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Effects of Ultraviolet Radiation on Predatory Mites and the Role of Refuges in Plant Structures

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ABSTRACT Most studies on ecological impact of solar ultraviolet (UV) radiation generally focus on plants. However, UV radiation can also affect organisms at other trophic levels. Protection against mortality induced by solar UV has, therefore, been hypothesized as one of the reasons why *Typhlodromalus aripo* hides in the apex of cassava plants during the day and comes out at night to prey on spider mites on leaves. In laboratory experiments using UV lamps, we determined the impact of UVA and UVB radiation on survival and oviposition of two leaf-inhabiting mites (*Amblydromalus manihoti*, *Euseius fustis*) and the apex-inhabiting mite (*T. aripo*), all three species being predators used for controlling the cassava green mite *Mononychellus tanajoa* in Africa. Whereas on leaf discs UVA has no negative impact on survival of the three predators, UVB is lethal to all of them. In contrast, nearly 85% of *T. aripo* survived after exposure to UVB inside apex of cassava plants. Exposure of *A. manihoti* and *E. fustis* to UVB radiation on the lower surface of a cassava leaf resulted in 36% survival. Oviposition and hatching of eggs laid after exposure to UVB were not affected, but eggs directly exposed to UVB did not hatch. Although caution should be exercised to extrapolate laboratory studies to the field, our results support the hypothesis that lower side of leaves, but especially plant apices, represent refuges that protect predatory mites from UVB. This might explain why *T. aripo* moves out of the apex to forage on leaves only during the night.

KEY WORDS cassava green mite, *Typhlodromalus aripo*, *Amblydromalus manihoti*, *Euseius fustis*, Phytoseiidae

Whereas temperature and rainfall are known to be major climatic factors that shape terrestrial arthropod communities (Wolda 1978, Yaninek et al. 1989), little is known about other environmental factors such as the ultraviolet (UV) spectrum of solar radiation. Solar UV radiation is dominated essentially by UVA (90%) and UVB (Afaq et al. 2002). Whereas UVA (wavelengths 320–400 nm) is not harmful to arthropods, exposure to UVB (282–320 nm) is known to increase their mortality (Barcelo 1981). Despite this knowledge, the possibility of direct behavioral responses of animals to solar UVB has received little attention (but see Mazza et al. 1999). Indeed, studies dealing with the ecological impact of solar UVB have largely focused on plants (Day and Neale 2002), but there is now growing evidence that UVB can also affect organisms at other trophic levels (Rousseaux et al. 1998).

UVB can affect herbivores directly by causing corporal damage, or indirectly by mediating changes in

the morphology, physiology, and biochemistry of their host plant through increasing leaf thickness and specific leaf mass, and changes in tissue toughness (Bernays and Chapman 1994, Ballaré et al. 1996). In field and laboratory experiments, Rousseaux et al. (1998) found that filtering out solar UVB from the sunlight resulted in an increase in the number of leaf lesions caused by chewing insects feeding on the creeping perennial herb, *Gunnera magellanica* Lam., whereas exposure to solar UVB changed the attractiveness of *G. magellanica* leaf tissue to natural grazers. Some arthropod species can also detect and avoid exposure to UVB (Barcelo 1981, Mazza et al. 1999). It is recently shown that by residing on the lower leaf surfaces, the two-spotted mite *Tetranychus urticae* Koch avoids deleterious effects of solar UVB radiation, indicating that the leaves function as a shelter from UVB (Ohtsuka and Osakabe 2009, Suzuki et al. 2009). This mite also emigrates from UVB environment to UVB-free environment. The orange body color of diapausing females of *T. urticae*, because of accumulation of β -carotene, is also thought to protect them against deleterious effects of UVB during winter when leaves are absent (Suzuki et al. 2009).

Although all the above-mentioned examples were related to the first and second trophic levels, very few studies have focused on the effects of solar UV radiation on the behavior of predators and on how this

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could affect biological control of herbivorous arthropod species (Doukas and Payne 2007a). The few studies published show that the effect of UV radiation on natural enemies can be negative (Chiel et al. 2006) or absent (Doukas and Payne 2007b). In a recent cage experiment in Israel, Legarrea et al. (2010) showed that the predatory mite *Amblyseius swirskii* Athias-Henriot tended to avoid an environment with relatively high UVB radiation, thereby suggesting a deleterious effect of UVB.

The reasons to conduct studies on the effect of UV radiation on predatory mites on cassava plants in Africa were provided by the biological control campaign launched by the International Institute of Tropical Agriculture, against the cassava green mite *Mononychellus tanajoa* (Bondar), a major mite pest in Africa discovered first in the 1970s. In the framework of this biological control campaign, various species of predatory mites (Acari: Phytoseiidae) have been tested for predation on *M. tanajoa*. Two species from the Neotropics, *Amblydromalus* (= *Typhlodromalus*) *manihoti* (Moraes) (see Chant and McMurtry 2005, Moraes et al. 2006) and *Typhlodromalus aripo* De Leon, were introduced in Africa: *A. manihoti* in 1989 (Yaninek et al. 1998) and *T. aripo* in 1993 (Yaninek and Hanna 2003, Hanna et al. 2005). These two exotic predator species have now established in cassava crops and they have spread across the cassava belt in Africa, where they share *M. tanajoa* as prey with several species of indigenous predatory mites, among which *Euseius fustis* (Pritchard & Baker) is the most common species (Onzo et al. 2003a). Whereas all the other predatory mite species inhabit the lower surface of cassava leaves, *T. aripo* hides in the apex of cassava plants during the day and comes out to forage for *M. tanajoa* on young cassava leaves during night hours only (Onzo et al. 2003b). Hiding in the apex during the day is a costly strategy for a predatory mite, because it reduces the time available to forage for prey on leaves. Therefore, we wondered why the apex is selected as a microhabitat and not the lower side of a leaf. We hypothesized that *T. aripo* hides in the apex for protection against harsh environmental conditions such as harmful solar UV radiation, especially UVB (Onzo et al. 2003b).

The objective of the current study is to compare the effects of UV rays (UVA and UVB) on survival, oviposition, and egg hatching of the apex-inhabiting mite *T. aripo* with two leaf-inhabiting predators, *A. manihoti* and *E. fustis*. The main purpose of this study is to help explain why *T. aripo* chooses to inhabit the apex during the daylight hours and forages on the leaves during the night hours only.

Materials and Methods

Test Organisms. Adult *M. tanajoa* females were collected from a culture initiated from field-collected individuals and maintained on potted cassava in a greenhouse for 1–3 wk. Individuals of *A. manihoti* and *E. fustis* were also collected from cassava fields in southern Benin and maintained in the laboratory at

International Institute of Tropical Agriculture-Benin on a diet of all stages of *M. tanajoa*, whereas individuals of *T. aripo* used in the experiments were collected from a cassava field 1 d before the start of each experiment.

Production of UV Radiation. UVB radiation was generated by a 6W lamp with a specific filter (Fisher Bioblock Scientific, Strasbourg, France; serial number 06 15489, 6W 312NM 220V, 680 $\mu\text{W}/\text{cm}^2$). UVA radiation was produced by a 6W lamp with another filter (Fisher Bioblock Scientific; serial number 06 15485, 365NM 220V, 700 $\mu\text{W}/\text{cm}^2$). Each lamp was placed in an individual portable UV-viewing cabinet (L $\times$ D $\times$ H: 300 $\times$ 280 $\times$ 240 mm). The opening of the cabinet (H $\times$ W: 260 $\times$ 140 mm) was equipped with a plastic curtain that isolated UV radiation from the external environment. The white lamp (natural light) was produced by a fluorescent neon tube 18W/230V, positioned at ≈ 1 m above the table on which the UV-viewing cabinets were installed.

Experimental Procedures. Two series of laboratory experiments were conducted to determine whether direct exposure to UV radiation could induce mortality in *T. aripo* and the other predatory mites, and whether hiding in the apex or residing on the lower surface of cassava leaves could reduce the deleterious effects of UV radiation on the predators. Direct exposure to UV radiation was accomplished by placing the test predatory mite on water-saturated cotton in a petri dish that was placed in the UV-viewing cabinet. The protective effect of the cassava apex or leaf (lower surface) was tested by placing the test mites in the apex or on the lower surface of a cassava leaf and exposing them from above to UV radiation in the UV-viewing cabinet. All of the experiments were conducted in separate UV-viewing cabinets that allowed exposure to UV radiation in the wavelengths of 312 nm (UVB) or 365 nm (UVA). Exposures to UV radiation were accomplished between 10 a.m. and 4 p.m.

Direct Exposure of Predatory Mites to UV Radiation

In this series of experiments, individuals of *T. aripo*, *E. fustis*, and/or *A. manihoti* were directly exposed in a petri dish (i.e., out of the apex) to either UVA or UVB for different periods of exposure. The experimental unit consisted of a cassava leaf disc (2 cm diameter) placed abaxial-surface up on water-saturated cotton wool in an open petri dish (8.8 cm diameter). Five adult females of the test predatory mites were placed on each leaf disc (and hence received no protection from incoming UV radiation). The experiment was replicated five times. Because of limited space in the UV-viewing cabinets, the leaf discs of all five replicates per treatment were placed in the same petri dish, with a minimum of 1 cm distance between leaf discs. Conditions within the cabinets were uniform in time and space. In the UV-viewing cabinet, the distance between the leaf disc holding the predators and the light source was 14 cm. Temperature inside the UV-viewing cabinet was 20°C. After exposure, the predators were

removed from the UV-viewing cabinets and kept in the laboratory at 25–27°C and 70–90% RH. They were fed daily with all stages of *M. tanajoa*. Cassava leaf discs were replaced every other day. Survival and oviposition as well as hatching of *T. aripo*, *E. fustis*, and *A. manihoti* eggs were monitored daily for consecutive 8 d. The different tests conducted were as follows.

Direct Exposure of Adult Female *T. aripo* to UVA Radiation. In this experiment, the two main treatments tested were as follows: 1) exposure to UVA and 2) exposure to white light (room light, UV-free control). The four sub-treatments relate to the period of exposure as follows: 1) 30-min exposure, 2) 1-h exposure, 3) 3-h exposure, and 4) 5-h exposure. The experiment was replicated five times, as described above.

Direct Exposure of Adult Female *T. aripo* to UVB Radiation. In this experiment, the three treatments tested were as follows: 1) exposure to UVB, 2) exposure to no light (i.e., darkness), and 3) exposure to white light (room light, UV-free control). For each treatment exposure periods tested were 30 min, 1 h, and 3 h, and the treatments were replicated five times.

Direct Exposure of Eggs of *A. manihoti*, *E. fustis*, and *T. aripo* to UVA and UVB Radiations. Because previous experiments focused on the viability of eggs laid by predators after their exposure to radiation, this series of experiments served to assess whether viability of predator eggs was affected by direct exposure to UV radiation. For each predatory mite species, 20 eggs were directly exposed (in a petri dish) to white light (room light, control), UVA, and UVB for 30 min, 1 h, 3 h, and 5 h in the UV-viewing cabinets. Eggs were removed from the cabinets after the exposure and kept in the laboratory (25–27°C and 70–90% RH), where their hatchability was assessed daily for consecutive 5 d.

UV Exposure of Cassava Apices or Full Leaves With Predatory Mites

In this series of experiments, apices or cassava leaves containing *T. aripo*, *E. fustis*, or *A. manihoti* were exposed to UVB for different periods. Leaves and apices used in these experiments were detached from the plant. The petiole of each leaf was then placed in a water-filled glass vial (0.8 cm in diameter and 4 cm deep) sealed with parafilm to keep it turgid throughout the exposure period. As for the apex and for the same reason, it is the end of the stem that was placed in a water-filled glass vial. Each glass vial contained one leaf or one apex. Five adult females of the test-predatory mite species were placed on each apex or on lower surface of each leaf. Each treatment was replicated five times. In the UV-viewing cabinet, apices and leaves were kept straight to mimic their natural posture on a cassava plant. The distance between the top of the apex or the leaf containing the predators and the light source was ≈8–10 cm. After exposure, the apex was dissected. Survival of predatory mites in apex or on lower surface of leaves was then assessed. Surviving individuals were transferred on a cassava leaf disc (2

cm diameter) on water-saturated cotton wool inside a petri dish (8.8 cm diameter) and kept in the laboratory at 25–27°C and 70–90% RH. All five leaf discs with predators from each of the five replicated apices were kept in the same petri dish. Similarly, all five leaf discs with predators from the five replicated leaves were kept in the same petri dish. Predators were fed daily with all stages of *M. tanajoa*, and their survival, oviposition, as well as egg hatch were monitored for consecutive 8 d.

Comparative Impact of UVB Radiation on *T. aripo* in Cassava Apex or Leaf Disc in Petri Dish. The objective of this experiment was to compare the effect of UVB radiation on *T. aripo* inside the apex of cassava plants with the effect when directly exposed to UVB radiation on cassava leaf discs in a petri dish. In this experiment, the two main treatments tested were as follows: 1) *T. aripo* in cassava apex and 2) *T. aripo* on cassava leaf disc in a petri dish. For each treatment, the two sub-treatments were exposure to white light (room light, UV-free control) and exposure to UVB radiation. The period of exposure was 3 h for each sub-treatment.

Comparative Impact of UVB Radiation on *T. aripo* in Cassava Apex or on Cassava Leaves With Petiole in a Glass Vial. The objective of this experiment was to determine whether residing in the apex of cassava plants offers the same level of protection against UVB as residing on the lower surface of cassava leaves, which is the common habitat of leaf-inhabiting phyto-seiid species. In this experiment, the two main treatments tested were as follows: 1) *T. aripo* in cassava apex and 2) *T. aripo* on the lower surface of a cassava leaf whose petiole was inserted in a glass vial containing water. For each treatment, the two sub-treatments consisted of the following: 1) exposure to white light (i.e., room light, control) and 2) exposure to UVB radiation. The two exposure periods tested were 3 h and 5 h.

Comparative Impact of UVB Radiation on *A. manihoti* and *E. fustis* on Cassava Leaves With Petiole in a Glass Vial or on Cassava Leaf Discs in a Petri Dish. This series of experiments aimed at determining whether residing on the lower surface of a cassava leaf offers protection to *A. manihoti* or *E. fustis* against UVB radiation compared with direct exposure to UVB radiation on the upper surface of cassava leaf discs in a petri dish. In this experiment, the two main treatments tested were as follows: 1) *A. manihoti* or *E. fustis* on the lower surface of a cassava leaf whose petiole is inserted in a glass vial containing water, and 2) *A. manihoti* or *E. fustis* on top of a cassava leaf disc on water-saturated cotton wool in a petri dish. For each treatment, the two sub-treatments were exposure to white light (i.e., room light, control) and exposure to UVB radiation. In each sub-treatment, the periods of exposure were 3 h and 5 h.

Statistical Analyses. Proportions of surviving predatory mites were calculated for each replicate and day of observation. Mean number of eggs laid by each female after exposure and proportions of eggs that hatched were also calculated per replicate per day. In each trial (or experiment), these trait variables were

Table 1. Mean ($\pm$ SE) of proportion of *T. aripo* survival, egg production, and proportion of eggs hatched after exposure to UVA radiation in a petri dish

Trait variables	Period	Treatment	
		Control	UVA
Survival	30 min	0.96 $\pm$ 0.01b(a)	0.98 $\pm$ 0.01a(a)
	1 h	1.00 $\pm$ 0.00a(a)	1.00 $\pm$ 0.00a(a)
	3 h	1.00 $\pm$ 0.00a(a)	0.98 $\pm$ 0.01a(a)
	5 h	0.97 $\pm$ 0.01b(a)	1.00 $\pm$ 0.00a(a)
Eggs/female	30 min	0.18 $\pm$ 0.04a(a)	0.31 $\pm$ 0.05a(a)
	1 h	0.24 $\pm$ 0.04a(a)	0.27 $\pm$ 0.04a(a)
	3 h	0.22 $\pm$ 0.05a(a)	0.28 $\pm$ 0.06a(a)
	5 h	0.28 $\pm$ 0.06a(a)	0.30 $\pm$ 0.05a(a)
Eggs hatched	30 min	0.91 $\pm$ 0.04a(a)	0.94 $\pm$ 0.03a(a)
	1 h	0.96 $\pm$ 0.02a(a)	0.89 $\pm$ 0.01a(a)
	3 h	0.92 $\pm$ 0.04a(a)	0.96 $\pm$ 0.03a(a)
	5 h	0.97 $\pm$ 0.02a(a)	0.91 $\pm$ 0.05a(a)

In rows, means followed with different letters that are in parentheses are significantly different among UV treatments at $P < 0.05$. In columns, means followed with different letters that are not in parentheses are significantly different among exposure durations within UV treatment at $P < 0.05$.

compared among treatments using analysis of variance (ANOVA) when the number of treatments to compare exceeded two or using the Student *t* test when only two treatments were involved. All statistical analyses were performed in SAS (SAS Institute 2003). Data on proportions were transformed using arcsine square root, whereas count data were transformed using $\log_{10}(x + 1)$ before use in the statistical analyses. When ANOVA revealed significant treatment differences, treatment means were separated using the Student-Newman-Keuls multiple range test in SAS.

Results

Impact of Direct Exposure to UVA on Survival and Fecundity of *T. aripo*. Table 1 shows that UVA has no impact on the survival of *T. aripo* ($df = 1$, $F = 0.77$, $P = 0.381$). UVA also did not affect egg production ($df = 1$, $F = 3.52$, $P = 0.062$) and hatchability of eggs produced by females after their exposure to UVA ($df = 1$, $F = 0.80$, $P = 0.377$). In most cases, the duration of exposure to UVA did not affect the above results. Similarly, survival and egg production by *A. manihoti*

Table 3. Mean ($\pm$ SE) of proportion hatched of eggs of *A. manihoti*, *E. fustis*, and *T. aripo* exposed to UVA and UVB radiation on leaf disc for 30 min, 1 h, 3 h, and 5 h

Species	Proportion of eggs hatched		
	Control	UVA	UVB
<i>A. manihoti</i>	0.83 $\pm$ 0.02a(a)	0.86 $\pm$ 0.03a(a)	0.00 $\pm$ 0.00b(a)
<i>E. fustis</i>	0.89 $\pm$ 0.03a(a)	0.92 $\pm$ 0.02a(a)	0.03 $\pm$ 0.03b(a)
<i>T. aripo</i>	0.92 $\pm$ 0.02a(a)	0.86 $\pm$ 0.02b(a)	0.00 $\pm$ 0.00c(a)

For each predator species (i.e., row), means followed with different letters that are not in parentheses are significantly different among UV treatments at $P < 0.05$. For each UV treatment (i.e., column), means followed with different letters that are in parentheses are significantly different among predator species at $P < 0.05$.

and *E. fustis* (data not presented) were also not affected by UVA radiation. In most cases, the duration of exposure to UVA did not affect the above results.

Impact of Direct Exposure to UVB on Survival and Fecundity of *T. aripo*. Table 2 shows that UVB treatments and durations of the exposure period have significant impact on the survival of *T. aripo* ($df = 2$, $F = 244.4$, $P < 0.001$; $df = 2$, $F = 92.3$, $P < 0.001$, respectively, for UVB treatments and period of exposure). No *T. aripo* survived after 3 h of exposure to UVB. Survival rates were 80% after 30 min and 76% after 1 h, whereas in the control (white light) and no-light treatments, survival rates were above 93%. Predator fecundity (i.e., number of eggs per female per day) also differed among UVB treatments ($df = 2$, $F = 3.88$, $P = 0.022$). Whereas there were no significant differences between the control and the no-light treatments, fecundity was significantly lower when *T. aripo* was exposed to UVB radiation independent of exposure period (Table 2). UVB had no impact on hatching of eggs laid after exposure to the radiation ($df = 2$, $F = 0.39$, $P = 0.680$).

Effects of Direct Exposure to UVA and UVB Radiations on Viability of Eggs of *A. manihoti*, *E. fustis*, and *T. aripo*. Table 3 shows that for the three predator species, UV treatments had significant impact on egg hatching ($df = 2$, $F = 145.4$, $P < 0.001$ for *A. manihoti*; $df = 2$, $F = 159.8$, $P < 0.001$ for *E. fustis*; $df = 1$, $F = 230.8$, $P < 0.001$ for *T. aripo*), and that the effect differed among phytoseiid species ($df = 2$, $F = 4.83$,

Table 2. Mean ($\pm$ SE) of proportion of *T. aripo* survival, egg production, and proportion of eggs hatched after exposure to UVB radiation in a petri dish

Trait variables	Period	Treatment		
		Control	No light	UVB
Survival	30 min	0.96 $\pm$ 0.01a(a)	0.96 $\pm$ 0.01a(a)	0.80 $\pm$ 0.05a(b)
	1 h	0.97 $\pm$ 0.01a(a)	0.95 $\pm$ 0.01a(a)	0.76 $\pm$ 0.05a(b)
	3 h	0.93 $\pm$ 0.02a(a)	0.99 $\pm$ 0.01a(a)	0.00 $\pm$ 0.00b(b)
Eggs/female	30 min	0.15 $\pm$ 0.03a(a)	0.20 $\pm$ 0.05a(a)	0.10 $\pm$ 0.03a(b)
	1 h	0.18 $\pm$ 0.04a(a)	0.12 $\pm$ 0.02a(a)	0.07 $\pm$ 0.03a(b)
	3 h	0.13 $\pm$ 0.03a(a)	0.17 $\pm$ 0.04a(a)	—
Eggs hatched	30 min	0.72 $\pm$ 0.06b(a)	0.74 $\pm$ 0.08a(a)	0.60 $\pm$ 0.17a(a)
	1 h	0.88 $\pm$ 0.06ab(a)	0.83 $\pm$ 0.05a(a)	0.70 $\pm$ 0.13a(a)
	3 h	0.93 $\pm$ 0.04a(a)	0.92 $\pm$ 0.04a(a)	—

In rows, means followed with different letters that are in parentheses are significantly different among UV treatments at $P < 0.05$. In columns, means followed with different letters that are not in parentheses are significantly different among exposure durations within UV treatment at $P < 0.05$.

Table 4. Comparison of mean ($\pm$ SE) of proportion of *T. aripo* survival, egg production, and proportion of hatched eggs after 3-h exposure to UVB radiation on leaf disc petri dish or cassava apex

Trait variables	Plant part	Treatment	
		Control	UVB
Survival	Apex	0.97 $\pm$ 0.01a(a)	0.85 $\pm$ 0.01a(b)
	Leaf disc	0.98 $\pm$ 0.01a(a)	0.00 $\pm$ 0.00b(b)
Eggs/female	Apex	0.25 $\pm$ 0.04b(a)	0.35 $\pm$ 0.06(a)
	Leaf disc	0.42 $\pm$ 0.05a(a)	—
Eggs hatched	Apex	0.83 $\pm$ 0.05b(a)	0.89 $\pm$ 0.05(a)
	Leaf disc	0.95 $\pm$ 0.03a	—

In rows, means followed with different letters that are in parentheses are significantly different among UV treatments at $P < 0.05$. In columns, means followed with different letters that are not in parentheses are significantly different among plant parts within UV treatment at $P < 0.05$.

$P = 0.009$). Hatching of *A. manihoti* and *E. fustis* eggs was not affected by UVA. In contrast, egg hatching was zero or nearly zero after exposure to UVB. For *T. aripo*, egg hatching was significantly different among the three UV treatments, with the highest proportion occurring in the control, followed by the exposure to UVA treatment and zero hatching after exposure to UVB.

Comparative Impact of UVB Radiation on *T. aripo* in Cassava Apex or Leaf Disc in Petri Dish. Table 4 shows that plant parts (i.e., apex or leaf discs) had significant impact on the effects of UVB on *T. aripo* survival ($df = 1$, $F = 598.4$, $P < 0.001$). Exposure to UVB also had significant impact on survival of the predator ($df = 1$, $F = 1359.3$, $P < 0.001$). Under white light (i.e., room light), plant parts had no significant impact on the survival of *T. aripo* ($df = 1$, $F = 0.38$, $P = 0.537$). In contrast, under exposure to UVB radiation, survival of *T. aripo* was significantly lower on cassava leaf disc (0.0%) compared with the apex ($df = 1$, $F = 1527.0$, $P < 0.001$). Because there were no surviving females under UVB, no oviposition was obtained; thus, statistical comparisons could not be made. However, under white light, oviposition was significantly better in the leaf disc treatment than in the apex treatment ($df = 1$, $F = 7.26$, $P < 0.009$). Egg hatch was not affected by any of the different treatments ($P > 0.05$).

Comparative Impact of UVB on *T. aripo* in Cassava Apex or on Cassava Leaves With Petiole in a Glass Vial. Table 5 shows that under white light (i.e., control), residing in the apex or on the lower surface of a cassava leaf had significant impact on the survival of *T. aripo* ($df = 1$, $F = 8.98$, $P < 0.003$). Survival of *T. aripo* was lower in the apex than on the lower surface of cassava leaves. In contrast, under exposure to UVB, there was no significant difference in the survival of *T. aripo* in the apex or on the lower surface of cassava leaf ($df = 1$, $F = 2.67$, $P < 0.105$). Whether exposed to UVB radiation or not, residing on the lower surface of cassava leaf or in the apex did not significantly affect oviposition of *T. aripo* ($df = 1$, $F = 0.05$, $P < 0.821$ under white light; $df = 1$, $F = 2.04$, $P < 0.155$ under UVB radiation). Egg hatch was not affected by any of the different treatments ($P > 0.05$).

Table 5. Comparison of mean ($\pm$ SE) of proportion of *T. aripo* survival, egg production, and proportion of eggs hatched after 3-h and 5-h exposure to UVB radiation on cassava apex or on lower cassava leaf surface

Parameters	Plant part	Treatment	
		Control	UVB
Survival	Apex	0.90 $\pm$ 0.02b(a)	0.93 $\pm$ 0.02a(a)
	Leaf in vial	0.96 $\pm$ 0.01a(a)	0.89 $\pm$ 0.02a(b)
Eggs/female	Apex	0.32 $\pm$ 0.04a(a)	0.28 $\pm$ 0.04a(a)
	Leaf in vial	0.33 $\pm$ 0.04a(a)	0.21 $\pm$ 0.03a(b)
Eggs hatched	Apex	0.96 $\pm$ 0.03a(a)	0.98 $\pm$ 0.01a(a)
	Leaf in vial	0.95 $\pm$ 0.03a(a)	0.95 $\pm$ 0.02a(a)

In rows, means followed with different letters that are in parentheses are significantly different among UV treatments at $P < 0.05$. In columns, means followed with different letters that are not in parentheses are significantly different among plant parts within UV treatment at $P < 0.05$.

Comparative Impact of UVB on *A. manihoti* and *E. fustis* on Cassava Leaves With Petiole in a Glass Vial or on Cassava Leaf Discs in a Petri Dish. Table 6 shows that plant parts (i.e., leaves in glass vial or leaf discs) had a significant impact on the effects of UVB on the survival of both *A. manihoti* ($df = 1$, $F = 104.0$, $P < 0.001$) and *E. fustis* ($df = 1$, $F = 96.2$, $P < 0.001$). Under white light (i.e., control), plant parts had no significant impact on the survival of any of the two predatory mite species ($df = 1$, $F = 0.01$, $P < 0.910$ for *A. manihoti*; $df = 1$, $F = 0.00$, $P < 0.972$ for *E. fustis*). In contrast, when exposed to UVB radiation, survival of *A. manihoti* and *E. fustis* was significantly lower on top of a cassava leaf disc (0.0%) in a petri dish compared with full cassava leaf (with lower side accessible to predatory mites) in a glass vial ($df = 1$, $F = 467.1$, $P < 0.001$ for *A. manihoti*; $df = 1$, $F = 434.6$, $P < 0.001$ for *E. fustis*). The period of exposure did not significantly affect the above results ($df = 1$, $F = 0.14$, $P = 0.708$ for *A. manihoti*; $df = 1$, $F = 0.16$, $P = 0.694$ for *E. fustis*).

Because of no surviving females under UVB on cassava leaf discs, no oviposition was obtained; thus, statistical comparisons could not be made. However, under white light (i.e., room-light conditions) and for both predators, oviposition was not significantly affected by plant part ($df = 1$, $F = 0.36$, $P = 0.548$ for *A. manihoti*; $df = 1$, $F = 0.16$, $P = 0.896$ for *E. fustis*). For each predatory mite species, egg hatch was affected neither by exposure to UVB, nor by plant part ($P > 0.05$, Table 6).

Discussion

Whereas many studies had focused on the impact of UV radiation on the first trophic level (Rousseaux et al. 1998, Day and Neale 2002), our study is among the first few that provide quantitative data on the impact of UV radiation on arthropod life history traits. Moreover, it is certainly the first study that shows how UV radiation can affect the spatial arrangement of arthropod species within a plant. By doing so, this study provides insight in the role of UV radiation in explaining the diurnal pattern of refuge use by the predatory mite *T. aripo* on cassava plants.

Table 6. Mean ($\pm$ SE) of proportion of *A. manihoti* or *E. fustis* survival, egg production, and proportion of eggs hatched after 3-h and 5-h exposure to UVB radiation on leaf disc or on full leaf in a water-filled vial

Species	Parameters	Plant part	Treatment	
			Control	UVB
<i>A. manihoti</i>	Survival	Leaf in vial	0.72 $\pm$ 0.03a(a)	0.62 $\pm$ 0.03a(b)
		Leaf disc	0.72 $\pm$ 0.03a(a)	0.00 $\pm$ 0.00b(b)
	Eggs/female	Leaf in vial	1.15 $\pm$ 0.10a(a)	1.21 $\pm$ 0.13(a)
		Leaf disc	1.08 $\pm$ 0.10a	—
	Eggs hatched	Leaf in vial	0.99 $\pm$ 0.01a(a)	0.99 $\pm$ 0.01(a)
		Leaf disc	0.99 $\pm$ 0.00a	—
<i>E. fustis</i>	Survival	Leaf in vial	0.65 $\pm$ 0.04a(a)	0.67 $\pm$ 0.03a(a)
		Leaf disc	0.65 $\pm$ 0.03a(a)	0.00 $\pm$ 0.00b(b)
	Eggs/female	Leaf in vial	1.16 $\pm$ 0.11a(a)	1.32 $\pm$ 0.15(a)
		Leaf disc	1.28 $\pm$ 0.15a	—
	Eggs hatched	Leaf in vial	0.99 $\pm$ 0.01a(a)	0.96 $\pm$ 0.02(a)
		Leaf disc	0.98 $\pm$ 0.01a	—

For each species, in rows, means followed with different letters that are in parentheses are significantly different among UV treatments at $P < 0.05$. In columns, means followed with different letters that are not in parentheses are significantly different among plant parts within UV treatment at $P < 0.05$.

Our laboratory experiments showed that whereas exposure to UVA had no lethal impact on the survival of adult stages of any of the three predatory mite species tested (i.e., *A. manihoti*, *E. fustis*, and *T. aripo*), direct exposure to UVB radiation is lethal to all of them. Three hours of direct exposure to UVB resulted in 100% mortality and the loss of egg viability for all three phytoseiid species tested. Residing in the apex of cassava plants provides almost 85% survival to *T. aripo* compared with the 0% survival under direct exposure to UVB. Interestingly, oviposition of female predators that survived the exposure to UVB was not affected, nor was the hatching capacity of the eggs that they subsequently laid. Protection against solar UVB radiation may well be one of the main reasons for *T. aripo*'s choice to forage on cassava leaves only during the night hours, as observed by Onzo et al. (2003b). Solar UV radiations are at their highest dose at noon under clear sky conditions, but completely absent during the night hours (Bordewijk et al. 1995).

Our study also shows that UV radiation can also affect the leaf-inhabiting predators *A. manihoti* and *E. fustis*. Their survival increased to 36% when on the lower surface of leaves compared with 100% mortality when directly exposed to UVB radiation. These results confirm the observations by Suzuki et al. (2009), that most UV radiation is absorbed and reflected by leaves. The underside of leaves therefore should be considered a better environment for the predatory mites when they need to avoid UV radiation (Ohtsuka and Osakabe 2009). We asked why *T. aripo* does not also inhabit the lower surface of cassava leaves like the other phytoseiids, but instead decides to reside in the apex of hairy cassava varieties (Hanna et al. 2000). Our results show that *T. aripo* gains additional protection from UV radiation when inside the apex of the cassava plant, i.e., higher survival than on the lower surface of leaves.

Another argument in favor of the use of apex could be found in the response of predator eggs to UVA exposure. Indeed, our experiments show that although exposure to UVA had no deleterious impact on the

survival of the three predator species tested, the hatching of *T. aripo* eggs was significantly lower when exposed to UVA than when exposed to white light (i.e., room light). This suggests that exposure to UVA still could negatively affect the increase of *T. aripo* populations. So, because solar UV radiation is predominantly composed of UVA (Afaq et al. 2002, Bordewijk et al. 1995), it pays for *T. aripo* to avoid exposure to UVA to maximize egg-hatching success by deciding to reside in the apex of (especially hairy) cassava cultivars.

Because in our experiments we used UV lamps to generate UVB and UVA radiations, our results cannot be directly used to predict outdoor effects of natural solar UV, as our experiments may overestimate the impact (Day and Neale 2002). This is even more important because the design used did not allow the test individuals to escape from exposure to UV radiation. Experimental limitations notwithstanding, our study provides valuable quantitative data that could help in explaining the foraging behavior of predatory mites inhabiting cassava plants and, more specifically, the diurnal use of the apical domatia of cassava plants by *T. aripo*. Based on these results, we conclude that staying in the apex of cassava plants or on the lower surface of cassava leaves protects predatory mite species from UVB-induced mortality. However, residing in the apex of cassava plants is, for *T. aripo*, more protective against UV radiations than residing on the lower surface of leaf. This might explain why *T. aripo* uses the apex as a refuge only during the day and moves out to forage on leaves during night.

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