality and photochemical efficiency data are presented as means analyzed over all three experimental periods. Mean differences were ascertained using Fisher's protected LSD ($P = 0.05$).

Results

All kentucky bluegrass plants began the trials with equivalent photochemical efficiency and similar visual quality (Table 1). Exposure of kentucky bluegrass to UV-B caused a rapid decline in photochemical efficiency and quality regardless of treatment. However, following 4 or 5 d of continuous UV-B, photochemical efficiencies of plants treated with HA + SWE and SA were greater than the control by 29% and 21%, respectively. At 10 or 12 d of exposure, SA-treated bluegrass had 33% higher photochemical efficiency, while HA + SWE-treated bluegrass had 42% greater photochemical efficiency. At the end of a recovery period (28 or 42 d), only the SA-treated plants continued to exhibit greater photochemical efficiency.

Similar to the photochemical efficiency results, visual quality was greater due to HA + SWE treatment at all sample dates after exposure to UV-B (Table 1); SA had positive effects on visual quality at the 10 to 12 d rating periods. Following UV-B removal, both treatments provided greater recovery of visual quality. When averaged over all sample dates and experiments, photochemical efficiency readings were positively correlated ($r = 0.77^{**}$) with quality ratings, providing good confidence for our visual assessments of turfgrass injury or recovery.

Leaf tissue samples for antioxidant analyses were only collected during the third experimental trial. One day after UV-B initiation, AT leaf concentration was equivalent across all treatments (Table 2). However, at day 5, HA + SWE treated bluegrass had higher endogenous AT levels relative to the control. At day 10, the SA and HA + SWE treatments resulted in AT concentrations that were 40% to 43% higher than the control. Higher visual quality ratings were correlated with greater endogenous AT concentrations over the 10-d treatment period due to exogenous treatments of HA + SWE ($r = 0.96^{**}$) or SA ($r = 0.69^*$).

Table 1. Quality and Photochemical Efficiency responses of kentucky bluegrass to UV-B irradiation and hormone supplement treatment analyzed over three experimental periods

Supplement	Day			
	1	4 or 5	10 or 12	28 or 42
	Photochemical efficiency (Fv/Fm)			
Control	0.60 a ^z	0.34 b	0.14 b	0.36 b
HA + SWE ^y	0.64 a	0.48 a	0.21 a	0.40 b
Salicylic acid	0.63 a	0.43 a	0.24 a	0.53 a
	Quality (1 = dead; 9 = ideal)			
Control	8.8 a	5.6 b	2.9 b	5.4 b
HA + SWE	8.9 a	6.6 a	4.1 a	6.7 a
Salicylic acid	8.9 a	5.7 b	4.4 a	7.4 a

^zValues within the same column marked with same letters are not different significantly at $\alpha = 0.05$.

^yHA = humic acid; SWE = seaweed extract.

Table 2. Kentucky bluegrass antioxidant and pigment responses to hormone supplement treatments and UV-B irradiance over 10 d; Expt. 3

Supplement treatment	Rate (mg·m ⁻²)	Days of UV-B exposure		
		1	5	10
Alpha-tocopherol (μg·g ⁻¹ FW)				
Control	0	6.4 a ^y	4.0 b	2.4 b
HA + SWE ^z	150 + 50	6.9 a	5.9 a	4.0 a
Salicylic acid	150	5.8 a	4.6 ab	4.2 a
SOD activity (unit/mg protein)				
Control	0	17.2 a	15.1 b	10.7 b
HA + SWE	150 + 50	17.5 a	18.2 a	15.9 a
Salicylic acid	150	19.9 a	21.6 a	16.7 a
Catalase activity (unit/mg protein)				
Control	0	84.5 b	44.5 c	18.8 b
HA + SWE	150 + 50	85.5 b	55.8 b	45.3 a
Salicylic acid	150	117.5 a	77.1 a	45.6 a
APX activity (unit/mg protein)				
Control	0	0.5 a	0.5 a	0.5 a
HA + SWE	150 + 50	0.7 a	0.6 a	0.7 a
Salicylic acid	150	0.7 a	0.9 a	1.0 a
Total Chlorophyll (μg·mL ⁻¹)				
Control	0	13.4 b	6.5 a	2.8 b
HA + SWE	150 + 50	13.3 b	8.6 a	5.6 a
Salicylic acid	150	15.3 a	8.2 a	5.0 a
Total Carotenoids (μg·mL ⁻¹)				
Control	0	2.7 b	1.3 a	0.7 b
HA + SWE	150 + 50	2.6 b	1.7 a	1.5 a
Salicylic acid	150	2.9 a	1.5 a	1.2 a
Anthocyanin (A ⁵³⁰ - (0.25 × A ⁶⁵⁷))				
Control	0	0.28 b	0.45 b	0.23 b
HA + SWE	150 + 50	0.34 b	0.45 b	0.42 a
Salicylic acid	150	0.56 a	0.61 a	0.36 a

^yHA = humic acid; SWE = seaweed extract.

^zValues within the same column marked with same letters are not different significantly at $\alpha = 0.05$.

^xSOD = superoxide dismutase; APX = ascorbate peroxidase.

Superoxide dismutase activity was equivalent across treatments at day 1 (Table 2). At day 5, SA- and HA + SWE-treated plants had greater SOD activity. From day 1 to 10, SOD activity decreased by 38% in control plants, while SA- and HA + SWE-treated plants only lost 16% and 9% SOD activity, respectively. Correlation between turf quality and SOD activity was not significant over the 10-d period.

Catalase activity declined sharply following 5 d of UV-B irradiation (Table 2). However, relative to the control, bluegrass pretreated with HA + SWE or SA maintained 25% and 73% higher catalase activity, respectively, at 5 d after UV-B initiation. When measured at 10 d, HA + SWE or SA resulted in 2.4-fold greater catalase activity. Accordingly, HA + SWE ($r = 0.97^{**}$) and SA ($r = 0.78^{**}$) were correlated with greater quality ratings over the 10-d UV-B exposure period. Ascorbate peroxidase activity was unaffected by UV-B irradiation and supplement pretreatment (Table 2).

Greater total chlorophyll content (i.e., chl a + b) remained following 10 d of UV-B due to HA + SWE and SA (Table 2); both treatments also resulted in greater carotenoids at day 10. Anthocyanin content for all three treatments increased under continuous UV-B from day 1 to 5, and decreased from day 5 to d 10 (Table 2). Relative to the control, SA-treated bluegrass had greater anthocyanin concentrations at all sampling dates, while HA + SWE plants had greater anthocyanin only at day 10. Patterns of anthocyanin concentration suggest control plants had less ability to maintain this defense with prolonged exposure to UV-B radiation.

Discussion

Similar to results reported in the companion paper (Ervin et al., 2004), pretreatment with SA or SWE + HA before continuous UV-B exposure alleviated decline of Kentucky bluegrass photochemical efficiency and visual quality. In general, the magnitude of protection was similar for SA and HA + SWE treatments across all three experiments. Schmidt and Zhang (2001) reported similar protection of Kentucky bluegrass photosynthetic function under UV-B stress due to SA and SWE + HA treatments. However, our data expand these findings by indicating that damage mitigation was associated with higher AT concentration, higher SOD and catalase activity, and greater leaf pigment concentrations.

Increased SOD activity with exogenous application of SA has been shown with *Nicotiana glauca* (Bowler et al., 1989). Mackerness (2000) pointed out that while UV-B exposure leads primarily to oxidative stress, these reactive oxygen species also act as second messengers that trigger SA production. Salicylic acid functions as a key signaling compound involved in the activation of plant defense responses such as induction of pathogenesis-related genes and the expression and activity of antioxidant enzymes such as ascorbate peroxidase and SOD (Mackerness, 2000; Jordan, 1996).

Our results indicate increased anthocyanin content for all treatments following 5 d of UV-B irradiation, with SA-treated bluegrass having the highest concentration. Anthocyanins are reported to function in preventing photo-oxidative damage as leaves senesce (Field et

al., 2001) and many species have been noted to up-regulate anthocyanin production in response to increased UV radiation (Holton and Cornish, 1995). In general, hormone-supplement treated plants maintained greater overall pigment concentrations over the 10-d irradiation period. Less pigment destruction was most likely associated with the more robust antioxidative protection systems reported herein due to HA + SWE and SA treatments.

The hormone-like activities of seaweed extract and humic acid have been identified with bioassay and GC-MS techniques (Cacco and Dell'Agola, 1984; Sanderson et al., 1987; Yan, 1993). Indirect ELISA indicates that the SWE used in these experiments contained 70 mg·kg⁻¹ of the cytokinin, zeatin riboside (Zhang and Ervin, 2004). Applications of a combination of SWE and HA have been previously shown to increase antioxidant concentrations and activities of drought-stressed Kentucky bluegrass (Zhang and Schmidt, 1999). Our results also indicate that antioxidant increases are correlated with reduced UV-B irradiation damage. Based on our reading of the literature, it is possible that the SWE + HA treatment affected cell membrane integrity either directly, by altering membrane components, or indirectly, by increasing antioxidative protective mechanisms. Yan et al. (1997) reported that perennial ryegrass (*Lolium perenne* L.) pretreated with SWE fortified with HA and Fe had increased drought tolerance associated with increased membrane fluidity (i.e., greater levels of unsaturated fatty acids). It is also clear that cytokinins directly function to scavenge free radicals and prevent their formation (Leshem, 1981; Musgrave, 1994). A further role of cytokinins in antioxidative protection has recently been shown by Liu and Huang (2002) who reported that treatment of creeping bentgrass roots with zeatin riboside reduced lipid peroxidation and senescence of leaves exposed to high temperature stress by suppressing loss of SOD and catalase activity.

In summary, our data indicate that increasing the robustness of the antioxidative protection system in Kentucky bluegrass through the application of phytohormone supplements prior to UV-B stress served to mitigate pigment destruction, alleviate decline of photochemical efficiency, delay senescence, and improve the rate of visual quality recovery. As terrestrial UV-B levels continue to increase, our approach of boosting plant defense systems through direct application of antioxidants (Ervin et al., 2004) or application of hormone supplements may prove of high utility for improving the abiotic stress resistance of cool-season turfgrasses. However, further research is required to confirm our results in field environments and fine-tune application protocols.

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