



Biological impact of ultraviolet-B radiation on spider mites and its application in integrated pest management

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Abstract

Many plant-dwelling mites reside on lower leaf surfaces. The biological impact of solar ultraviolet-B (UV-B) radiation on spider mites has been demonstrated over the last decade. Due to the serious problem of acaricide resistance in spider mites, the development of alternative control methods and establishment of an integrated pest management (IPM) strategy are urgently needed, especially for greenhouse horticultural crops such as strawberries. A physical control method for spider mites using UV-B lamps (UV-B method) has been established. Using the UV-B method, simultaneous control of spider mites and powdery mildew, a major disease, is possible, making it a favorable IPM strategy. Here, I introduce general findings regarding the biological impact of UV radiation on spider mites and phytoseiid mites, useful natural enemies for biological control, over the last decade, including dose response, effective wavelengths, and photoreactivation. Moreover, I introduce the application of UV-B to spider mite control in strawberry greenhouses, including the possibility of concurrent use with biological control via phytoseiid mites, and discuss its possible contributions to IPM.

Keywords UV damage · Photoreactivation · *Tetranychus urticae* · *Neoseiulus californicus* · Acari

Introduction

The near ultraviolet (UV) wavelengths are divided into UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (200–280 nm). As UV-C and the majority of UV-B are absorbed by the atmosphere and ozone layer, solar UV radiation at ground level is composed of UV-A with a small proportion of UV-B. At shorter wavelengths, UV exerts stronger inhibition on organisms (Slieman and Nicholson 2000), resulting in a spectrum of biological activity of solar UV radiation that peaks in the range of 305–315 nm (Coohill and Sagripanti 2009; Munakata et al. 1996).

The biological impact of solar UV-B combined with the effects of climate change has heightened awareness of ozone layer destruction including the ozone hole in Antarctica (Ballaré et al. 2011; Bornman et al. 2019; Paul and Gwynn-Jones 2003). Meanwhile, attenuation of solar UV-B radiation has resulted in an increase in herbivory by insects at high latitudes in both the southern and northern hemispheres

(Ballaré et al. 2001; Gwynn-Jones et al. 1997; Rousseaux et al. 2001, 2004). Conversely, enhanced UV-B radiation increases the deleterious effects on insect behavior and health and affects their interactions with plants via induction of defensive material production and photomorphogenic changes (Burdick et al. 2015; Caldwell et al. 2007; Escobar-Bravo et al. 2017; Kuhlmann and Müller 2009a, 2009b; Yin et al. 2018). Solar UV radiation is generally higher at lower latitudes, except in the ozone hole region, and has greater impacts on organisms living in low latitudes (Meador et al. 2009), leading to evolution of protective systems and other adaptations against ambient UV-B radiation in insects (Abram et al. 2015; Gaudreau et al. 2017).

Plant-dwelling mites frequently reside on the lower leaf surfaces of their host plants (Sudo and Osakabe 2011). In addition to topographic differences between adaxial (upper) and abaxial (lower) leaf surfaces (Chien and Sussex 1996; Price 1980; Sakai et al. 2012a; Sudo and Osakabe 2013), the preference for lower leaf surfaces by tiny mites (Jeppson 1975; Kiritani 2012, 2013) has been attributed to avoidance of harsh environments on upper leaf surfaces such as radiant heat (Lu et al. 2014; Perring et al. 1984), desiccation (Ferro and Chapman 1979; McEnroe 1961) and rain (Boyne and Hain 1983; Ho 2000; Osakabe 1965; Régo et al. 2013).

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Detrimental effects of solar UV-B on plant-dwelling mites and avoidance of these effects by occupying lower leaf surfaces on sunny days have been reported previously by Barcelo (1981). Over the last decade, numerous studies have revealed significant biological impacts of UV-B radiation on plant-dwelling mites (Ohtsuka and Osakabe 2009; Suzuki et al. 2009). Genus *Tetranychus*, which includes the two-spotted spider mite *T. urticae* Koch (Acari: Tetranychidae), comprises the most important spider mites acting as horticultural pests because of their vigorous fertility, extremely broad host range, and development of acaricide resistance worldwide (Jeppson 1975; Osakabe et al. 2009; Van Leeuwen et al. 2010, 2015). Therefore, the use of UV-B (as well as UV-C) for spider mite control has raised interest (Short et al. 2018; Tanaka et al. 2016).

Below, I review the biological impacts and adaptations of herbivorous spider mites and their natural enemy, phyto-seiid mites. Then, I introduce the challenges associated with application of UV-B lamps for spider mite management in greenhouses and discuss the potential contribution of UV-B technology to integrated pest management (IPM) strategies for greenhouse cultivation.

Hiding from solar radiation

The majority of mites use lower leaf surfaces

Tetranychus urticae pierces both adaxial and abaxial leaf surfaces with its stylet (Bensoussan et al. 2016). In field observations by Osakabe et al. (2006), ~99% of *T. urticae* females resided on lower (abaxial) leaf surfaces in an apple orchard from mid-June to early-August in Hiraka, Akita, Japan (39°23' N, 140°3' E). Ohtsuka and Osakabe (2009) revealed that egg hatching and juvenile development were significantly suppressed on upper (adaxial) leaf surfaces or on leaf discs that were placed under UV-transparent film, while most eggs hatched and larvae developed on lower (abaxial) leaf surfaces or on leaf discs that were placed under UV-attenuating film. Plants accumulate UV-B-absorbing compounds, including leaf phenolics (e.g., flavonoids), in epidermal cells that reduce UV-B penetration via protection of sensitive targets in mesophyll cells, possibly acting as selective sunscreens for small arthropods on the lower leaf surfaces (Izaguirre et al. 2007; Lavola et al. 1998; Rousseaux et al. 2004; Tegelberg et al. 2004). Similar protective effects of host plant leaves have been demonstrated in the UV-sensitive freshwater snail *Planorbarius corneus* (Linnaeus) (Wahl 2008).

Several practical observations provide evidence that mites avoid solar UV radiation. For example, movement of *T. urticae* females from the upper to lower leaf surfaces of host plants under solar radiation was accelerated when covered

by UV-transparent film overhead compared with UV-opaque film (Sakai and Osakabe 2010). Conversely, movement from the lower to upper leaf surfaces of host plants covered by UV-opaque film overhead was accelerated after the lower leaf surfaces were irradiated with reflected solar UV radiation (Sakai and Osakabe 2010). On the other hand, in a UV irradiation experiment with a wavelength interval of 20 nm using a spectroscopic light source, Sakai and Osakabe (2010) found that *T. urticae* did not escape from leaf area irradiated with UV-B and UV-A at 300 and 360 nm wavelengths, while it escaped from the area irradiated with UV-A at 320 and 340 nm wavelengths. Based on this result, they supposed that *T. urticae* avoids UV-A at 320–340 nm wavelengths in the sun, thereby avoiding UV-B contained in it at the same time (Sakai and Osakabe 2010). Monochromatic analyses by Suzuki et al. (2009) also showed avoidance behavior by *T. urticae* females more often in the presence of UV-A (350 nm) than UV-B (300 nm). *Tetranychus urticae* females showed a maximum behavioral response along with a second peak at 375–525 nm wavelengths (Naegele et al. 1966). In contrast, Suzuki et al. (2013) showed that *T. urticae* avoids entering patches illuminated with UV-B (λ_{\max} 307 nm) from a light emitting diode under virtual field conditions provided by a micro-locomotion compensator, which is an equipment to keep and record a walking mite in an experimental area by complementing the movement of mites on the test table with the movement of the table (Kojima et al. 2003). Therefore, it is controversial how *T. urticae* avoids solar UV-B.

In addition to *T. urticae*, the eyeless predacious phyto-seiid mite *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae) avoids areas irradiated with solar UV (Tachi and Osakabe 2012). *Neoseiulus californicus* escapes rapidly from areas irradiated with monochromatic UV-B radiation at wavelengths ≥ 300 nm, in contrast to *T. urticae* (Tachi and Osakabe 2014). If the complicated thread webs produced by spider mites (prey) are present, *N. californicus* does not escape from areas irradiated with UV at ≥ 310 nm, whereas it escapes areas irradiated with dangerous UV-B at 300 nm (see section “Fatal wavelengths”) (Tachi and Osakabe 2014). Phytoseiid mites show escape behavior even from visible light (VIS) (Tachi and Osakabe 2012; Weintraub et al. 2007), causing them to remain on lower leaf surfaces and within domatia (Ghazy et al. 2016; Onzo et al. 2009, 2010).

The minority of mites use upper leaf surfaces

In contrast to many other mites, spider mites in the genus *Panonychus* (Acari, Tetranychidae) frequently occupy upper leaf surfaces (Foott 1963; Jones and Parrella 1984; Morimoto et al. 2006; Osakabe et al. 2006). Eggs of the citrus red mite *Panonychus citri* (McGregor) (Acari: Tetranychidae) show greater resistance to UV-B radiation

than do those of *T. urticae* (Fukaya et al. 2013; Osakabe et al. 2006). The herbivorous false spider mite, *Brevipalpus obovatus* Donnadieu (Acari: Tenuipalpidae), is another occupier of upper leaf surface (Sudo and Osakabe 2011), and it shows greater UV-B resistance than *P. citri* (Sudo and Osakabe 2015). Sudo and Osakabe (2013) suggested that *B. obovatus* has a reduced risk of egg predation by phytoseiid mites such as *Phytoseius nipponicus* Ehara (Acari: Phytoseiidae), present on the lower leaf surfaces of *Viburnum erosum* Thunb. var. *punctatum* Franch. et Sav. (Adoxaceae), by ovipositing on the upper leaf surfaces (Sudo and Osakabe 2013). However, it is difficult for *B. obovatus* eggs to survive on upper leaf surfaces in summer due to strong detrimental effects of both UV-B radiation and radiant heat from the sun, limiting the field occurrence of this mite to autumn (Sudo and Osakabe 2015).

UV irradiation and radiant heat from the sun both induce the formation of reactive oxygen species (ROS), which cause oxidative damage in organisms, such as lipid peroxidation (Girotti 1985, 1998) as well as DNA base damage (Cadet and Wagner 2013). Although the protective effects of enzymatic antioxidant responses have not been clarified (Yang et al. 2010), *P. citri* possesses astaxanthin, an efficient scavenger of ROS (Camera et al. 2009), as its main pigment (Atarashi et al. 2017; Metcalf and Newell 1962). Atarashi et al. (2017) observed a higher survival rate at high temperature in wild type than albino *P. citri*, which lacks astaxanthin, although no difference was detected under UV-B irradiation. On the other hand, summer-form *Tetranychus* mites also possess astaxanthin but the distribution of astaxanthin is restricted to the mites' eye spots; when they enter diapause, ketocarotenoids including astaxanthin are synthesized and accumulate throughout the body (Kawaguchi et al. 2016; Veerman 1972, 1974a). As a result, *Tetranychus* mites have increased UV resistance in their diapause form than in their summer form (Suzuki et al. 2009).

Panonychus ulmi Koch (Acari: Tetranychidae) exhibits a reddish body and egg coloration similar to *P. citri*, likely due to carotenoids such as astaxanthin or complexes thereof (Putman 1965). Generally, *Panonychus* mites are inferior competitors to *Tetranychus* mites, as the complicated webs of fine threads created by the latter significantly inhibit the activity and development of the former (Morimoto et al. 2006). Field observations in an apple orchard revealed that *P. ulmi* females tended to avoid lower leaf surfaces on which *T. urticae* was present and to move to the competitor-free upper leaf surfaces (Osakabe et al. 2006). Solar radiation may have non-negligible effects on the evolution and seasonal dynamics of plant-dwelling mites via the effects of oxidative stressors, namely UV-B radiation and radiant heat.

Seasonal differences in the biological impacts of solar UV-B radiation

In general, the UV-B irradiation intensity and daily cumulative dose of solar radiation are high in summer and low in winter. Therefore, we tend to assume that the biological impact of solar UV-B radiation is strongest in summer. However, a semi-field experiment performed in Kyoto, Japan, from spring (mid-April) to autumn (end of October) revealed the highest ovicidal effect of solar UV radiation on *T. urticae* eggs in spring (Sakai et al. 2012b). The hatchability of eggs exposed to solar UV radiation (placed under UV-transparent film) was lowest in April (10.7%) and increased toward October (74.9–92.3%). In contrast, the hatchability of eggs placed under UV-opaque film was 96.2–99.8% throughout the experimental period from spring to autumn (Sakai et al. 2012b), indicating a strong impact of solar UV radiation on spider mites. Sakai et al. (2012b) found a negative correlation between the hatchability of eggs exposed to solar UV radiation and the cumulative UV-B dose during the egg period.

From the data reported by Sakai et al. (2012b), the LD₅₀ value of solar UV-B radiation for *T. urticae* eggs was estimated as ~50 kJ/m², which is equivalent to the cumulative irradiation dose over 3 days in April or October or <2.5 days in summer (June–August) in Kyoto. The reason for the peak mortality of eggs in spring (April) and the minimum mortality in autumn (October) remain unclear. However, it is likely that the higher temperature in autumn shortened the egg period and thereby reduced the cumulative UV-B dose received during the egg period in autumn relative to spring. If this speculation is true, the combined effect of UV-B dose and temperature is an important factor for identifying the optimal conditions for practical UV-B control of spider mites.

The effect of temperature on UV damage to organisms remains controversial (see section “Effects of air temperature on mite mortality due to daily nighttime UV-B irradiation”), and in particular, the impacts of global climate change are largely unknown (Alton and Franklin 2012, 2017). In Japan, the temperature increase in 2015–2018 relative to 1981–2010 was greater in spring than in autumn (Fig. 1). Such meteorological changes may influence the seasonal occurrence of spider mites via both the effect of temperature on developmental rate and UV damage mitigation.

Fatal effects and reciprocity law

Fatal wavelengths

The fatal effects of solar UV-B radiation on *T. urticae* were shown by Ohtsuka and Osakabe (2009). In the sun,

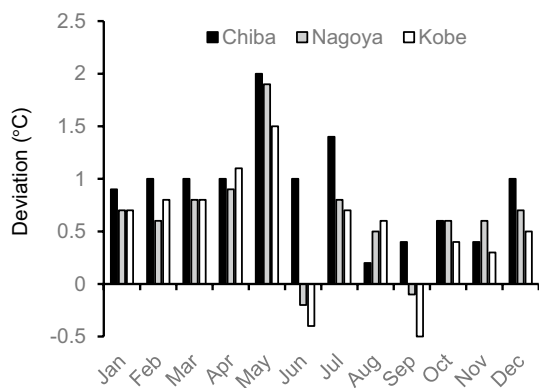


Fig. 1 Deviation of monthly mean temperature in 2015–2018 from that in 1981–2010. Data from the Japan Meteorological Agency (<https://www.data.jma.go.jp/gmd/cpd/cgi-bin/view/index.php>)

egg hatching and juvenile development were significantly suppressed on the upper (adaxial) leaf surfaces, while most eggs hatched, and larvae on lower (abaxial) leaf surfaces or under UV-attenuating film developed normally. Experiments on the effects of single-wavelength acute irradiation using artificial monochromatic UV radiation indicated that the extent of damage changed dramatically between wavelengths of 300 nm and longer; all eggs of *T. urticae* and *N. californicus* died from exposure to 300 nm wavelength while all eggs hatched upon exposure to 310 nm and longer wavelengths in *N. californicus* (Tachi and Osakabe 2014) and 320 nm and longer wavelengths in *T. urticae* (310 nm has not been tested) (Sakai and Osakabe 2010). A similar response has been reported in marine zooplankton (Copepoda) eggs (Kouwenberg et al. 1999b). UV-C causes greater damage to spider mites (Suzuki et al. 2009), but solar radiation at wavelength below 290 nm scarcely reaches ground level. Meanwhile, UV-A shows no lethal effects on mites (Ohtsuka and Osakabe 2009; Sakai and Osakabe 2010; Suzuki et al. 2009; Tachi and Osakabe 2014). Therefore, the wavelengths fatal to mites lie within a very narrow range (290–300 nm) that accounts for a small portion of the total solar radiation at ground level.

Reciprocity law in the lethal effect

Several studies have been conducted on aquatic organisms to determine the mechanism of UV damage. Reciprocity might be applicable to the mortality of shrimp zoea (Wübgen 2000), sea urchin (early stages; Nahon et al. 2009), and fish eggs (Kouwenberg et al. 1999a). However, divergence from reciprocity was observed at low UV-B radiation in shrimp zoea and several aquatic animals (Cywinska et al. 2000; Wübgen 2000), and thus the applicability of the reciprocity law to UV damage in those organisms remains questionable. In contrast, mortality due to UV-B

irradiation is strictly determined by the cumulative UV-B dose (= UV-B irradiance [W/m^2] \times irradiation time [s]) in *T. urticae* (Murata and Osakabe 2013). Moreover, Murata and Osakabe (2013) found strong linear regression between mortality probit and the log-transformed UV-B dose, which was useful for determining LD_{50} values of 0.58, 1.19, 1.01, and 26.12 kJ/m^2 for the egg, larva, teleiochrysalis, and adult female, respectively. Egg production by females decreased linearly, and the developmental duration from larvae to adult emergence increased linearly, with increasing cumulative UV-B dose (Murata and Osakabe 2013). Murata and Osakabe (2013) performed these experiments in a laboratory illuminated by fluorescent lights. Therefore, UV-B damage may be underestimated compared to dark conditions due to effects of photoreactivation discussed in “DNA lesions and repair” section. The UV damage in this spider mite generally followed the reciprocity law, suggesting that the effect of UV-B application on spider mite management will be predictable.

The large difference in LD_{50} values between the laboratory experiment using a UV-B lamp and the semi-field experiment under solar UV radiation (86-fold greater; Sakai et al. 2012b) described above is noteworthy. In the laboratory experiment, eggs were illuminated with a moderate-intensity fluorescent lamp (Murata and Osakabe, 2013), whereas the amount of VIS in the natural sunlight was overwhelming. This difference in the LD_{50} values may be explained by photoreactivation efficiency, as described below.

Stage-specific vulnerability to UV-B damage

UV-B sensitivity of eggs varies among developmental stages; for example, Atlantic cod eggs are vulnerable during post-fertilization (mid-gastrulation) and hatching stages in comparison with the middle embryonic stages (Kouwenberg et al. 1999a). The UV-B vulnerability of *T. urticae* eggs peaks at 24–48 h after oviposition at 25 °C (Murata and Osakabe 2014; Yoshioka et al. 2018), corresponding to when the larval body is formed based on the germinal disk (Dearden et al. 2002). Then, the UV-B tolerance of the eggs increases, reaching a maximum just prior to hatching (Murata and Osakabe 2014). *Neoseiulus californicus* eggs show their highest UV-B vulnerability at similar embryonic development periods as those of *T. urticae* eggs (Sugioka et al. 2018). Interestingly, the goldfish *Carassius auratus* (L.) embryo shows a similar time course of sensitivity and resistance to UV-B as that of mites (Wiegand et al. 2004).

The high UV-B resistance of mature embryos just before hatching is related to the fact that most *T. urticae* larvae irradiated with UV-B do not die immediately, and instead enter the protochrysalis stage (Murata and Osakabe 2017b). The damaged larvae die during the protochrysalis stage or molting (Murata and Osakabe 2014, 2017b), indicating the

vulnerability of the chrysalis stage. This finding is supported by the smaller LD₅₀ of the teleiochrysalis than that of larvae, although adult *T. urticae* females may have higher values than those of larvae due to their larger body size, as described above (Murata and Osakabe 2013). Interestingly, greater numbers of quiescent stage European red mites, *Panonychus ulmi* (Koch), occupied lower leaf surfaces than upper leaf surfaces, as reported by Foott (1963). Similarly, many larvae and nymphs of *P. citri* reside on the lower surfaces of citrus leaves, despite higher juvenile development rates and egg production levels in females, indicating a nutritional advantage of residing on the upper leaf surface (Fukaya et al. 2013).

DNA lesions and repair

Accumulation of DNA damage

Ambient UV-B radiation frequently causes DNA lesions in organisms in the forms of cyclobutane pyrimidine dimers (CPDs), (6–4) photoproducts (6–4 PPs), and their Dewar valence isomers, which interrupt the processes of gene transcription and replication (Cadet et al. 2012; Pfeifer 2020; Rastogi et al. 2010; Sinha and Häder 2002). Although 6–4 PPs may have more serious lethal effects on organisms due to the formation of DNA bends, CPDs are more common and therefore responsible for most cytotoxic effects (Mitchell and Nairn 1989; Sinha and Häder 2002).

Studies on *Daphnia* and bacteria suggest that DNA lesions accumulate in a dose-dependent manner (Connelly et al. 2009; Riley and Kaufman 1972). Murata and Osakabe (2017a) observed increased mortality and simultaneous accumulation of DNA lesions (CPDs and 6–4 PPs) with increasing UV-B doses in irradiated *T. urticae* larvae. The levels of CPDs and 6–4 PPs are linearly correlated with the UV-B dose (Murata and Osakabe 2017a).

DNA repair systems

Nucleotide excision repair (NER) and photoenzymatic repair (PER) are the major repair systems for DNA lesions in organisms (Rastogi et al. 2010; Sinha and Häder 2002; Thoma 1999; Weber 2005). Multiple enzymes act in NER to replace damaged DNA with undamaged nucleotides, using ATP for energy (Sinha and Häder 2002). In contrast, PER is a relatively simple repair system in which DNA lesions are directly repaired by photolyases using energy from blue light (400–450 nm wavelength) and UV-A (Kalthoff 1975; Sancar 2003; Shiroya et al. 1984; Sinha and Häder 2002). The *T. urticae* genome includes four highly homologous copies of the CPD photolyase gene (*tetur12g04440*, *tetur12g04460*, *tetur35g00010*, and *tetur35g00030*), the product of which

repairs CPDs, but it contains no gene encoding a (6–4) photolyase for repairing 6–4 PPs (Grbić et al. 2011), which has been found in limited organisms, such as *Drosophila* (Todo et al. 1996). A single-copy gene encoding the xeroderma pigmentosum group A protein (*tetur05g03450*), one of the core factors for NER, is present in the *T. urticae* genome (Grbić et al. 2011; Murata and Osakabe 2017a). Murata and Osakabe (2017a) suggested that UV-B-induced 6–4PPs disappeared 1 day after UV-B irradiation in *T. urticae* larvae kept in the dark. Thus, 6–4 PPs may be repaired by mechanisms other than PER including NER in *T. urticae*.

Recovering from fatal UV-B damage using light energy

Photoreactivation via repair of DNA lesions such as CPDs and 6–4 PPs via PER is essential, and the reactivation system is present in a wide range of organisms, including bacteria (Ikenaga et al. 1970; Peccia and Hernandez 2001), rotifers (Grad et al. 2003), crustaceans (Connelly et al. 2009; Damkaer and Dey 1983; Grad and Williamson 2001), algae (Pakker et al. 2000; Pescheck 2019), plants (Hada et al. 2003; Kaiser et al. 2009; Manova et al. 2016; Takahashi et al. 2002), amphibians (Blaustein et al. 1994; Morison et al. 2020), and fishes (Applegate and Ley 1988; Lawrence et al. 2020; Mitchell et al. 2009; Wiegand et al. 2004), but not in placental mammals, which may rely on other repair systems: base excision repair, NER, and so on (Sinha and Häder 2002). In spider mites, Santos (2005) observed photoreactivation of UV-B damage in *T. urticae*, the mortality rate of *T. urticae* adult females irradiated with UV-B at 46.8 kJ/m² was reduced from 46% (when kept in the dark after UV-B irradiation) to 26% with VIS illumination after UV-B irradiation. As the adult female is the most resistant to UV-B radiation, more dramatic photoreactivation effects are observed egg and larval stages. UV-B-irradiated *T. urticae* eggs and larvae recovered at rates of 57% and ~100% with subsequent VIS radiation (Murata and Osakabe 2014).

In a midge *Smittia* sp. (Chironomidae, Diptera) and a bacterium *Escherichia coli* (Migula) (Enterobacteriaceae, Enterobacterales), VIS intensity has been suggested as a factor that affects the efficiency of photoreactivation (Kalthoff et al. 1978; Kelner 1951). In contrast, correlation of the photoreactivation efficiency with the cumulative VIS irradiance after UV-B irradiation has been reported in the long-nosed potoroo *Potorous tridactylus* (Kerr) (Potoroidae, Diprotodontia) and a bacterium *Streptomyces griseus* (Krausky) (Streptomycetaceae, Actinomycetales) (Chiang and Rupert 1979; Kelner 1951). Murata and Osakabe (2014) suggested that the photoreactivation of *T. urticae* also depends on the cumulative VIS irradiation (a reciprocity law), though the regression curve was analyzed by a nonlinear least-squares method.

Efficient wavelengths for photoreactivation

For activation of PER, radiation at wavelengths of 350–450 nm generally provides an effective energy source (Baalen and O'Donnell 1972; Chiang and Rupert 1979; Kalthoff et al. 1978; Kelner 1951; Sancar 2003). Murata and Osakabe (2014) assessed the effects of UV-A and wavelength-filtered VIS (blue, green, yellow, and red) on photoreactivation of *T. urticae* eggs. They estimated the effective radiation range as UV-A to green light (≤ 500 nm) (Murata and Osakabe 2014), roughly corresponding to those of other organisms. Intensification of solar UV-B radiation occurs later than UV-A (morning) and is negligible earlier in the evening (Fig. 2). Because lower leaf surfaces also exposed to low-intensity UV-B rays scattered in the air, survival rate and egg production of *Typhlodromalus aripo* De Leon, the most UV-B vulnerable phytoseiid mite species, decrease on lower leaf surfaces when the leaves are irradiated with UV-B (Onzo et al. 2010). UV-A and visible lights also seem to be scattered in shadows such as lower leaf surfaces frequently. Thus, solar radiation in the early morning and late evening may enhance the recovery from UV damage via photoreactivation in mites.

Application of UV-B for mite control in strawberry greenhouses

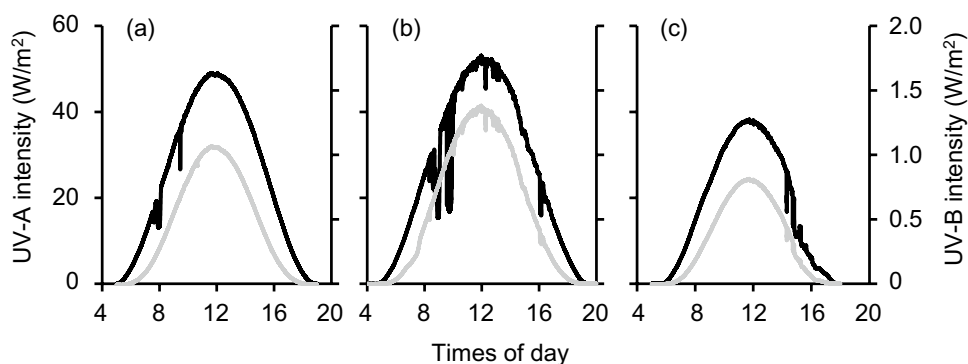
Spider mites have long been major pests affecting strawberry production in Japan (Aida 1987; Yanagita 2019). Moreover, the recent development of acaricide resistance in *T. urticae* has become a serious problem in Japanese strawberry greenhouses, hindering the selection of chemicals for rotation spraying (Yamamoto 2012; Yanagita 2019). Therefore, the development of alternative control technologies is urgently needed. The UV-B method (Tanaka et al. 2016) may be a promising addition to IPM in greenhouse strawberry cultivation.

UV-B ray delivery to lower leaf surfaces

Along with many other plant-dwelling mites, most *T. urticae* individuals reside on the lower leaf surfaces of host plants in the field (Osakabe et al. 2006). Thus, for practical use of UV-B for spider mite control in strawberry greenhouses, UV-B delivery to the lower leaf surfaces on which spider mites reside is important. For this reason, Tanaka et al. (2016) used a combination of overhead UV-B lamps and light-reflecting sheets in a strawberry greenhouse. The light-reflecting sheet was a flash-spun nonwoven fabric sheet (Tyvek 700AG; DuPont-Asahi Flash Spun Products, Tokyo, Japan), which diffusely reflected solar radiation, including UV-A and UV-B, and VIS with high efficiency ($> 90\%$; Sakai and Osakabe 2010). As a result, the UV-B radiation was 0.023 – 0.053 W/m^2 on the lower leaf surface and 1.61 – 1.87 W/m^2 on the upper leaf surface of greenhouse strawberry plants (Tanaka et al. 2016). For the reasons described in the following section, UV-B irradiation was performed at midnight every day for 3 h. Therefore, the daily cumulative irradiation on the lower leaf surfaces was 0.25 – 0.57 kJ/m^2 .

UV-B irradiation affects plant-dwelling arthropods and pathogens not only directly, but also through indirect pathways involving plant responses to UV irradiation, such as the accumulation of phenolic compounds (Escobar-Bravo et al. 2017; Neugart and Schreiner 2018) and the induction of protective signaling systems (Ballaré 2014; Kunz et al. 2006). In strawberries, UV-B irradiation induces disease resistance and strongly prevents the development of powdery mildew caused by *Sphaerotheca aphanis* (Wallroth) Braun var. *aphanis* (Erysiphales: Erysiphaceae) (Kanto et al. 2009). Although the effects of plant defense systems on spider mites have been reported (Kant et al. 2008; Ozawa et al. 2017), indirect effects of UV-B radiation acting through host plants on spider mites have not been reported to date. Tomimori et al. (2020) detected no effect of pre-irradiation with UV-B on the perilla plants *Perilla frutescens* (L.) Britton var. *crispa* (Thunb.) H. Deane (Lamiales: Lamiaceae), which produces abundant essential oil containing various

Fig. 2 Daily fluctuations of solar UV-A (solid line) and UV-B (gray line) in Kyoto, Japan on **a** 25 April, **b** 21 July, and **c** 7 October in 2010. Data from the Solar Radiation and Weather Monitoring Project at Kyoto Women's University ($34^{\circ}59' N$, $135^{\circ}47' E$; http://db.cger.nies.go.jp/gem/ja/uv/uv_sitedata/kyoto/index.html)



secondary metabolites that act as a biological protective mechanism, on the juvenile development and egg production of *T. urticae*. This highlights the importance of delivery of UV-B rays to spider mite locations for practical application.

Diminished photoreactivation by midnight UV-B irradiation

Suzuki et al. (2014) and Koveos et al. (2017) showed that simultaneous white light and UV-B irradiation reduced the mortality of *Tetranychus* spider mite eggs and phytoseiid mite eggs caused by UV-B damage. The photoreactivation efficiency increased with increasing cumulative VIS irradiation, as did the reciprocity effect on the accumulation of UV-B damage (Murata and Osakabe 2014). These results indicate less effective control of spider mites by UV-B irradiation during the daytime; therefore, nighttime irradiation is preferred in greenhouses (Masui et al. 2013; Tanaka et al. 2016).

Moreover, increasing lag time between UV-B irradiation and light irradiation for photoreactivation reduces the photoreactivation efficiency in *T. urticae* eggs, and a lag longer than 4 h inactivates the photoreactivation system (Murata and Osakabe 2014; Yoshioka et al. 2018). In contrast, no effect of lag time was observed in UV-B-exposed larvae; even after a 4-h lag, all larvae exposed to photoreactivation light developed to adulthood, but no larvae developed if they were not exposed to light (Murata and Osakabe 2014). Therefore, the effect of UV-B irradiation on controlling spider mites in greenhouse production might be due to an ovicidal mechanism.

Concurrent use of UV-B and biological control

Reversal of vulnerability to UV-B between spider mites and phytoseiid mites under daily nighttime irradiation for practical application

According to egg mortality after a single period of acute UV-B irradiation, phytoseiid mites appear to be more vulnerable to UV-B damage than spider mites (Ghazy et al. 2016; Tachi and Osakabe 2012). Interestingly, it was recently reported that resistance to daily UV-B irradiation at midnight is higher in *N. californicus* eggs than *T. urticae* eggs (Nakai et al. 2018; Yuan and Osakabe 2020). Yuan and Osakabe (2020) found a linear regression between the logarithmic daily cumulative level of UV-B radiation and probit mortality in *T. urticae* eggs ($y = 6.54x + 11.7$, $R^2 = 0.867$, $P = 4.38 \times 10^{-3}$) and *N. californicus* eggs ($y = 6.99x + 8.76$, $R^2 = 0.978$, $P = 1.17 \times 10^{-4}$) in laboratory experiments that simulated practical UV-B irradiation conditions in strawberry greenhouses (Tanaka et al. 2016). The LD₅₀ value of *N. californicus* eggs was 0.29 kJ/(m² day) at 25 °C, which

was three times higher than that in *T. urticae* (0.095 kJ/(m² day); 25 °C). The mortality of eggs irradiated with 0.15, 0.17, and 0.2 kJ/(m² day) were estimated from the regression lines as 90, 95, and 98%, respectively, in *T. urticae* and 2, 5, and 15%, respectively, in *N. californicus*. Therefore, cumulative irradiation in the range of 0.15–0.2 kJ/m² (0.014–0.019 W/m² for 3 h/day) is advantageous for applying UV-B for spider mite control in combination with *N. californicus* at 25 °C. However, Nakai et al. (2018) reported that a UV-B dose of 0.27 kJ/(m² day) at 25 °C reduced the developmental success of hatched *N. californicus* larvae, indicating that lower UV-B doses within the cumulative radiation range may be preferable for controlling spider mites using phytoseiid mites.

The mechanism behind the difference in the UV-B vulnerability of spider mites and phytoseiid mites between a single UV-B irradiation and daily nighttime UV-B irradiation remains unclear. Koveos et al. (2017) reported higher hatchability under continuous UV-B irradiation without VIS irradiation in the eggs of four of phytoseiid mite species compared with *T. urticae* eggs. Considering the reciprocity of UV-B-induced mortality (Murata and Osakabe 2013), the difference in vulnerability could be attributed to the shorter egg duration of phytoseiid mites relative to spider mites. Moreover, variations in UV-B vulnerability among the embryonic developmental stages (Murata and Osakabe 2014; Sugioka et al. 2018; Yoshioka et al. 2018) may be involved. This topic may be related to the interaction between UV damage and temperature and thus linked to the issue of global climate change.

Effects of air temperature on mite mortality caused by daily nighttime UV-B irradiation

Laboratory experiments revealed that daily nighttime UV-B irradiation in greenhouses is more effective for controlling spider mites at low than high temperatures (Nakai et al. 2018; Yuan and Osakabe 2020). Mortality of *T. urticae* eggs caused by UV-B irradiation at 0.097 kJ/(m² day) was 7.0, 28.6, and 78.2% at 30, 25, and 18 °C, respectively (Yuan and Osakabe 2020). The air temperatures (monthly average) 0.15 m above a ridge in greenhouse reported by Tanaka et al. (2016) in Hyogo Prefecture, Japan (34.9° N, 134.9° E) were lower than 18 °C from December to April, and reached 21–22.6 °C in May, indicating that the cumulative radiation on lower leaf surfaces was sufficient for control of *T. urticae* eggs.

Like *T. urticae*, the biological impact of daily nighttime irradiation on *N. californicus* is stronger at relatively low temperature. The rates of egg mortality caused by UV-B irradiation at 0.27 kJ/(m² day) were 13.7, 31.1, and 80.3% at 30, 25, and 18 °C, respectively (Yuan and Osakabe 2020). Analyzing the relationship between temperature and probit

mortality by linear regression, strong correlations ($R^2 > 0.95$) were detected in both *T. urticae* and *N. californicus* eggs (Fig. 3). The regression line was similar between *N. californicus* UV-B irradiated at 0.27 kJ/(m² day) and *T. urticae* UV-B irradiated at 0.097 kJ/(m² day), indicating that *N. californicus* eggs have stronger resistance to daily nighttime UV-B irradiation than do *T. urticae* eggs, at least within the temperature range of 18–30 °C. Moreover, in the winter, daily cumulative UV-B radiation for spider mite control can be reduced, and this reduction is beneficial for the activity of phytoseiid mites. Vulnerability to UV-B radiation varies among phytoseiid mite species (Ghazy et al. 2016; Onzo et al. 2010). *Phytoseiulus persimilis* Athias-Henriot is more resistant to UV-B radiation compared with other phytoseiids that are potential biological control agents, such as *N. californicus*, *Neoseiulus womersleyi* Schicha, and *Amblyseius swirskii* Athias-Henriot (Koveos et al. 2017; Tachi and Osakabe 2012). *Phytoseiulus persimilis* eggs show orange–red color that might be due to keto-carotenoids derived from prey spider mites (Veerman 1974b), while eggs of *Neoseiulus* phytoseiid mites are colorless or milky white. Keto-carotenoids, especially astaxanthin, has strong antioxidant activity (Camera et al. 2009), and have the effects reducing lipid peroxidation in spider mites (Atarashi et al. 2017). According to Croft et al. (1999), eggs of *P. persimilis* is larger in size (egg length: 0.24 mm) than that of *Neoseiulus* species (egg length: 0.20–0.21 mm), being advantageous in terms of UV-B resistance due to limitation of penetration. Moreover, according to Escudero and Ferragut (2005), egg duration of *P. persimilis* at 25 °C (1.4–1.8 days) is shorter

than that of *N. californicus* (1.9–2.4 days), though the effects on UV-B resistance is not clear so far.

Although a clear relationship between mortality and temperature was seen in mite eggs after daily nighttime UV-B irradiation, the thermal dependence of UV-B damage in various organisms remains controversial. UV damage in *E. coli* and tadpoles of the frog *Limnodynastes peronii* Duméril and Bibron is greater at lower temperature than at higher temperature (Mangoli et al. 2014; Van Uitregt et al. 2007). The cladoceran *Daphnia catawba* Coker and the calanoid copepod *Leptodiaptomus minutus* Lilljeborg show greater UV-B resistance with increasing temperature, whereas the rotifer *Asplanchna girodi* de Guerne shows reduced resistance at higher temperatures (Williamson et al. 2002). Moreover, in four *Daphnia* species, DNA repair occurs more rapidly at lower temperatures, but the opposite pattern is seen in *Daphnia pulicaria* Forbes (MacFadyen et al. 2004). Enzymes associated with DNA repair and ROS scavenging likely have high activity within the optimal temperature range. The studies described above suggest the involvement of multiple factors, such as developmental stage and timing of gene expression. In spider mites, some stages are specifically vulnerable, such as developing embryo and quiescent juvenile (Murata and Osakabe 2014, 2017b; Sugioka et al. 2018; Yoshioka et al. 2018). Research in the association of such stage-specific UV-B vulnerability with variation in the thermal dependence of UV damage will be worthwhile for elucidating adaptation to UV-B radiation in mites.

Differences in the behavioral responses of spider mites and phytoseiid mites to UV-B irradiation

Tachi and Osakabe (2012) showed that most *T. urticae* and *N. californicus* individuals escaped from solar UV radiation within 30 and 10 min, respectively. In laboratory experiments using monochromatic UV radiation, however, *T. urticae* females responded by escaping from UV-A irradiation at 320 and 340 nm wavelengths, but not from UV-B irradiation at 300 nm (Sakai and Osakabe 2010). In a monochromatic analysis by Suzuki et al. (2009), non-diapausing *T. urticae* females also escaped from safe UV-A radiation (350 nm) more often than from lethal UV-B radiation (300 nm). Barcelo and Calkins (1980) and Barcelo (1981) showed strong dose-dependent responses of *T. urticae* escape from leaf areas irradiated with UV-B at the beginning of experiments. Then, the mite distribution between areas with and without UV-B radiation became constant at ~2 h after the start of UV-B irradiation (Barcelo and Calkins 1980). On the other hand, Suzuki et al. (2013) revealed that *T. urticae* increased the frequency of turning behavior when it entered an area irradiated with monochromatic UV-B (307 nm) using a virtual field system, suggesting that *T. urticae* perceives

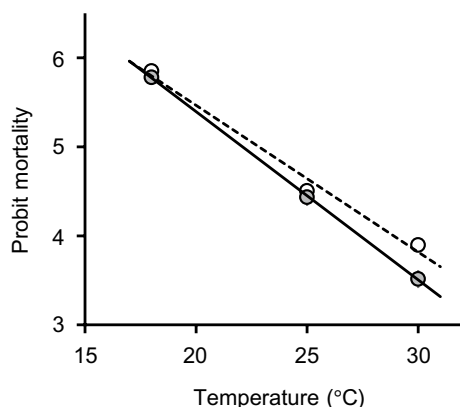


Fig. 3 Correlation of probit mortality with temperature in the eggs of *Tetranychus urticae* (gray circles) and *Neoseiulus californicus* (open circles) irradiated with 0.097 and 0.27 kJ/(m² day), respectively. Regression lines: $y = -1.65x + 8.76$, $R^2 = 0.95$, $P = 5.32 \times 10^{-6}$ for *T. urticae* (solid line) and $y = -1.89x + 9.18$, $R^2 = 0.979$, $P = 2.69 \times 10^{-7}$ for *N. californicus* (broken line). This graph was created using the data from Yuan and Osakabe (2020)

UV-B radiation visually, as thrips (Mazza et al. 2010), or via another mechanism, as phytoseiid mites.

Although phytoseiid mites are eyeless, they escape from solar UV radiation more quickly than spider mites (Tachi and Osakabe 2012). Photoreceptors distributing brains have been known in a wide range of classes of nonmammalian vertebrates (Bertolucci and Foà 2004). In insects, multiple extraocular photoreceptive areas including brains and genitalia have been reported (Arikawa et al. 1980; Spaethe and Briscoe 2005). Elucidation of extraocular photoreceptor in the eyeless phytoseiid mites is interesting but not yet so far.

The arresting effects of spider mite webs on predacious phytoseiid mites have long been known. When phytoseiid mites encounter the webs or their remnants, they walk slowly and turn frequently, entering a “search mode” for their prey, spider mites (Hoy and Smilanick 1981). This behavior may result in the phytoseiid mite trailing silks or residues left by dispersed spider mites (Shinmen et al. 2010; Yano and Osakabe 2009). In the experiments performed in Kyoto City, Japan (35° N, 136° E) from 7 September to 8 October, 2011, females of *N. californicus* escaped from solar VIS radiation (Tachi and Osakabe 2012) as well as from artificially provided monochromatic UV-A and UV-B radiation (Tachi and Osakabe 2014). They are also arrested by residue from *T. urticae* females (web and eggs), even when irradiated with monochromatic UV of wavelength ≥ 310 nm, which is not harmful to *N. californicus* (Tachi and Osakabe 2014). In contrast, they escaped quickly from an area irradiated with harmful UV-B at 300 nm, regardless of the presence of spider mite residue (Tachi and Osakabe 2014), indicating that phytoseiid mites perceive this deleterious UV radiation. Interestingly, prey eggs without webs do not arrest *N. californicus* females in UV-irradiated areas (Tachi and Osakabe 2014), showing the importance of webs in their behavioral response to predation (Furuichi et al. 2005). I suppose that phytoseiid mites likely escape and hide more quickly than spider mites when UV-B lamps are turned on in a greenhouse. Spider mites flee to and are saved in a safe place, such as the shadows on host plant leaves, which phytoseiid mites possibly enter to escape from UV-B irradiation. Consequently, the phytoseiid mite may efficiently forage on prey in these hidden areas in a greenhouse subjected to UV irradiation.

Potential protection of phytoseiid mites from UV-B irradiation by pollen feeding

The removal of ROS by antioxidants is generally considered a UV protective mechanism. However, protection via the ROS-scavenging effects of antioxidants has been tested mainly in vitro (Camera et al. 2009; Kootstra 1994), and the effects of antioxidants on the survival of organisms under ambient UV radiation remain vague (Heath et al. 2013).

Indeed, diapausing *T. urticae* females, which are more resistant to UV-B radiation than the summer form of this species (Suzuki et al. 2009), accumulate keto-carotenoids such as astaxanthin, a very powerful ROS scavenger (Kawaguchi et al. 2016; Veerman 1974a). This suggests that the carotenoid composition and dose affect their survival under ambient UV-B radiation. In phytoseiid mites, Nakai et al. (2018) found that *N. californicus* eggs and hatched larvae produced by females feeding on *P. citri*, which contains abundant astaxanthin, were more resistant to UV-B radiation than those produced by females feeding on *T. urticae*.

Plant pollen is a possible alternative food for many phytoseiid mites (Castagnoli and Simoni 1999; Kishimoto et al. 2014; Osakabe 1988; Osakabe et al. 1987). The germ cells contained in pollen must be protected from ambient UV-B, and therefore, pollen contains UV-B-protective compounds (Feng et al. 2000; Wang et al. 2010; Žilić et al. 2014). Sugioka et al. (2018) identified tri-coumaroylspermidine and catechins as the major antioxidants in peach pollen and tea pollen, respectively. *Neoseiulus californicus* females fed pollen showed increased survivorship after exposure to artificial UV-B irradiation, and the viability of eggs produced by pollen-fed females was higher than that of *T. urticae*-fed females (Sugioka et al. 2018). The transmission of those antioxidants into eggs has not been proven unfortunately. However, I consider that such transmission is not surprising, because transmission of dietary obtained carotenoids, which is essential for diapause induction, from mother to eggs is known for a long time in phytoseiid mites and spider mites (Van Zon et al. 1981; Veerman 1980, 1992).

Later, Yuan et al. (2020) identified five types of hydroxycinnamoyl spermidine derivatives in strawberry pollen. The majority of the content was comprised of three derivatives containing a caffeoyl group or both caffeoyl and feruloyl groups (Yuan et al. 2020). The caffeoyl and feruloyl groups confer higher antioxidant capacity than does the coumaroyl group in spermidine derivatives (Castelluccio et al. 1995; Shahidi and Chandrasekara 2010). Yuan et al. (2020) observed the development of juveniles including egg periods on strawberry pollen was faster than that on *T. urticae* and found enhanced survival of females and hatching of eggs in *N. californicus* after UV-B irradiation combined with a strawberry pollen diet. This finding may help maintain *N. californicus* within strawberry greenhouses equipped with UV-B lamps.

UV-B lamps as an IPM strategy in greenhouses

One advantage of UV technology in IPM is that it enables simultaneous control of spider mites and powdery mildew, both of which are economically important pests of

strawberry (Kanto et al. 2009, 2011, 2014; Sugeno et al. 2018) and wide range of horticultural crops including rose (Kobayashi et al. 2013; Suthaparan et al. 2012) and cucumber (Suthaparan et al. 2014, 2017). Powdery mildew fungi have developed resistance to a wide range of fungicides due to their frequent application (Elderfield et al. 2018; Nakano et al. 1992; Sombardier et al. 2010; Wyenandt et al. 2018).

A comparison of UV damage and photoreactivation between mites and powdery mildew fungi drawn from the literature is provided in Table 1. The UV-B wavelength range that can effectively suppress infection by powdery mildew fungi is less than 310 nm (Suthaparan et al. 2012, 2016a). The effect of UV-B at 290–310 nm on powdery mildew fungi depends on the duration of exposure (Suthaparan et al. 2016a). The effectiveness of UV-B by direct irradiation rather than by indirect effects by UV-B via host plants, decreasing photoreactivation with lag time between UV-B irradiation and VIS irradiation in powdery mildew fungi (Janisiewicz et al. 2016a; Suthaparan et al. 2012, 2016b, 2018) are similar to those in spider mites. Janisiewicz et al. (2016b) reported a similar decrease in photoreactivation with lag time in the gray mold fungus *Botrytis cinerea* Pers. These similarities in symptoms and protective responses to UV-B radiation between spider mites and fungi are advantageous for the development of IPM strategies against both pests. The mechanism by which the time lag between UV-B irradiation and VIS radiation diminishes photoreactivation capacity is currently under investigation.

UV-C radiation (wavelength ≤ 280 nm) strongly inhibits fungal development (Janisiewicz et al. 2016a; Suthaparan et al. 2016a) as well as *T. urticae* population growth (Short et al. 2018). However, irradiation at a wavelength of 280 nm inhibits the walking ability of both *N. californicus* and *T. urticae* in an intensity-dependent manner (Sakai and Osakabe 2010; Tachi and Osakabe 2014). The proportions of *N. californicus* females incapable of walking normally (i.e., of escaping from UV) after UV radiation at 280 nm wavelength were 95.1% (37/39 ♀♀), 100% (41/41 ♀♀) and 0% (0/28 ♀♀) at intensities of 1.26, 0.73 and 0.29 W/m², respectively (Tachi and Osakabe 2014). The intensity of UV-C (254 nm) used by Short et al. (2018) for *T. urticae* control was 0.237 W/m². Although this is lower than the intensity that caused no damage to phytoseiid mite behavior at 280 nm, the shorter wavelength might have a greater effect on the behavior and health of phytoseiid mites. Conversely, the benefit of UV-C is the short irradiation time required for control of spider mites. The *T. urticae* population was suppressed by only 60 s of irradiation per day (Short et al. 2018). Therefore, information about the interaction between UV-C and phytoseiid mites is likely to be helpful for supporting the practical application of UV-C. In the future, it is worth considering how each UV wavelength can be optimized for IPM.

Table 1 Comparison of UV damage and photoreactivation between mites and fungi causing powdery mildew

UV effects	Spider mite and phytoseiid mite	Powdery mildew fungus	References
Direct (D) and indirect (I) effects	D > I	D > I	Ohtsuka and Osakabe (2009), Suthaparan et al. (2012, 2016b, 2018), Janisiewicz et al. (2016a), Tomimori et al. (2020)
Deleterious wavelength	< 310 nm	< 310 nm	Sakai and Osakabe (2010), Tachi and Osakabe (2014), Suthaparan et al. (2016a)
Reciprocity in deleterious effects	Yes	Effects depend on duration of exposure (UV-B)	Tachi and Osakabe (2012), Murata and Osakabe (2013), Suthaparan et al. (2016a), Yuan and Osakabe (2020)
Photoreactivation from UV damage	Yes	Yes	Murata and Osakabe (2014, 2017a), Janisiewicz et al. (2016b), Koveos et al. (2017), Nakai et al. (2018), Sugioka et al. (2018), Suthaparan et al. (2018)
Effective wavelength for photoreactivation	From UV-A to green (≤ 500 nm; <i>T. urticae</i>)	350–500 nm (<i>Oidium neolycopersici</i>)	Murata and Osakabe (2014), Suthaparan et al. (2018)
Dark period after UV irradiation to invalid photoreactivation	≥ 4 h	> 4 h	Murata and Osakabe (2014), Janisiewicz et al. (2016a), Suthaparan et al. (2018), Yoshioka et al. (2018)

Future perspectives

The UV-B method is a control technique that exploits the behaviors and physiologies of spider mites related to UV adaptation to exploit their weaknesses. Although increased shadowing due to plant growth may reduce the effectiveness of this method, phytoseiid mites avoiding UV-B may prey on spider mites surviving in the shadows. Consequently, the UV-B method can suppress overgrowth of the spider mite population in excess of the control capacity of phytoseiid mites, and phytoseiid mites can complement the weakness of the UV-B method in shaded areas. Moreover, nighttime UV-B irradiation allows workers to avoid unwanted exposure to UV-B. Thus, the concurrent use of the UV-B method and biological control is an extremely promising management method.

On the other hand, the physiological processes of UV damage and adaptation to it in spider mites require more works. Mites are organisms with a remarkable life-and-death reaction to UV damage, making them an ideal subject for study of the mechanism of UV adaptation.

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