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Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi

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Abstract

Increases in UV-B radiation have been shown to slow the rate of litter decomposition in ecosystems. However, it is unclear if this is a result of direct UV-B effects on saprobic microorganisms, or a result of UV-B-induced changes in litter quality that indirectly affect decay by saprobes. In this study, we evaluated the magnitude of direct and indirect effects on litter decomposition of *Brassica napus* by soil fungi, under growth chamber conditions. We found that, both, direct and indirect UV-B negatively influenced litter decomposition, however, direct effects were much more pronounced. We then tested whether UV-B radiation would have species-specific effects on fungal colonization and competitive ability, rather than influencing all fungal species equally. We predicted that darkly pigmented fungi would increase their relative competitive ability under high UV-B. The test fungi were all isolated from field soil under *Brassica napus.* Two fungi were hyaline (*Aspergillus terreus*, *Trichoderma koningii*), two were darkly-pigmented (*Cladosporium sphaerospermum*, *Epicoccum purpurascens*) and one had a hyaline mycelium but darkly-pigmented conidia (*Aspergillus niger*). Elevated UV-B radiation had differential direct and indirect effects on fungal growth, and caused shifts in the competitive balances between pigmented and non-pigmented fungi. However, in only two of six pair-wise challenges did the pigmented species increase their relative competitive ability under UV-B conditions. It is clear that UV-B profoundly influence fungal community structure in soil, but the direction of such effects remains unpredictable.

Keywords: Ultraviolet radiation; Global change; Soil fungi; Litter decomposition; *Brassica napus*

1. Introduction

Since the late 1970s, there has been a significant reduction in the stratospheric ozone layer. As a consequence the amount of ultraviolet-B (UV-B: 320–280 nm) radiation reaching the earth's surface has increased (Kerr and McElroy, 1993). This additional UV-B radiation has been shown to negatively influence the growth of plants, by damaging DNA and cell membranes, altering phytohormone production, and causing morphogenetic changes (Rozema et al., 1997b). Furthermore, there is increasing evidence that such effects on plant growth can lead to inefficiencies at the ecosystem level, particularly with regards to primary production and the cycling of nutrients. Plants growing in the presence of UV-B tend to produce higher levels of protective compounds such as lignins, flavonoids and condensed tannins (Rozema et al., 1997b). This typically results in plant litter that is more recalcitrant to decay by microbes and, thus, leads to reduced rates of decomposition and nutrient availability.

Such indirect influences of UV-B on litter decomposition have been well documented, however, since

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litter on the soil surface is also exposed to solar radiation, the microbes themselves may also be directly affected by UV-B. For example, using a factorial experiment, Gehrke et al. (1995) showed that decomposer organisms may be directly and indirectly affected by UV-B radiation. When enhanced UV-B was directly applied to decomposing *Vaccinium* spp. litter, microbial respiration decreased. A similar indirect effect was found when plants were initially grown under enhanced UV-B but litter was decomposed under ambient conditions. Plants grown under enhanced UV-B contained decreased levels of cellulose, and increased amounts of tannins. Decomposer microbes were directly sensitive to UV-B, but they were also sensitive to change in litter chemistry that resulted after plants were grown under enhanced UV-B. Similar results were detected by Newsham et al. (1997) and Rozema et al. (1997a) using different plant species, *Quercus robur* and *Calamagrostis epigeios*, respectively. Furthermore, Gehrke et al. (1995) and Newsham et al. (1997) also detected changes in the species composition of saprophytic fungi when litter was decomposed under enhanced UV-B. They suggested that this likely resulted from the ability of some fungal species to tolerate UV-B, possibly with the help of protective pigments.

If saprophytic fungi differ in their tolerance to UV-B radiation, then it is also possible that this will alter the extent and direction of competitive interactions among species. Any such changes in competitive ability under enhanced UV-B conditions may lead to altered microbial community structure and nutrient cycling. Yet to date, the potential of UV-B to influence competitive interactions among saprophytic fungi has not been assessed. In this study, experiments were performed with the plant, *Brassica napus*, to test whether UV-B directly and indirectly influences (a) the decomposition of litter by a select group of saprophytic fungi, and (b) the relative competitive abilities of pigmented and hyaline (non-pigmented) fungal species.

2. Materials and methods

2.1. Fungi

Five soil fungi were isolated from under *B. napus* L. growing at the Elora Agricultural Research Station, University of Guelph in November of 1996. They where subsequently maintained at 4°C on 2% Malt Extract Agar (MEA) in the laboratory. This included two darkly-pigmented species, *Cladosporium sphaerospermum* Penz. and *Epicoccum purpurascens* Ehrenb. Ex Schlecht., two hyaline species, *Aspergillus terreus* Thom and *Trichoderma koningii* Oudem., and a fifth species, *Aspergillus niger* van Tieghem, that produced a hyaline mycelium but darkly-pigmented conidia.

2.2. Plant litter

B. napus stem litter was collected after harvest of a previous UV-B experiment conducted in the field at the Elora Agricultural Research Station of the University of Guelph (Newlands, 1997). In that experiment, the set-up consisted of a completely randomized split plot design with four treatments, each replicated three times. The four treatments were: elevated UV-B irradiance (bulbs emitted approximately 5.7 kJ m^{-2} per day, and UV-C was blocked out using cellulose diacetate filters), ambient UV-B irradiance (no frame of bulbs overhead), no UV-B irradiance (UV-B and UV-C was blocked out using Mylar plastic sheets), and a 'frame only' control to determine shading effects. The 12 plots were each 1.8 m × 1.2 m. Elevated UV-B radiation was supplied by pre-aged (100 h), UV-emitting fluorescent lamps (UV-B 313, Q-panel), turned on from 09:00 to 17:00 hours. Each frame contained 12 lamps, each 0.3 m apart and 1.5 m high. *B. napus* was planted on 1 June 1996 and harvested on 18 September 1996. Stems were collected for the present study from two treatments only (ambient and elevated UV-B).

2.3. Decomposition study

The experiment was set up using a 2 × 2 factorial design. The two factors included conditions under which the plants were grown (indirect: ambient or elevated UV-B) and conditions under which the litter was decomposed (direct: no UV-B at 5.5 kJ m^{-2} per day). Each experimental unit consisted of a glass microcosm (10.5 cm × 7.5 cm) containing 50 ml of sterile silica quartz sand, twenty 2 cm long *B. napus* litter fragments, and 10^6 spores of each *E. purpurascens* and *T. koningii*, in 10 ml of sterile distilled water.

B. napus stem fragments were gamma-irradiated (259 rad/min) for 24 h and then added to the microcosms. Half the microcosms were covered with a 10 cm × 10 cm piece of 3 mm thick plexiglass that transmitted all UV wavelengths (Panagopoulos et al., 1992), and a 10 cm × 10 cm piece of cellulose diacetate that blocked out UV-C radiation. They were secured to the microcosm with vacuum grease (Dow Corning). The remaining microcosms were covered with a 10 cm × 10 cm piece of 3 mm thick window glass that blocks out all radiation above 280 nm. The elevated UV-B radiation was supplied in growth cabinets by pre-aged (approximately 100 h) UV-emitting fluorescent lamps (UV-B 313, Q-Panel, Cleveland, OH). The distance of 1.2 m above the stem litter provided 5.5 kJ m^{-2} per day of biologically effective UV-B irradiance (Caldwell, 1971). Lamps were turned on from 09:00 to 17:00 hours.

Each treatment was replicated 10 times. The replicates were split between two growth cabinets, and randomized within each. The litter was allowed to decompose for 62 days. Fungal respiration was measured at Days 18, 32, 48, and 62 using an infrared gas analyzer (LI-6251 Li-Cor). Three controls were also included to ensure that nothing else within the sealed microcosm produced CO_2: (a) sealed microcosms containing only air, (b) sealed microcosms containing air and several sterile stem fragments, and (c) sealed microcosms containing air and 50 ml sterile silica Quartz sand. Both, before and after the decomposition study, 20 litter fragments were oven-dried at 60°C for 48 h to determine dry weight. Percent mass loss was calculated as <initial weight−final weight/initial weight>.

2.4. Competition study

The experimental set-up was similar to that above, and was repeated for all possible pair-wise combinations of pigmented and hyaline fungal species, for a total of six competition experiments. One million conidia of each species were inoculated into the microcosms containing 10 pieces of *B. napus* litter. Microcosms were placed in one of two growth cabinets and fungi were allowed to compete for litter substrates for 10 days. We picked 10 days because in a preliminary experiment, each species growing on its own was able to colonize 100% of litter fragments by Day 6 (with and without UV-B), and allowing an additional 4 days for competitive interactions. Stem fragments were then cut into 2 mm pieces, surface sterilized in 20% household bleach for 1 min, rinsed in distilled water, and plated on 2% MEA. They were then incubated at room temperature for 7 days, after which the growth of each fungus from each stem fragment was recorded. Percent colonization for each species was calculated as the number of fragments colonized/total number of fragments × 100.

2.5. Statistical analyses

In the decomposition study, both, production of CO_2 and percent colonization were analyzed using a repeated measures factorial analysis of variance (ANOVA), whereas mass loss was analyzed using a factorial ANOVA. In the competition study, percent colonization was analyzed using a factorial ANOVA.

3. Results

UV-B radiation did affect fungal respiration (Fig. 1) and litter mass loss (Fig. 2) in the microcosms. We detected a strong direct (p=0.001) and weak indirect (p=0.043) UV-B effect on fungal respiration, but no significant direct × indirect interaction (p=0.798). CO_2 concentration in the microcosms ranged from greater than 25,000 ppm in the absence of UV-B radiation to less than 700 ppm with UV-B radiation. Overall, CO_2 concentration was decreased by 85% in the presence of UV-B radiation. Similarly, we detected a direct effect (p=0.013) of UV-B radiation on the percent mass loss of *B. napus* stem litter (Fig. 2). A 22% decrease in mass loss was detected in the presence of UV-B radiation. However, indirect and interaction effects were not statistically significant ($p < 0.05$).

The results of the competition study are presented in Fig. 3 and Table 1. Direct UV-B radiation affected the outcome of competition in all pair-wise challenges, except for *A. terreus* versus *E. purpurascens* (Fig. 3c, Table 1). Even so, under direct UV-B exposure, the pigmented species did not always increase their relative competitive ability. This only occurred in two

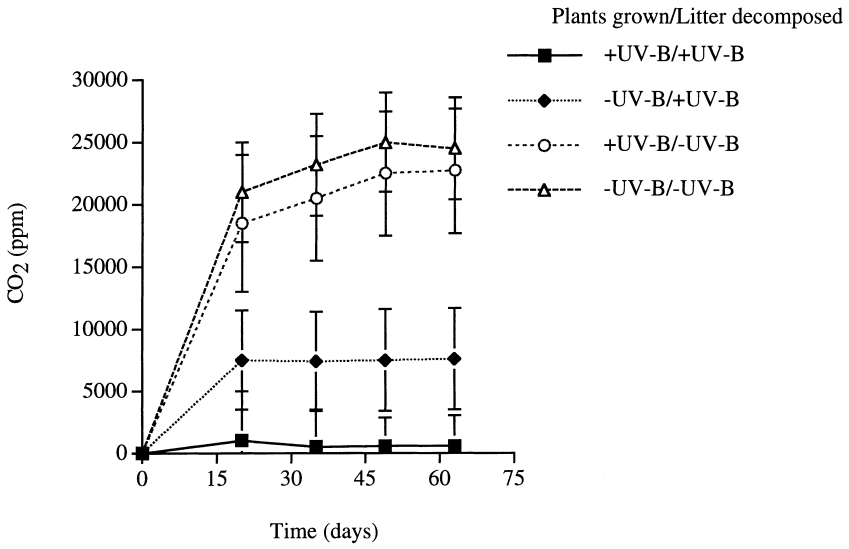

Fig. 1. Direct and indirect effects of UV-B radiation on fungal respiration. Symbols represent means +/−1 S.E.

pair-wise challenge combinations (*C. sphaerospermum* versus *T. koningii* and *E. purpurascens* versus *T. koningii*) (Fig. 3e, f, Table 1). In the other combinations, direct UV-B decreased the relative competitive abilities of pigmented fungi (Fig. 3a, b, d, Table 1). We also detected an indirect effect of UV-B on fungal competition in two of the six pair-wise challenges, indicating that litter quality also had an influence on the outcome of competition. *A. niger* increased its relative competitive ability against *A. terreus* (Fig. 3a, Table 1), and so did *C. sphaerospermum* when challenged with *T. koningii* (Fig. 3e, Table 1). Furthermore, we detected significant interactions between direct and indirect UV-B on the outcome of competition between pigmented and hyaline fungi. In two pair-wise challenge combinations (*A. niger* versus *A. terreus* and *A. niger* versus *T. koningii*), the direct UV-B effect was reduced when plants were initially grown under elevated UV-B, whereas it was enhanced in two other combinations (*C. sphaerospermum* versus *T. koningii* and *E. purpurascens* versus *T. konigii*) (Table 1).

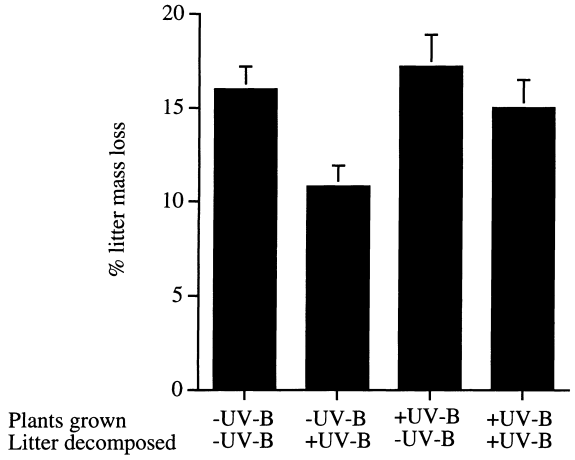

Fig. 2. Direct and indirect effects of UV-B radiation on the percent litter mass loss of *Brassica napus* stem litter. Each bar represents the mean +/−1 S.E.

4. Discussion

The results clearly show that fungi are differentially sensitive to UV-B, and this can influence fungal activity and decomposition directly during the decomposition process. The results also illustrate the presence of indirect effects by exposure to UV-B during plant growth and development, and that direct and indirect effects can strongly interact to influence fungal community structure. Strong direct effects are not surprising, particularly since UV-B radiation can directly inhibit various aspects of fungal development

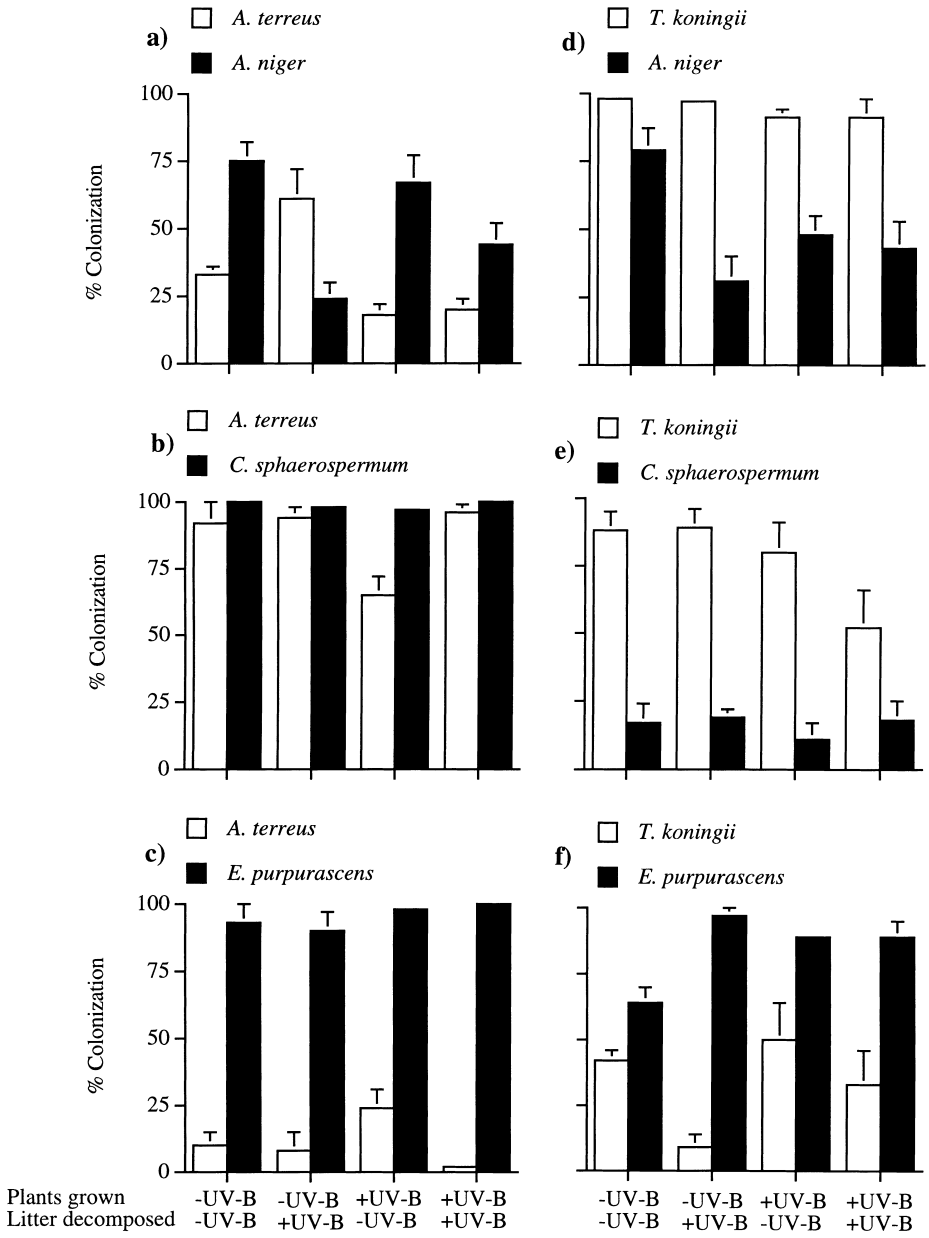

Fig. 3. Direct and indirect effects of UV-B radiation on the competitive abilities of pigmented (*Aspergillus niger*, *Cladosporium sphaerospermum*, *Epicoccum purpurascens*) vs. hyaline (*Aspergillus terreus*, *Trichoderma koningii*) fungi. Each bar represents the mean percent fungal colonization of *Brassica napus* litter +/−1 S.E.

such as spore germination and hyphal elongation (Maddison and Manners, 1972; Rotem et al., 1985; Wang and Casedevall, 1994; Rasanayagam et al., 1995). Of course, the relative impact of direct versus indirect effects will also largely depend on the extent to which plant secondary metabolism is affected, and this is genotype dependent (Rozema et al., 1997b). In the present study, *B. napus* did produce higher levels of flavonoids when grown under enhanced UV-B (Newlands, 1997), and these compounds

Table 1
Direct and indirect effects of UV-B radiation on the relative growth of pigmented vs. hyaline fungi

Plants grown (UV-B)	−	−	+	+			
Litter decomposed (UV-B)	−	+	−	+			
Pair-wise challenge	Difference in % colonization between pigmented and hyaline fungi				*p*-values		
					Indirect effect	Direct effect	Interaction effect
A. Niger×*A. Terreus* (Fig. 3a)	47	−30	50	24	0.008	0.001	0.021
C. Sphaerospermum×*A. Terreus* (Fig. 3b)	−21	−63	−51	−47	0.088	0.020	0.065
E. Purpurascens×*A. Terreus* (Fig. 3)	80	80	76	98	0.525	0.117	0.090
A. Niger×*T. Koningii* (Fig. 3d)	24	87	35	55	0.728	0.001	0.002
C. Sphaerospermum×*T. Koningii* (Fig. 3e)	10	6	32	5	0.006	0.042	0.049
E. Purpurascens×*T. Koningii* (Fig. 3f)	−76	−75	−60	−35	0.427	0.002	0.049

typically make plant tissues more recalcitrant to decay by microbes.

The present study shows that UV-B differentially influences fungal saprobes, particularly when they co-exist in communities. This implies that the influence of UV-B on decomposition rates partly depends on the fungi involved. Fungi do differ in their abilities to decompose materials. For example, primary fungal invaders typically lack the enzymes to utilize more complex carbohydrates, such as starch, cellulose and lignin, and are capable of inhibiting other organisms by producing antibiotics. On the other hand, secondary invaders are better capable of utilizing more complex substrates (Widden, 1997). The two species used in the decomposition study, *E. purpurascens* and *T. koningii*, were secondary invaders that contain enzymes capable of decomposing cellulose and lignin, as well as litter phenolics (Arsvoll, 1975; Dix and Webster, 1995). However, they do differ in other ways, for example, *T. koningii* produces phenol oxidase enzymes and can utilize tannins (Domsch et al., 1980), whereas *E. purpurascens* can be inhibited by leaf tannins (Harrison, 1971). Clearly, the suite of fungi chosen in such a study will influence the strength of any observed indirect effects.

The exact magnitude of direct and indirect UV-B effects cannot properly be assessed in this study, since the plants were grown in the field and the litter was decomposed in growth chambers. UV-B treatments applied in growth chambers typically lead to exaggerated effects, because of low PAR:UV-B ratios that are produced by artificial light and UV-B sources (Rozema et al., 1997b). Also, direct field exposure is often modified by partial shading by the plant canopy. Nevertheless, the presence of, both, direct and indirect effects did occur and these did influence colonization of litter by competing species of saprophytic fungi.

Direct photodegradation of litter is also possible under UV-B radiation. In one study, decomposition was increased under UV-B (Rozema et al., 1997a). They reported enhanced mass loss of *C. epigeous* leaf material decomposing under enhanced solar UV-B in a dune grassland ecosystem. This was not correlated with a stimulation of microbial activity. Evidence is accumulating which suggests that photochemical reactions may make a substantial contribution to litter decay in nature (Moorhead and Callaghan, 1994; Schoeman and Dickinson, 1997). However, we can likely rule out any significant photodegradation effects in the present study, since none of the UV-B treatments directly increase litter decay.

We predicted that under direct UV-B, pigmentation would convey a competitive advantage for the pigmented species. However this did not appear to be the case. Only in the pair-wise challenges between *E. purpurascens* and *T. koningii* and *C. sphaerospermum* and *T. koningii* did the pigmented species increase their relative competitive ability relative to the hyaline species under UV-B radiation. A possible reason for this was the criteria used for choosing representative pigmented and non-pigmented species. In some species, the entire thallus was not consistently pigmented, and furthermore, the type of pigments differed among species. For example, *A. niger* produces pigmented conidia

but hyaline hyphae, and the pigment is mainly composed of aspergilline, which is not a melanin-like compound. In contrast, the vegetative hyphae, conidiophores, and conidia of *C. sphaerospermum* are heavily and equally pigmented (Domsch et al., 1980), and the dark, olivaceous pigment is located in the cell wall and is known to be a melanin compound (Margalith, 1992). The third pigmented species, *E. purpurascens*, contains carotenoid pigments in the vegetative hyphae (Gribanovki-Sassu and Foppen, 1967), and indole melanins in the conidia (Ellis and Griffiths, 1974). It has been shown that non-melanin compounds are not efficient at protecting against ultraviolet radiation (Durrell and Shields, 1960). All of this could explain the decrease in competitive ability exhibited by pigmented species under UV-B. Indirect UV-B effects should also alter competitive balances between different fungal species, particularly between primary and secondary saprophytes. Different fungi have unique enzymatic capabilities, and so their involvement in litter decomposition depends quite significantly on the nature of the resources present (Carreiro and Koske, 1992; Wardle et al., 1993). We did observe indirect effects of UV-B on litter colonization, but more pronounced effects may have been found if a larger suite of common soil fungi was compared, one that includes primary and secondary saprobes (Kendrick and Burges, 1962).

Competitive saprophytic ability is defined by Garrett (1963) as being substrate specific and is comprised of one or more fungal attributes: ability to germinate and grow rapidly when stimulated by soluble nutrients, appropriate enzyme equipment for digesting resistant carbon constituents, ability to produce fungistatic and/or bacteriostatic compounds, and ability to tolerate fungistatic compounds. Competition does occur in fungal communities (Widden, 1997), and the extent to which each attribute contributes to competitive ability is not well understood. There are several reasons why one fungal species might out-compete another and pigmentation is only one variable that might render one species a better competitor. For example, *A. terreus* is known to be highly cellulolytic, and also releases numerous antifungal substances (Brian and Hemming, 1947; Vasudeva and Roy, 1949). Many antibiotic compounds are synthesized via the polyketide pathway, which is also responsible for the synthesis of fungal melanins. It is unknown whether these antifungal antibiotics are produced in greater amounts under elevated UV-B conditions. However, UV-B radiation does stimulate this pathway to synthesize fungal melanins; it is also possible that other substances such as antibiotics that are controlled by this pathway could also be influenced. Although only a speculation, this may explain why *A. terreus* increased its relative competitive ability under UV-B radiation in pair-wise challenges with *C. sphaerospermum* and *A. niger*.

In conclusion, this study shows that UV-B can directly and indirectly influence litter decomposition and the outcome of competition between saprophytic fungi. However, we have not provided evidence to support the hypothesis that pigmentation will confer a competitive advantage under UV-B radiation. However, we grouped all pigment types (melanins, carotenoids, etc...) together, and additional research on the different types of pigments may show stronger trends. We hypothesize that fungi that contain melanins, in particular, should increase their competitive abilities under elevated UV-B. Further research is needed on this topic because UV-B can profoundly alter the structure and function of fungal communities in soil, which can have long-term effects on nutrient availability and primary productivity.

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