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Effect of Enhanced UV-B Radiation on Reniform Nematode (*Rotylenchus reniformis* Linford and Oliveira) Populations in Cotton (*Gossypium hirsutum* L.)

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Abstract: To understand the effects of increased UV-B radiation on reniform nematode (*Rotylenchus reniformis* Linford and Oliveira) populations, cotton (*Gossypium hirsutum* L.) plants were exposed to three levels of UV-B radiation [0 (control), 6 and 12 kJ m^{-2} day^{-1}] in a glasshouse from emergence to early square stage. At each UV-B treatment, four populations [0 (N_0), 2500 (N_{2500}), 5000 (N_{5000}) and 7500 (N_{7500})] of reniform nematodes were incorporated into the sterilized rooting medium. Plant growth, development, photosynthetic parameters, pigments, phenolics and the number of eggs and nematode numbers in the rooting medium were recorded at the end of the experiment, 40 DAS. Even though, UV-B radiation did not significantly affect plant growth and development, it did significantly increase leaf and root phenolic concentrations. UV-B treatments significantly decreased both the egg and nematode numbers in all the nematode population treatments. Significant negative correlation was found between cotton leaf phenolic concentration and egg (slope = -69.4; R^2 = 0.72) and nematode (slope = 103; R^2 = 0.53) numbers. Similarly, root phenolics also showed negative correlation with egg (slope = -3184; R^2 = 0.26) and nematode numbers (slope = -5857; R^2 = 0.30). Therefore, current and projected UV-B radiation levels may have an important regulatory influence on nematode populations.

Key words: Cotton, *Gossypium hirsutum* L., nematodes, phenolics, reniform nematode, *Rotylenchus reniformis*, UV-B radiation

INTRODUCTION

Depletion of the stratospheric ozone has lead to substantial increases in the ultraviolet-B radiation (UV-B) (300-320 nm) reaching the Earth's surface (McKenzie *et al*., 2003). Since the 1980s, ground-level UV-B radiation has increased by 6-14% at mid- and high latitude sites over both hemispheres (UNEP/WMO, 2002). The synergistic effect between climate change factors, particularly global warming and ozone depletion could further exacerbate conditions conducive to higher UV-B radiation in the coming years. A recent study indicates a strong synergism between global warming and ozone depletion (Aldhous, 2002) and the UV-B radiation is projected to further increase in the future. Zerefos *et al*. (1997) reported a 27% per decade increase in the ground-level UV-B radiation over northern Europe. More recently, Hicke *et al*. (2004) found a 15% increase in Georgia and

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10% in New Mexico states of USA over a nine year period starting from 1995, with maximum increases occurring during the summer crop growing season.

Because UV-B is highly energetic radiation, increases in ground-level will have potential consequences for plants, animals and microbes. Therefore, effects of UV-B radiation on field crops have been extensively studied over the last two decades demonstrating that UV-B is detrimental to crops (as reviewed by Kakani *et al*., 2003). To date, there are very few studies that have reported UV-B effects on biotic responses in the crop environment (Ballare *et al*., 1996; Rousseaux *et al*., 1998; Zavala *et al*., 2001). Ballare *et al*. (1996) found that current levels of UV-B substantially decreased insect herbivory on crop foliage, while Zavala *et al*. (2001) found that solar UV-B resulted in a two-fold increase of feeding by various species of chewing insects in soybean. Similarly Gwynn-Jones (1999) found that increased UV-B radiation reduced herbivory of snails and slugs. However, there are no studies on UV-B effects on nematodes, which are pests that significantly reduce yields of crops in major agricultural regions of the world (Sasser, 1989).

One potential effect of increased UV-B radiation on plants is a change in the secondary chemistry (Bassman, 2004), particularly the accumulation of phenolic compounds (Rozema *et al*., 1997; Mazza *et al*., 2000) as a defense mechanism through induction of enzymes of the shikimic acid pathway (Caldwell and Flint, 1994). Most plant phenolics are produced via the phenylpropanoid and phenylpropanoid acetate pathways, which begin with the action of phenylalanine ammonia lyase upon the amino acids phenylalanine and tyrosine. These compounds, which are accumulated as a response to high UV-B radiation levels, are also considered to serve as plant signals to the biotic and abiotic environment (Dakora and Phillips, 1996). Secondary metabolites are also important in plant-herbivore interactions (Rosenthal and Janzen, 1979; Bernays *et al*., 1989) and may affect pathogens (Newsham *et al*., 1997; Horner *et al*., 1988). The phenolics are an extensive group of plant substances which possess a common aromatic ring bearing one or more hydroxyl substituents. Phenolic compounds can be converted into several derivatives including phytoalexins (antimicrobial compounds), coumarins (oral anticoagulants), lignins (cell wall strength), various flavonoids and condensed tannins (feeding deterrents) (Swain, 1977).

Plant roots are normally exposed to a variety of soil microorganisms, which grow on roots as a food resource or habitat niche. The soil microorganisms such as bacteria, fungi and nematodes invade plant roots (Hirsch *et al*., 2003) and cause damage to plant system. Plant defense responses to nematodes, however, involve chemicals rather than nutritional or structural penetration barriers and specific enzymes of phenylpropanoid pathway are implicated (Zacheo *et al*., 1982; Brueske, 1980). Phenolics are known to induce resistance in host plants against pathogenic microorganisms (Swain, 1977). They often act as signal molecules to facilitate or to discourage interactions with other organisms. Symbiotic microbes such as rhizobia are attracted to certain phenolics and their nod (nodulation) genes are induced by phenolics (reviewed by Schultze and Kondorosi, 1998). Plant phenolics also act as repellents of herbivores including insects, birds and mammals (Dixon and Palva, 1995). Plant parasitic nematodes have a well-developed nervous system that includes chemo-, thermo- and mechano-sensory neurons (Bird and Bird, 1991). This finding underscores the importance of chemical signaling to nematode ecology.

The reniform nematode is an important problem in United States, particularly, in the south and southeast regions and all (current and obsolete) Upland cotton cultivars are susceptible to nematodes (Jenkins *et al*., 1993; Robinson *et al*., 1999; Koenning *et al*., 2001). The current yield losses vary from region to region, 2.2% across the US Cotton belt and over 5% in the Arizona and New Mexico regions (Blasingame and Patel, 2005; Robinson *et al*., 1999), depending on management practices such as crop rotation, application of pesticides and use of resistant cultivars. However, breeding and evaluation of germplasm for nematode resistance have been hampered by lack of reliable and efficient evaluation methods (Zhang *et al*., 2006). Both nematode egg counting and gall index have been used extensively in breeding and evaluation tests (Zhang *et al*., 2006). The interrelationships between chemical compounds produced under high UV-B radiation and biotic environments remains elusive. Therefore, we hypothesize that higher concentrations of phenolic compounds in the tissues may be detrimental to reniform nematode (*Rotylenchus reniformis* Linford and Oliveira) reproduction in cotton (*Gossypium hirsutum* L.). Our objective was to determine whether the phenolic compounds produced under higher UV-B radiation levels have any effect on the nematode populations.

MATERIALS AND METHODS

Plant culture: The experiment was conducted in a greenhouse located at R.R. Foil Plant Science Research Center, Mississippi State University, Mississippi, USA to examine the effects of UV-B radiation on nematode plant parasite numbers in cotton. Seeds of Upland cotton,

Paymaster 1218 B/RR, were sown in 2.5 L pots filled with sterilized soil on 2 May 2003. Soil was sterilized by autoclaving at 121°C and 103.4 kDa for 2 h on 2 consecutive days. Plants were irrigated three times a day with half-strength Hoagland's nutrient solution delivered at 0800, 1200 and 1700 h with an automated and computer-controlled drip system to provide favorable nutrient and water conditions for plant growth. The greenhouse was maintained at constant temperature of 28±3°C during the experimental period. The final harvest was 40 day after sowing (DAS).

Treatments: The UV-B radiation treatments of 0 (control, no UV-B) and a total daily dose of biologically effective UV-B radiation of 6 and 12 kJ m^{-2} day^{-1} were imposed starting from emergence, 8 DAS. The UV-B doses of 6 and 12 kJ m^{-2} day^{-1} in the experiment simulated ambient solar UV-B levels during June-July months in Mississippi (http://uvb.nrel.colostate.edu/UVB/) and 30% depletion of stratospheric ozone, respectively, based on the empirical model of Green *et al.* (1980).

The UV-B radiation was delivered to plants for 8 h from 0800 to 1600 h by UV-313 lamps (Q-Panel Company, Cleveland, Ohio, USA) powered by 40 W dimming ballasts. To filter UV-C radiation (<280 nm), the lamps were wrapped with solarized 0.07 mm cellulose diacetate (CA) film (JCS Industries Inc., La Mirada, California, USA). The CA on the lamps was changed at 3-4 day intervals to account for the degradation of the CA properties. The UV-B energy delivered at the top of the plant canopy was checked daily with a UVX digital radiometer (UVP Inc., San Gabriel, California, USA) and calibrated against an Optronic Laboratory (Orlando, Florida, USA) Model 754 Spectroradiometer, which was used to initially quantify lamp output. The lamp power was adjusted, as needed, at 1000 h each day to maintain the respective UV-B radiation levels. The distance from lamps to the plant tops was maintained at 0.5 m throughout the experiment. Unilluminated lamps with frame were placed on the control set of plants to simulate equivalent shading. The average daily biologically effective UV-B radiation delivered during the experiment was 6.07±0.04 for 6 kJ m^{-2} day^{-1} and 11.72±0.06 for 12 kJ m^{-2} day^{-1} treatments.

The reniform nematode race was originally isolated from a cotton field in Tallahatchie County, Mississippi, USA and maintained on cotton. The nematodes were extracted by combined gravity screening and sucrose centrifugal flotation (specific gravity = 1.13) and enumerated with the dissecting microscope (Jenkins, 1964). Four initial nematode inoculum treatments were imposed, 0 (N_0), 2500 (N_{2500}), 5000 (N_{5000}) and 7500 (N_{7500}) nematodes pot^{-1} at each UV-B treatment. The nematode extract was added by pipeting the appropriate nematode suspension into three depressions of 1 cm in diameter ×3 cm deep and 2-3 cm away from base of the plant. After inoculation, the depressions were filled with sterilized soil to prevent dehydration of the inoculum.

Measurements: At final harvest, plant component dry weights were determined after oven drying at 70°C until it weighed constant over a period of 72 h. One day before the final harvest, leaf photosynthesis components such as net photosynthesis (Pn), stomatal conductance (g_s) and intercellular carbon dioxide concentration [CO_2] (Ci) were measured using LICOR-6400 photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) on each of the selected leaves, 4th or 5th leaf from the terminal. The leaf Pn measurements were made using a red: Blue light source (LI-6400-02B) and adjusted to provide a fixed photosynthetic photon flux density of 1500 μmol photons m^{-2} sec^{-} .[1] Cuvette block temperature was maintained to match the glasshouse temperature using a computer controlled Peltier module mounted on the cuvette. The airflow entering the cuvette was maintained at [CO_2] of 360 μL CO_2 L^{-1}.

Pigment extraction was made from the same leaves after the photosynthetic measurements. The photosynthetic pigments (chlorophyll *a*, chlorophyll *b* and carotenoids) were extracted by placing five 38.5 mm^2 leaf discs in a vial with 5 mL of dimethyl sulfoxide and extracting for 24 h. The absorption of the extracts was determined at 470, 648 and 664 nm using the Bio-Rad UV/VIS spectrophotometer (Pharmacia, Cambridge, England) with a resolution of 1 nm by scanning from 200 to 900 nm. The equations by Litchenthaler (1987) were used to obtain the pigment concentrations. The pigment concentrations were expressed on a leaf area basis (μg cm^{-2}).

The leaf phenolic compounds were extracted from five 38.5 mm^2 leaf discs placed in a vial with 10 mL of a mixture of methanol, water and hydrochloric acid in 79:20:1 ratio by volume. The vials were incubated at room temperature for 24 h in dark to allow for complete extraction of phenolics. The absorbance of the extracts from different treatments was measured at 300 nm. The phenolic content was calculated using the equation, C = 16.05 * A, where A is absorbance at 300 nm and C is phenolic compound concentration (μg mL^{-1} of extract) and expressed as equivalents of p-coumaric acid (Mirecki and Teramura, 1984) on a dry weight basis. Similarly, root phenolics were extracted from oven-dried ground samples of plant roots (Chimphango *et al.*, 2003). A dried sample of 0.3 g was placed in 10 mL of the extractant and the phenolic concentration was estimated using the same procedure described earlier.

After final harvest, the juveniles and vermiform adults were extracted from the soil in the pots by gravity screening and centrifugal flotation methods (Jenkins, 1964) and counted using a Nikon SMZ 800 microscope (Nikon Instruments, Kanagawa, Japan). Eggs were extracted from roots by immersing roots into 0.525% of sodium hypochlorite for 240 sec (Hussey and Barker, 1973). The solution was then poured through a 75 μm pore sieve nested over a 25 μm sieve and enumerated in a graded petridish using a stereomicroscope (Nikon Scientific, Kanagawa, Japan).

Statistical analysis: To test the significance of the both UV-B radiation, nematode treatments and their interactive effects on growth, photosynthesis, pigments and nematode populations, the data was statistically analyzed using two way analysis of variance (ANOVA) by Genstat 6 for Windows (Genstat 6 Committee 1997). The least significant difference (LSD) tests at p = 0.05 were employed to distinguish treatment difference means of the parameters measured in this study. For correlation analysis of leaf and root phenolics and nematode population, the zero nematode treatments were removed before the analysis.

RESULTS

Dry matter production and photosynthetic rates: Neither ambient nor elevated UV-B levels had effect on whole plant dry matter and individual part dry weights (Table 1). Stomatal conductance and intercellular CO_2 concentrations were not affected by either UV-B radiation or by nematode treatments whereas UV-B radiation had a significant effect on photosynthesis ($p<0.05$) (Table 2).

Pigments and phenolics: The chlorophyll and carotenoid concentrations were not significantly different among UV-B radiation treatments (Table 3). Total chlorophyll content significantly ($p<0.05$) decreased by 7-8% with N_{2500}, N_{5000} and N_{7500} nematode treatments with no additional UV-B. Carotenoids also had a similar trend, where nematode treatments reduced carotenoids by 6% when compared to plants grown with no nematodes in the treatment. However, leaf phenolic concentrations significantly increased by 28 and 32% with increasing UV-B levels of 6 and 12 kJ m^{-2} day^{-1}, respectively. There was a significant interaction between UV-B radiation and nematode treatments ($p<0.001$) for leaf phenolics. The highest leaf phenolic concentration was observed under 12 kJ m^{-2} day^{-1} of UV-B and N_0 nematode treatment. Root phenolic concentrations also significantly ($p<0.001$) differed with increasing UV-B radiation, nematode treatments and their interaction. UV-B radiation treatments of 6 and 12 kJ m^{-2} day^{-1} produced 10% more root phenolics than that of 0 kJ m^{-2} day^{-1} treatment and high nematode treatments decreased the root phenolic concentrations by 43%.

Nematode populations: With increasing UV-B radiation, averaged over all the nematode treatments, eggs produced by the nematodes significantly ($p<0.01$) decreased by 32 and 16% with 6 and 12 kJ m^{-2} day^{-1} UV-B treatments, respectively (Table 4). Similarly, the 6 and 12 kJ m^{-2} day^{-1} UV-B radiation treatments

Table 1: Biomass production and partitioning of cotton plants as influenced by ultraviolet-B (UV-B) radiation and nematode treatments at 40 days after sowing. Values are means±standard error (n = 5)

Treatments		Dry matter production			
UV-B kJ m^{-2} day^{-1}	Nematodes No. pot^{-1}	Total	Leaf	Stem	Root
		g $plant^{-1}$			
0	0	8.26±1.82	3.80±0.68	3.63±0.94	0.82±0.21
	2500	8.44±1.56	3.94±0.27	3.60±0.67	0.90±0.22
	5000	8.56±0.65	3.94±0.70	3.75±0.33	0.86±0.08
	7500	8.67±1.00	3.87±0.43	3.83±0.42	0.98±0.16
6	0	6.75±0.92	3.25±0.45	2.74±0.36	0.76±0.14
	2500	9.24±1.18	4.33±0.56	3.92±0.50	0.99±0.14
	5000	7.66±1.11	3.57±0.54	3.35±0.50	0.74±0.11
	7500	8.94±0.84	4.17±0.34	3.80±0.45	0.97±0.08
12	0	8.12±1.16	3.89±0.48	3.49±0.58	0.75±0.11
	2500	7.27±1.11	3.38±0.68	3.15±0.44	0.74±0.16
	5000	8.25±1.03	3.99±0.52	3.52±0.42	0.74±0.11
	7500	7.52±1.28	3.60±0.59	3.29±0.53	0.73±0.17
p (UV-B)		NS	NS	NS	NS
p (Nematode)		NS	NS	NS	NS
p (UV-B x Nematode)		NS	NS	NS	NS

NS: Not significant at the 0.01 probability level

Table 2: Photosynthesis (Pn), stomatal conductance (gs) and intercellular CO_2 concentration (Ci) of cotton plants as influenced by ultraviolet-B (UV-B) radiation with nematode treatments at 40 days after sowing. Values are means±standard error (n = 5)

Treatment		Photosynthesis parameters		
UV-B kJ m^{-2} day^{-1}	Nematodes No. pot^{-1}	Pn (µmol m^{-2} sec^{-1})	g_s (mol m^{-2} sec^{-1})	C_i (µmol mol^{-1})
0	0	26.5±0.4	0.569±0.2	284.5±5.7
	2500	23.9±1.4	0.912±0.03	303.7±2.0
	5000	27.1±0.7	1.183±0.10	310.7±3.1
	7500	25.9±1.0	1.157±0.30	301.3±9.1
6	0	30.3±0.6	0.985±0.04	298.3±1.5
	2500	32.1±0.5	1.124±0.10	299.7±6.6
	5000	30.7±1.3	0.809±0.02	285.8±2.1
	7500	31.8±1.1	0.929±0.10	292.2±1.5
12	0	29.4±0.6	0.865±0.10	290.2±5.9
	2500	27.5±2.0	0.612±0.10	267.0±9.9
	5000	29.5±0.9	0.884±0.10	291.3±5.6
	7500	28.6±3.6	1.038±0.20	303.5±2.4
p (UV-B)		***	NS	NS
p (Nematode)		NS	NS	*
p (UV-B x Nematode)		NS	**	***

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively. NS: Not significant at the 0.1 probability level

Table 3: Pigments and phenolic concentration of cotton plants as influenced by ultraviolet-B (UV-B) radiation and nematode treatments at 40 days after sowing. Values are means±standard error (n = 15)

Treatment		Pigments		Phenolics	
UV-B kJ m^{-2} day^{-1}	Nematodes No. pot^{-1}	Total chlorophyll	Carotenoids	Leaf	Root
		µg cm^{-2}		µg g^{-1}	
0	0	28.2±0.35	9.8±0.11	108.4±1.7	9.83±0.57
	2500	25.2±0.22	8.4±0.03	70.8±7.2	4.65±0.34
	5000	24.9±0.46	8.2±0.27	87.3±2.5	6.47±0.65
	7500	23.6±0.82	8.1±0.27	75.3±8.6	4.83±0.10
6	0	26.2±0.45	9.1±0.12	111.8±2.7	9.77±0.30
	2500	26.1±0.60	9.0±0.34	114.9±1.08	6.52±0.11
	5000	23.9±0.90	8.6±0.31	104.8±4.2	5.26±0.16
	7500	26.9±0.36	9.3±0.07	116.2±1.9	6.01±0.35
12	0	26.1±1.70	9.0±0.56	122.3±1.9	9.86±1.09
	2500	24.6±0.55	8.7±0.03	109.6±0.6	6.45±0.15
	5000	25.9±0.51	9.0±0.26	108.7±1.9	5.39±0.15
	7500	25.8±0.59	8.9±0.25	100.6±0.62	5.93±0.09
P (UV-B)		NS	NS	***	***
P (Nematode)		*	*	***	***
P (UV-B x Nematode)		*	*	***	***

*, *** Significant at the 0.05 and 0.001 probability levels, respectively. NS: Not significant at the 0.1 probability level

Table 4: Number of eggs and nematodes (juveniles and vermiform adults) in cotton as influenced by ultraviolet-B (UV-B) radiation and nematode treatments at 40 days after sowing. Values are means±standard error (n = 15)

Treatments		Nematodes	
UV-B kJ m^{-2} day^{-1}	Nematodes No. pot^{-1}	Eggs	Total (juveniles and vermiform adults)
		No. pot^{-1}	
0	0	622±104	356±101
	2500	26629±1525	35736±2541
	5000	22568±2514	30754±1599
	7500	24087±1896	40712±1528
6	0	248±25.4	387±88
	2500	13417±1865	29265±2514
	5000	21001±1124	36002±1632
	7500	15182±987	17839±1114
12	0	198±57	313±101
	2500	21364±2114	25411±1254
	5000	16524±998	21706±1896
	7500	23231±1251	22483±2082
P (UV-B)		**	***
P (Nematode)		***	***
P (UV-B x Nematode)		NS	***

, * Significant at the 0.01 and 0.001 probability levels, respectively. NS: Not significant at the 0.1 probability level

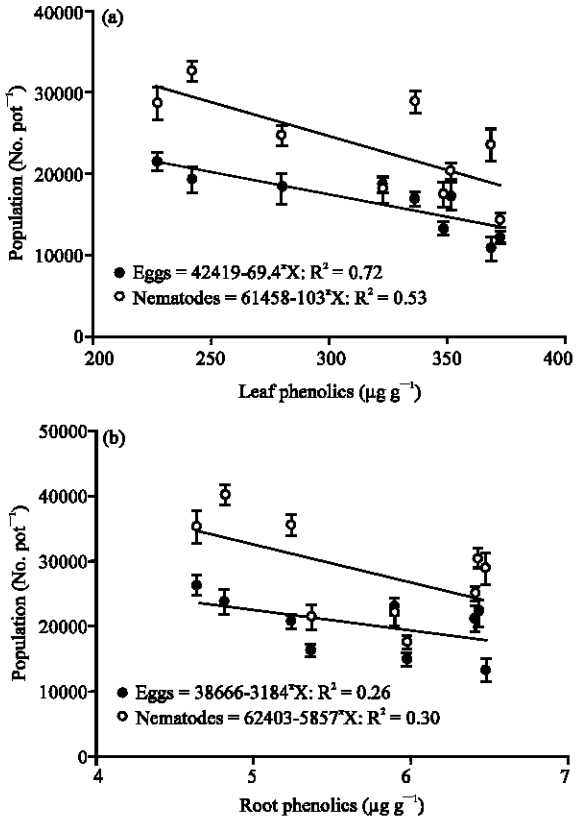

Fig. 1: Relationship of cotton (A) leaf and (B) root phenolic concentrations with eggs and final nematode populations in the soil medium for plants grown under three ultraviolet-B (UV-B) radiation treatments (0, 6 and 12 kJ m^{-2} day^{-1}) and three initial nematode (2500, 5000 and 7500 nematodes pot^{-1}) populations. Bars show SE (n = 12). The zero nematode treatments were not used in the analysis

decreased final nematode numbers, i.e., the number of juveniles and vermiform adults decreased by 19 and 35%, respectively compared to the) UV-B control.

Phenolics and their correlations with nematode populations: Leaves accumulated more (~15 times) phenolics than the roots when averaged across treatments (Table 4). Negative correlations were obtained between leaf and root phenolic concentrations and final nematode numbers, R^2 = 0.53 and 0.30, respectively (Fig. 1). Similar negative correlations were obtained between leaf and root phenolic concentrations and eggs produced by the nematodes, R^2 = 0.72 and 0.26, respectively.

DISCUSSION

Over the past two decades, considerable attention has been given to UV-B radiation effects on plants, while few studies have addressed UV-B induced changes in plant chemistry and their influence on biota such as insects, snails and slugs. This is the first report on the UV-B radiation effects on nematode populations in crops. In this study, we present the results of how increasing UV-B radiation affects the nematode and their egg populations in cotton. Our results show reductions in the number of nematodes (juveniles and vermiform adults) and eggs under enhanced UV-B radiation. Even though UV-B radiation cannot penetrate into the soil where these nematodes are active, changes in chemistry of the plant might have been the reason for the reductions in nematode populations and their reproductive capacity.

In the current study, UV-B radiation increased the phenolic concentrations in the UV-B irradiated plants, which was also previously reported by several others (Rozema *et al*., 1997; Mazza *et al*., 2000; Bassman, 2004). Accumulation of phenolics as a defense mechanism through induction of enzymes of the shikimic acid pathway has also been reported previously (Caldwell and Flint, 1994). In several studies, UV-B has been shown to affect several other characteristics of foliage that might play a role in the feeding preference of slugs by increasing epicuticular wax production (Gordon *et al*., 1998) and increased leaf hair density (McCloud and Berenbaum, 2000). Ultraviolet-B could cause changes in the distribution of these substances within plant tissues such as accumulation of phenolics in the upper epidermal cell layers (Grammatikopoulos *et al*., 1998), which could conceivably alter herbivory patterns.

Correlation analysis in the present study showed that the leaf and root phenolics accumulated in response to UV-B levels had a negative relationship with both nematode and egg numbers. Similarly, other studies showed that resistant cultivars of banana (Valette *et al*., 1998) and alfalfa (Baldridge *et al*, 1998) with higher flavonoids in roots were associated with very low populations of nematodes. Phenolics accumulated at high UV-B radiation levels act as both UV protectants and also as feeding deterrents for many insects, snails and slugs (Warren *et al*., 2002; Zaller *et al*., 2003; Lavola *et al*., 1998). A correlation of elevated levels of some phenolics offering resistance to plants for nematode infection was previously shown by Chitwood (2002). A recent review by Hirsch *et al*. (2003) showed that certain chemical signals are required for nematodes to hatch and in the absence

of appropriate chemical signals dormancy can be maintained for years. For most of the nematode species development, the key recovery is a diffusible chemical signal from host root. This might be the reason for less number of juveniles and vermiform adults observed in this study. Detailed characterization of phenolics needs further investigations.

We observed that enhanced UV-B radiation has no effect on growth, pigment concentrations and dry matter production. The results are consistent with several other studies showing no significant reductions in photosynthesis, growth or biomass accumulation (as reviewed by Searles *et al*., 2001). The lack of growth response observed here is in agreement with similar studies conducted with legumes (Allen *et al*., 1998; Stephen *et al*., 1999). However, these findings are in contrast with reported reductions in plant biomass grown under elevated UV-B radiations in cotton (Reddy *et al*., 2003). These inconsistencies may be explained by genotypic differences in UV-B sensitivity (Jansen *et al*., 1998). It has been demonstrated that UV-A and PAR have moderating effect on UV-B damage by inducing photoreactivating processes that effectively repair DNA lesions resulting from UV-B radiation (Jagger, 1969).

In conclusion, the chemical constituents such as phenolics are produced in response to increased UV-B radiation. Higher phenolics significantly reduced both egg and nematode numbers at all nematode treatments. Increased root and leaf phenolic concentrations were negatively correlated with both egg and nematode populations showing potential chemo-deterrence. Further studies are needed to understand the influence of specific phenolic compounds on reniform nematode populations and screen varieties that can produce greater amounts of phenolic compounds in the tissues to exert effect on nematode population in the field.

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