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Daily light integral and day light quality: Potentials and pitfalls of nighttime UV treatments on cucumber powdery mildew

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ABSTRACT

Nighttime ultraviolet (UV) radiation, if applied properly, has a significant potential for management of powdery mildews in many crop species. In this study, the role of growth light duration, irradiance, a combination of both (daily light integral) and light spectral quality (blue or red) on the efficacy of UV treatments against powdery mildew caused by *Podosphaera xanthii* and the growth performance of cucumber plants was studied in growth chambers. Increasing daily light integral provided by high-pressure sodium lamps (HPS) decreased efficacy of nighttime UV treatments against *P. xanthii*, but it increased plant growth. Furthermore, the efficacy of nighttime UV decreased when day length was increased from 16 to 20 h at a constant daily light integral. The efficacy of nighttime UV increased if red light was applied after UV treatment, showing the possibility of day length extension without reducing the effect of UV. Increasing the dose of blue light during daytime reduced the efficacy of nighttime UV in controlling the disease, whereas blue deficient growth light (< 6% of blue) caused UV mediated curling of young leaves. Furthermore, application of blue light after nighttime UV reduced its disease control efficacy. This showed the importance of maintaining a minimum of blue light in the growth light before nighttime UV treatment. Findings from this study showed that optimization of nighttime UV for management of powdery mildew is dependent on the spectral composition of the photosynthetically active radiation.

1. Introduction

Powdery mildews cause significant yield losses in cucumber (*Cucumis sativus* L.). While *Podosphaera xanthii* is the most common and consistent problem in greenhouse and high tunnel cucumber production [1], *Golovinomyces cichoracearum* and *Leveillula taurica* are also known to cause powdery mildew in cucumber [2]. Wide ranges of strategies including but not limited to the use of resistant varieties, biocontrol agents, silicon and efficacious fungicides are available for management of this disease. However, difficulties in developing high yielding, resistant greenhouse cultivars with desirable commercial characteristics [3], along with emergent fungicide resistance in the pathogen population [4,5], and consumer concerns about pesticide residues in food, have required alternative/additional strategies.

Optical radiation is part of the electromagnetic spectrum and consists of ultraviolet (UV), visible and infrared regions. Optical radiation has been studied for its effects and potential in management of powdery mildews [6–8], including *P. xanthii* in greenhouse grown cucumbers [9]. While red light may suppress powdery mildews in a wide range of crops within the visible spectrum [8,10,11], the degree of disease suppression achieved when it was used as a sole treatment was insufficient to control disease under practical conditions (A. Suthaparan, unpublished data). However, the potential of UV in controlling powdery mildews on a range of host plants has been reported [6,7,9,12–14]. UV radiation can be subdivided into UV-A (315–400 nm), UV-B (280–315 nm), UV-C (200–280 nm) and vacuum UV (100–200 nm) [15]. The UV region within 250 to 400 nm was classified in three ranges based on their efficacies against *Oidium neolycopersici*, the cause of powdery mildew in tomato: i) effective (250–280 nm), ii) transition (290–310 nm), and iii) ineffective (310–400 nm) [16]. Development of *O. neolycopersici* was similarly suppressed within the effective range. In addition to wavelength, treatment time and frequency of treatments are also significant factors in determining the efficacy of UV (275 nm to 400 nm) against powdery mildews [6]. Application of UV (275 nm to 400 nm) during nighttime and in combination with red light significantly improved suppression of powdery mildew in cucumber [9], strawberry and rosemary [6].

Within the tested wavelengths and doses, the disease suppressive effect of UV was primarily upon the pathogen rather than persistence of induced systemic resistance in the host [7,16]. Therefore, direct

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exposure of the entire phyllosphere to UV is necessary to ensure efficacy against powdery mildews, which may partly be achieved using UV reflective aluminized bench or soil covers [6].

While UV has a great potential to suppress powdery mildews, optimizing its use in conjunction with practical growing conditions is necessary to achieve high efficacy with no phytotoxicity. The importance of high ratios of photosynthetic active radiation (PAR; 400–700 nm) or UV-A in ameliorating damage caused by UV-B in both terrestrial and aquatic plants, has been documented [17]. Plant protective mechanisms against UV applied during daytime have primarily been correlated with UV-induced flavonoid biosynthesis and its UV screening potential in the epidermal layer [17,18]. However, there are no reports of the effects of day length, daytime PAR level, and its spectral composition on efficacy of brief nighttime UV exposure for disease control and phytotoxic potential. Although red light suppresses powdery mildews alone or in combination with UV (275 nm to 400 nm) [9,19], its effect related with the timing of UV application and its potential as day extension light have not been studied.

A series of experiments were conducted in controlled environment growth chambers to examine the impact of growth light architecture on the efficacy of brief UV (275 nm to 400 nm) application on *P. xanthii* and its host, the cucumber plant. The growth light conditions of i) daytime PAR in terms of day length, level of irradiance, and spectral composition (end of day red light), ii) daily doses of blue light, and iii) daily application time of blue light were examined for their impact.

2. Materials and Methods

2.1. Experimental Plants and Experimental Setup

Cucumber seeds cv. Odeon, susceptible to powdery mildew, were sown in 12 cm diameter plastic pots filled with standard growth medium, and maintained in a greenhouse compartment as described in a previous study [9]. Healthy and vigorously growing plants, each at the growth stage with fully unfolded first true leaves were transferred to growth chambers having a completely controlled environment.

The experiments were conducted in a randomized complete block design (RCBD). Each experiment was conducted twice in succession and considered as block in data analysis. Each treatment was implemented in a separate growth chamber to avoid interference between light treatments. All treatments in each block were randomly assigned to growth chambers. Eight individual plants (replicates) receiving the same treatment in each study were randomly assigned to a different position within the growth chamber.

2.2. Growth Chamber Environmental Conditions and Recording

Growth light (GL) was provided by high-pressure sodium (HPS) lamps (Lucalox LU400/XO/T/40, GE lighting, Budapest, Hungary). Air temperature was 20 ± 1 °C and relative air humidity (RH) was 75 ± 5%. Plants were fertigated daily with a nutrient solution [9]. For UV treatments, 7.8 ± 0.2 μmol/m^2/s (3 ± 0.1 W/m^2) of UV irradiance (≤ 315 nm) at plant height was applied daily for 3 min by 120 cm UV-B fluorescent tubes (model UVB-313EL; Q-PANEL Lab Products, Cleveland, OH, USA). Air temperature, RH, irradiance level received at plant height, and the spectral composition of all radiation sources were measured as described in a previous study [9]. A Priva greenhouse computer (Priva, Zijlweg, The Netherlands) with dry and wet bulb thermo sensors deployed at plant canopy level in each growth chamber was used to record air temperature and RH at 5 min intervals. A digital Lambda LI-185B photometer (LI – COR Inc., Lincoln, NE, USA) with a quantum sensor LI-190 was used to measure photon irradiance within the PAR region received from HPS and light emitting diodes (LEDs) at plant height. An Optronic model 756 spectroradiometer (Optronic Laboratories, Orlando, FL, USA) was used to measure UV irradiance (≤ 315 nm). Spectral qualities of all lamps used in the present study were measured using an Optronic model 756 spectroradiometer. The HPS lamps emitted a broad light spectrum with multiple peaks at 575–600 nm, and contained around 6% blue light (400–500 nm) [7]. The blue LEDs (15 W GreenPower LED module HF blue; Philips, The Netherlands) had a spectral range of 400–500 nm, with a peak at 454 nm. The red LEDs (10 W GreenPower LED module HF deep red; Philips, The Netherlands) had a spectral range of 600–700 nm, with a peak at 660 nm. UV fluorescence tubes emitted at a spectral range of 275–400 nm, with a peak at 313 nm.

2.3. Inoculum Preparation and Inoculation

Colonies of *P. xanthii* were obtained by sequential transfers of the pathogen starting with a leaf containing powdery mildew from a greenhouse grown cucumber plant to clean leaf disks, and then to clean plants as described previously [9]. Ten-day-old inoculum (time from inoculation of a healthy cucumber leaf to harvesting newly formed conidia) was used for inoculation of cucumber leaves in all experiments with severity studies. The entire surface area of the first true leaf of the healthy cucumber plant was inoculated using a hand held sprayer and spraying conidial suspensions of 10 ml on each leaf as fine droplets with a concentration of 10^4 conidia/ml. Immediately following inoculation, the plants were moved to growth chambers to commence experimentation. The fine droplets with inoculum dried within an hour, and UV treatment was applied on a daily basis at the onset of darkness (3 h after inoculation for the first time).

2.4. Experiments With Inoculated and Non-inoculated Plants

All the experiments described below were conducted twice in succession with inoculated cucumber plants (for severity studies), and twice in succession with non-inoculated cucumber plants (for plant growth studies) of the same growth stage. Each treatment was accommodated in a separate growth chamber with eight plants per chamber at a time.

2.5. Effect of Growth Light Duration and Irradiance

In this experiment, the effect of growth light duration (day length), irradiance level, and their interaction (daily light integral = DLI) on efficacy of nighttime UV treatment was examined. A two-factor (irradiance and day length) factorial experiment with two levels was conducted as follows: i) Photosynthetic photon flux (PPF) of either 75 ± 5 or 150 ± 5 μmol/m^2/s and ii) day lengths of either 8 or 16 h were provided by HPS lamps as described above. The treatment combinations provided daily light integrals of 2.16, 4.32, 4.32 or 8.64 mol/m^2/day. UV irradiance of 7.8 ± 0.2 μmol/m^2/s was provided on a daily basis at the onset of darkness in all growth chambers. Based on the results of the above experiment, another single factor (day length) experiment was conducted with four levels of day length (8, 12, 16 and 20 h) but all with the same daily light integral of 4.32 mol/m^2/day. UV irradiance of 7.8 ± 0.2 μmol/m^2/s was provided on a daily basis at the onset of darkness in all growth chambers.

2.6. Effect of End-of-day Growth Light Spectrum Applied Before or After UV Treatment

Here we examined the potential of red light in lieu of HPS light for day extension, to be able to grow plants at 20 h day length without reducing UV efficacy, as compared to shorter day lengths, as studied above. We also wanted to ascertain the time (before or after UV treatment) when red light treatment should take place as day extension to achieve the most effective suppression of powdery mildew. A two-factor (end-of-day GL spectrum and its application time relative to UV treatment) factorial experiment was conducted with a daily light integral of 4.32 mol/m^2/day and 20 h with illumination (4 h dark),

including 16 h supplied with HPS lamps and 4 h of day extension light supplied by either HPS lamps or red LEDs, both applied either before or after UV treatment.

2.7. Effect of Blue Light Irradiance Enrichment of the Growth Light

The purpose of this experiment was to determine the amount of daytime blue light needed to eliminate/minimize UV mediated phytotoxicity without losing its efficacy for disease control. A single factor experiment of 16 h GL of 150 ± 5 μmol/m^2/s (daily light integral of 8.64 mol/m^2/day) with four levels of blue light was conducted as follows: i) 150 ± 5 μmol/m^2/s from HPS lamps only, ii) 125 μmol/m^2/s from HPS lamps and 25 μmol/m^2/s from blue LEDs, iii) 100 μmol/m^2/s from HPS lamps and 50 μmol/m^2/s from blue LEDs, iv) 75 μmol/m^2/s from HPS lamps and 75 μmol/m^2/s from blue LEDs. UV irradiance of 7.8 ± 0.2 μmol/m^2/s was provided on a daily basis at the onset of darkness in all growth chambers.

2.8. Effect of Time of Day for Blue Light Enrichment

This experiment was set up to reveal if blue light optimized in the above study ((in treatment ii); 25 μmol/m^2/s from blue LEDs for 16 h daily = 1.44 mol/m^2/day) can be added to growth light for a short period of time (early, mid-day or late) rather than during the whole daylight period and how this may interfere with disease control and potential phytotoxicity. A single factor experiment of 16 h GL (150 ± 5 μmol/m^2/s) was conducted with five levels of blue light as follows: i) 150 ± 5 μmol/m^2/s from HPS lamps only, ii) 125 μmol/m^2/s from HPS lamps and 25 μmol/m^2/s from blue LEDs (as mentioned above), iii) 125 ± 5 μmol/m^2/s from HPS lamps and 150 ± 5 μmol/m^2/s from blue LEDs for 160 min provided at start of the daytime, iv) as iii) but with blue LEDs on during mid-day, v) as iii) but with blue LEDs on during the end of the daytime. All treatments received the same daily light integral of 8.64 mol/m^2/day. UV irradiance of 7.8 ± 0.2 μmol/m^2/s was provided on a daily basis at the onset of darkness in all growth chambers.

2.9. Effect of End-of-day Blue Irradiance Applied Before or After UV Treatment

This experiment was conducted to reveal the effect on powdery mildew if blue light was applied either before or after UV treatment. Daily blue photon integral provided with LEDs was kept equal to the optimized level (1.44 mol/m^2/day) in the above experiment. To achieve this, 2 h and 40 min duration was selected. This ensured a 16-h daily light cycle and an irradiance of 150 μmol/m^2/s for all treatments (equal daylength, equal irradiance and equal DLI). A two-factor (end-of-day GL spectrum and time of light application relative to UV treatment) factorial experiment with two levels was set up with 16 h GL at an irradiance of 150 μmol/m^2/s supplied with HPS lamps for 13 h and 20 min. The remaining 2 h and 40 min of GL was provided by either HPS lamps or blue LEDs, either before or after UV treatment of 7.8 ± 0.2 μmol/m^2/s. All treatments had the same daily light integral of 8.64 mol/m^2/day.

2.10. Data Collection

In experiments with severity studies, the percentage of leaf area covered with powdery mildew was visually rated on the first true leaves of inoculated cucumber plants 12 days after inoculation. In experiments with growth studies, the following five growth parameters were recorded 12 days after start of each experiment on healthy plants: i) Relative chlorophyll content measured with a Hansatech Model CL-01 chlorophyll content meter (Hansatech Instruments, Pentney, Norfolk, England) of the third unfolded leaf of each plant (two measurements per leaf, one for each side of the mid rib), ii) plant height (distance from the node of the cotyledons to the top fully unfolded true leaf with lamina length ≥ 4 cm), iii) number of leaves per plant (all unfolded true leaves with lamina length ≥ 4 cm), iv) leaf area (measured with an LI-3100 area meter; Li-Cor Inc. Lincoln, NE, USA) per plant, and iv) dry weight (dried at 70 °C for 10 days) of leaves and other above ground plant parts (hereafter named shoot dry weight).

2.11. Data Analysis

The general linear model was used for analysis of variance of mildew severity and plant biometric data (Minitab Version 17.0, Minitab Corp., State College, PA, USA). Treatment means were separated using Tukey's pairwise comparison at $P = 0.05$. In addition, trend analysis was performed for continuous variables to examine the trend. Figures were drawn using SigmaPlot 10 (Systat Software, Inc., Chicago, IL, USA). Prior to analysis, data were checked for homogeneity of variances.

3. Results

3.1. Level of Irradiance and Day Length

Irradiance, day length and their interaction all significantly affected the efficacy of UV in controlling powdery mildew ($P < 0.0001$). Treatment combinations of 75 or 150 μmol/m^2/s irradiance for 8 h resulted in < 0.06% disease severity, while the same irradiance levels for 16 h resulted in severities of 3.8% and 6.6%, respectively (Fig. 1A).

Irradiance ($P < 0.0001$), day length ($P < 0.0001$) and irradiance × day length interactions ($P = 0.007$, Fig. 1B) all significantly influenced the relative chlorophyll content. There were similar trends for leaf area ($P < 0.0001$) and shoot dry weight ($P < 0.0001$), for irradiance level or day length (data not shown) and the treatment combinations (Fig. 1C and D).

A polynomial regression showed that the efficacy of UV decreased significantly with increasing day length when similar daily light integral was provided ($R^2 = 0.87$, $P < 0.0001$) (Fig. 2A).

Polynomial regressions further showed that relative chlorophyll content ($R^2 = 0.7$, $P < 0.001$), total leaf area ($R^2 = 0.6$, $P < 0.001$) and shoot dry weight ($R^2 = 0.57$, $P < 0.001$) increased with increasing day lengths from 8 to 16 h and then declined at 20 h (Fig. 2B to 2D).

3.2. End-of-day Growth Light Spectrum Applied Before or After UV Treatment

The spectrum of the end-of-day light ($P = 0.03$) and time of application relative to UV treatment ($P < 0.0001$), and their interaction ($P < 0.0001$) all significantly influenced the efficacy of UV against powdery mildew. Disease severity was highest with treatment combinations of end of day HPS light applied after UV treatment (70.9%) and lowest with treatment combinations of end-of-day red light applied after UV treatment (2%) (Fig. 3A).

Independent of light spectrum, applying HPS or red light at the end of the day before UV treatments slightly but significantly reduced the relative chlorophyll content compared with application after UV treatments ($P = 0.027$, Fig. 3B). Applying UV after HPS gave a slight but significant reduction in leaf area ($P < 0.01$, Fig. 3C) and shoot dry weight ($P = 0.004$, Fig. 3D) compared to the other treatments.

3.3. UV Mediated Phytotoxicity in the Absence of Additional Blue Light

In all the above-mentioned experiments where HPS lamps and additional red light were used as the main sources of growth light, some curling of newly developing young leaves was noticed in treatments with UV (data not shown).

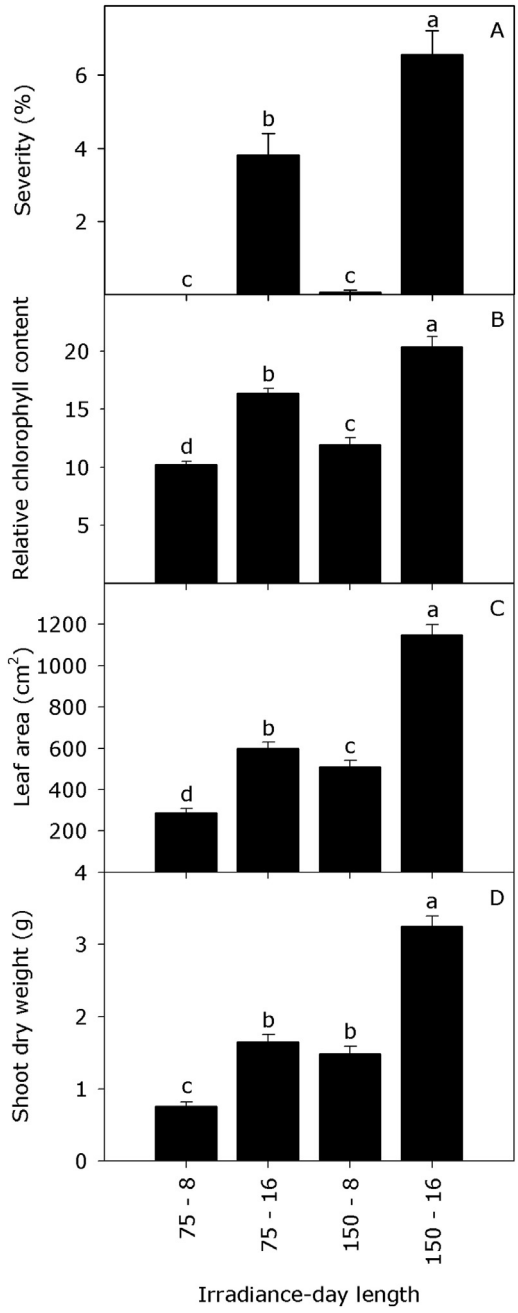

Fig. 1. Severity of powdery mildew (A), relative chlorophyll content (B), leaf area (C), and shoot dry weight (D) of cucumber plants treated daily with nighttime UV; treatments were either 75 or 150 µmol/m^2/s of irradiance from HPS lamps for either 8 or 16 h day length. Experiments were conducted twice in succession with inoculated plants for severity studies (A), and twice in succession with non-inoculated plants for plant growth studies (B to D), and assessed 12 days after start of the experiment. Values are mean ± standard error of 16 plants. Different letters indicate significant differences at P = 0.05.

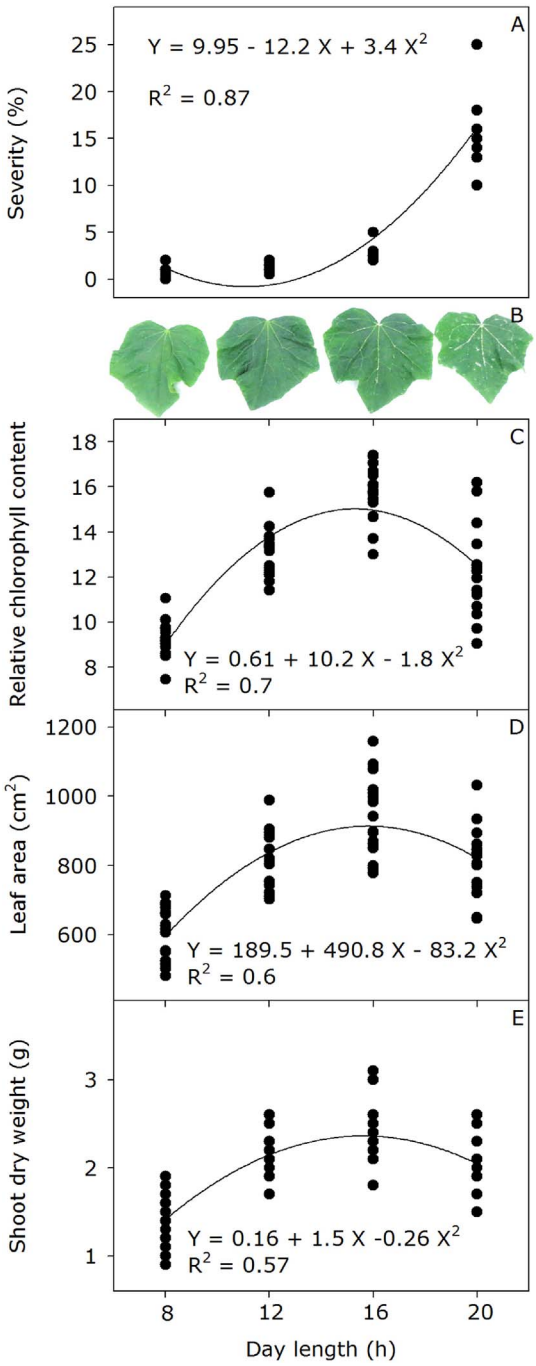

Fig. 2. Effect of day length (8, 12, 16, or 20 h) at a constant daily light integral of 4.32 mol/m^2/day on efficacy of nighttime UV treatment against powdery mildew (A), representatively diseased leaves (B), relative chlorophyll content (C), leaf area (D), and shoot dry weight (E) of cucumber plants treated daily with nighttime UV. Experiments were conducted twice in succession with inoculated plants for severity studies (A), and twice in succession with non-inoculated plants for plant growth studies (C to E), and assessed 12 days after start of the experiment. Values are mean ± standard error of 16 plants.

3.4. Blue Light Irradiance Enrichment

Daytime blue irradiance level had a significant effect on the efficacy of UV. The severity of powdery mildew was significantly lower with daytime blue irradiances of either zero or 25 µmol/m^2/s compared to 50 or 75 µmol/m^2/s ($P < 0.0001$, Fig. 4A), and a polynomial regression of blue light level vs. severity revealed an R^2 of 0.50 ($P < 0.0001$). Plant height, leaf area and shoot dry weight were all negatively affected by an increasing proportion of blue light, and regressions of blue light vs. severity yielded R^2 from 0.58 to 0.76 ($P < 0.0001$) (Fig. 4B to D).

3.5. Early, Mid or End-of-day Blue Light Enrichment

The effect of nighttime UV on disease severity was not affected by the time of the day when blue light was applied (data not shown). However, plant height ($P < 0.0001$), relative chlorophyll content ($P < 0.0001$), leaf area ($P < 0.0001$), and shoot dry weight ($P < 0.0001$) were all significantly affected by the time of day blue light was applied (Fig. 5). Tendencies were noted: early or late

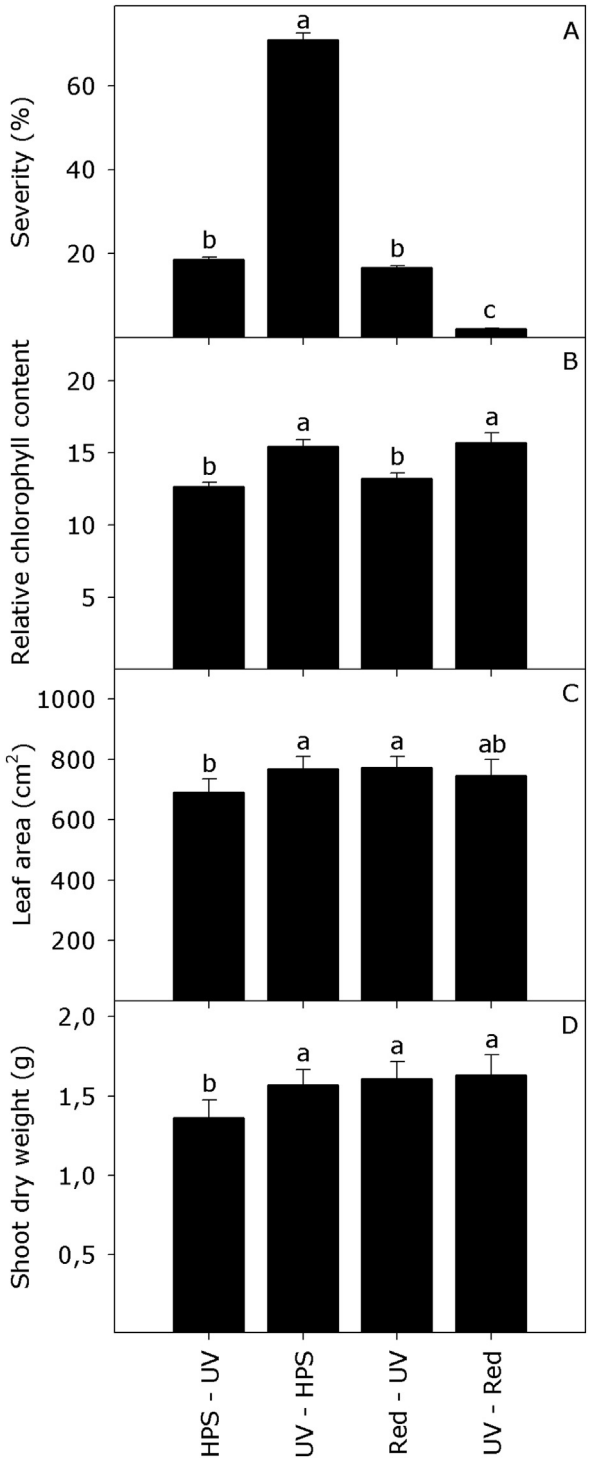

Fig. 3. Severity of powdery mildew (A), relative chlorophyll content (B), leaf area (C), and shoot dry weight (D) of cucumber plants grown with end-of-day growth light (last 4 h of 20 h day lengths) provided by either high pressure sodium lamps or red light emitting diodes, applied either before or after UV treatments. Other details are as explained in Fig. 1.

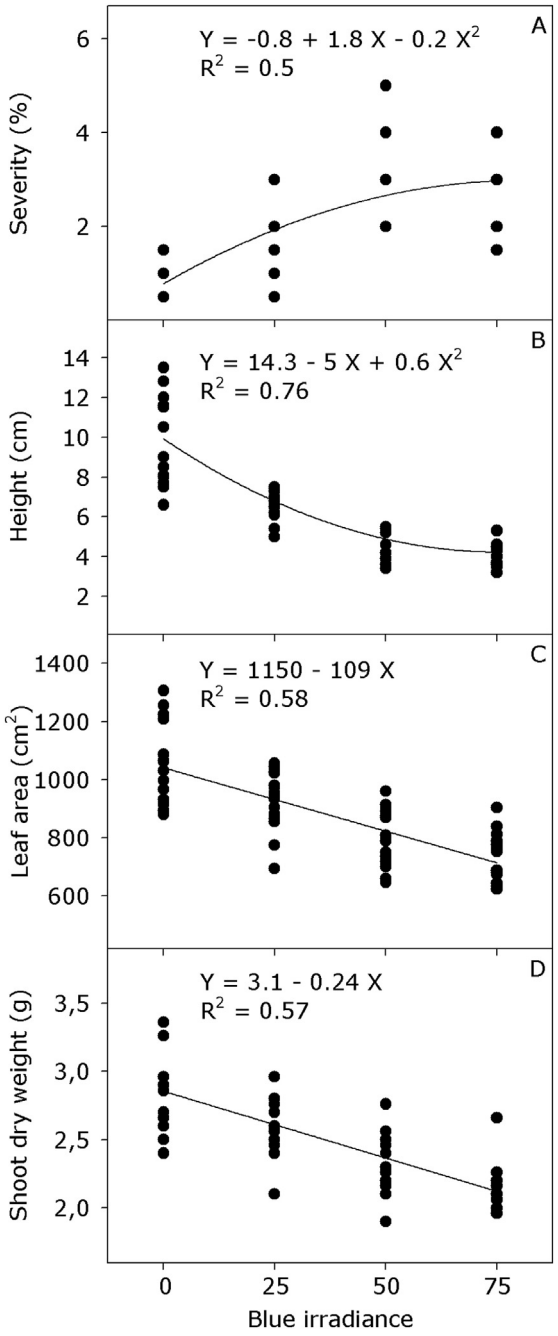

Fig. 4. Relationship between the amount of blue irradiance enrichment (0, 25, 50, or 75 μmol/m^2/s) provided as part of the growth light (light integral kept constant at 8.64 mol/m^2/day) and severity of powdery mildew (A), plant height (B), leaf area (C), and shoot dry weight (D) of cucumber plants treated daily with nighttime UV. Other details are as explained in Fig. 2.

applications of blue light reduced plant height, leaf area or dry weight compared to the other treatments, and all blue light treatments reduced plant height compared to non-application of blue light.

3.6. End-of-day Blue Irradiance Applied Before or After UV Treatment

The spectrum of light at the end of the day ($P = 0.013$) and its application time relative to UV ($P < 0.0001$), and their interaction ($P < 0.0001$) all significantly influenced the efficiency of UV against powdery mildew. Disease severity was greatest with treatment combinations of end-of-day blue light applied after UV treatment (66.3%) and lowest with treatment combinations of end-of-day HPS or blue light applied before UV treatment (≤ 2.8%) (Fig. 6).

4. Discussion

Specific effects of nighttime UV and application of red and blue light after UV treatments on suppression of cucumber powdery mildew were shown in our previous studies [9,19]. The present study sheds light on

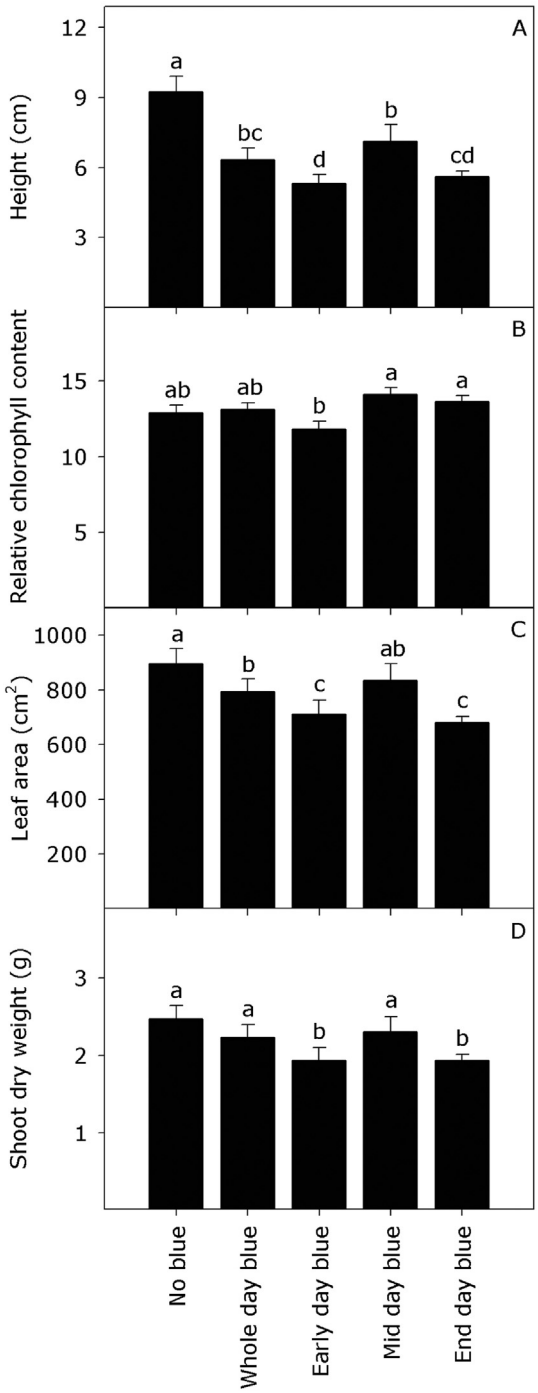

Fig. 5. Effect of blue irradiance enrichment at different times of the day on plant height (A), relative chlorophyll content (B), leaf area (C), and shoot dry weight of cucumber plants treated daily with nighttime UV. Other details are as explained in Fig. 1.

how day length, level of irradiance, the combination of both (daily light integral) and spectral quality of light (blue or red) affect the efficacy of nighttime UV in controlling powdery mildew and plant growth. These experiments clearly indicated that an increased day length (≥ 16 h) and irradiance level reduced the efficacy of nighttime treatments of UV against cucumber powdery mildew, if UV was kept at the same level. A trend was noted in that growth parameters peaked at 16 h compared to 12 or 20 h day length. Previous studies showed that dry matter accumulation and leaf area development were similar with daylengths of 12, 18 and 24 h, and lowest with 8 h with the same daily light integral [20]. This discrepancy may be due to plant age, light intensity and other

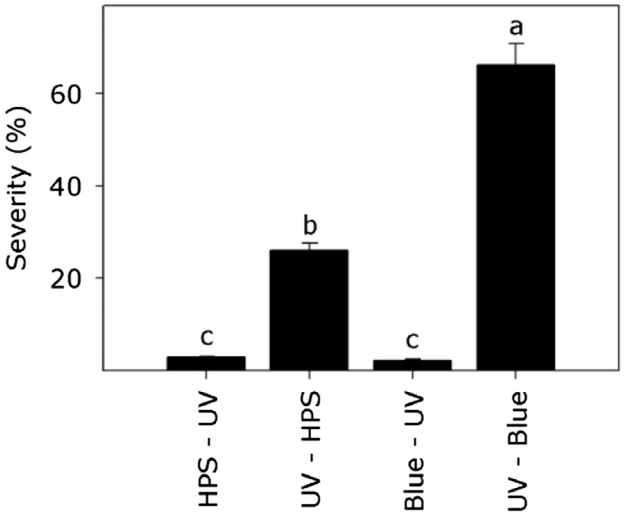

Fig. 6. Powdery mildew severity of cucumber plants grown with end-of-day growth light (last 2 h 40 min of 16 h day lengths) provided with either high pressure sodium lamps or blue light emitting diodes, applied either before or after nighttime UV treatment. Other details are as explained in Fig. 1.

conditions, and it was reported, for example, that the response of cucumber plants to photoperiod depends on plant age and light intensity in its pre-reproductive period [21].

If red light was used to increase day length from 16 to 20 h after UV treatments, there was a clear reduction in powdery mildew compared to UV treatments applied following 4 h of either HPS or red light as end-of-day treatments. However, there were no reductions in growth parameters if red light was applied after UV treatments, compared to HPS applied after UV. This means that red light application after UV treatment not only resulted in better control of powdery mildew under long day conditions (20 h), but it also provided sufficient light via extended day length to keep plant growth at a level provided by a broader spectrum light source (HPS). A recent study reported that the efficacy of nighttime UV-C against powdery mildew in strawberry plants is dependent on the dark period after UV application [12]. Our studies showed that the efficacy of nighttime UV did not depend on the length of the dark period, but rather on the spectral quality of light applied after UV treatment. This confirms our previous results that application of red light after brief UV treatment can improve the UV efficiency against powdery mildew [9]. However, the impact of day length and daily light integral on the UV efficacy by adding red light was not examined in that study.

The highest proportion of blue light applied during daytime significantly reduced the efficacy of nighttime UV treatments against powdery mildew. On the other hand, some leaf curling was observed in newly developed leaves, when plants were treated with UV and grown with day light supplied only by HPS or by HPS with day extension red light (blue light deficient growth light, data not shown). This indicated the need for a minimum of blue photons in plant growth light. At the same time, with an increasing amount of blue light, plants became more compact, with reduced height, leaf area and dry matter. Photosynthesis and photomorphogenesis are affected by day length, irradiance level, a combination of both and the spectral quality. The blue part of the light spectrum has been associated with leaf characteristics, and blue light is required for normal photosynthetic functioning of cucumber leaves. The photosynthetic capacity was twice as high for leaves grown at 7% blue light compared with no blue light, and continued to increase up to 50% blue light [22]. Increasing blue light proportion reduced stem length (more compact) of lettuce and radish [23], as was confirmed with cucumber plants in the present experiments.

If blue light of a similar dose was applied in the middle of the day, plant growth was better than if applied early or late in the day, but

there was no impact on nighttime UV treatments on powdery mildew. Applying blue light after UV treatments seemed to nullify the effect of UV on powdery mildew, confirming our previous findings [9]. A recent study shows that the application of wavelengths ranges from > 310 nm to < 525 nm following UV treatment can significantly recover the UV mediated damage in powdery mildews (Suthaparan et al., unpublished data).

For practical implications, it is clear that the higher light levels, especially with higher blue irradiances in day light, higher levels of UV may be needed during nighttime to be effective against powdery mildew, and thus nighttime UV levels may need to be adjusted according to daytime growth light level and its spectrum. To achieve the optimal effects in suppression of powdery mildew and promoting plant growth, nighttime UV treatments and growth light spectral composition should be adjusted according to time of year, latitude, cloud cover, etc. In greenhouses and plastic tunnels, further adjustments may be necessary based on the light transmitting properties of the covering materials.

Light is a predominant environmental factor in controlling growth, development and stress responses of plants [24,25]. Plants harvest light as a source of energy via mass pigments and as an environmental cue via sensory pigments. The use of light or UV as tools in management of powdery mildews should not negatively affect plant growth and development.

Plant growth responses to the light environment are influenced by quantity (irradiance level and lighting period) and quality (spectral composition) of the light. Some aspects of plant responses to daily light integral (irradiance × lighting period) have previously been examined intensively, and daily light integrals required for optimal plant growth differ considerably among plant species [20,26]. However, generalizing results of these studies have shown that for similar daily light integrals, plants exposed to a low irradiance for an extended day length generally accumulate more dry matter than plants exposed to a high irradiance over a shorter day length. Growth abnormalities of some plants with continuous lighting, for example tomato plants [27,28], inhibition or prevention of flowering in short day plants, and increased production costs entailed by day extension lighting have limited the use of day lengths around 20 h in many cases.

This study showed that the day length may be extended beyond 16 h, if needed, without reducing the efficiency of nighttime UV against powdery mildew. Under such conditions, UV may be applied after 16 h of regular growth light and then day length can be extended with light sources emitting red wavelengths, which may further suppress powdery mildew [9,29].

UV has been shown to have deleterious effects on all living organisms by damaging DNA, proteins (structural and functional) and other essential molecules affecting plant growth [30–35]. Although UV has a strong potential in the management of powdery mildews, improper use of UV may easily cause phytotoxic effects. Plants have evolved two major strategies for UV radiation tolerance; avoidance and repair. Avoidance mechanisms include epidermal screening of UV radiation via accumulation of phenolic compounds, preferentially in the vacuoles in the epidermal cells. Repair mechanisms include DNA damage repair by nucleotide excision and photo-reactivation mediated repair of photoproducts [36].

Lack of protective pigments for UV screening, aside from those of the outer ascocarp wall of the fruiting bodies of powdery mildews, leave repair mechanisms as the single strategy for UV tolerance, making powdery mildew fungi more vulnerable to UV than their host plants. Specific wavelengths of the growth light, notably UV-A and blue light, enhance the powdery mildew pathogens' ability to withstand short wavelength UV exposure [9].

In our study, we found that when a certain level of blue photons was ensured in the growth light, the risk of UV induced phytotoxicity was reduced. Because of blue light mediated plant tolerance to UV [36,37], application of blue photons may enable activation of similar repair mechanisms in fungi as well. When blue photons were applied after UV treatment in this study, the effect of UV against powdery mildew was strongly reduced, clearly indicating that blue light mediated repair mechanisms in powdery mildew. Providing certain level of blue photons in growth light before UV treatments minimized the risk of UV mediated phytotoxicity while maintaining a high efficacy against powdery mildew.

Powdery mildews are caused by obligate biotrophic fungal pathogens, co-evolved with their host plants. The environmental conditions optimal for host plant growth and development are also optimal for growth and development of the powdery mildews. This leaves a narrow window for UV and light regulated disease management. The success of UV treatments in powdery mildew management clearly depends on optimal combinations of spectral quality, day length and irradiance level combined with applications of UV that minimize pathogen tolerance and maximize plant tolerance against UV. This study provides a basis for optimizing growth light and UV for control of powdery mildews.

Conflict of Interest

The authors declare that there is no conflict of interest.

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