Effect of Light on the Behavior of *Alternaria tagetica* In Vitro and In Vivo

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ABSTRACT

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Light was found to affect growth, sporulation, and zinniol production by *Alternaria tagetica*, as well as the number of lesions formed on marigold inoculated with the fungus. Fungus growth was inhibited by both continuous and alternating light. The fungus sporulated only on one of the three test media and only under alternating light. The patterns of zinniol production in the dark and in the light were not the same. Zinniol production in the light occurred only during the active growth of the fungus; the bulk of the toxin was produced in the dark after cessation of growth. In both the light and the dark, the quantity of zinniol in filtrates rapidly declined once zinniol production ceased. More lesions were produced on inoculated plants kept in the dark than on those kept in the light. Low illuminance also was more conducive to lesion development than high illuminance and more lesions developed on plants exposed to low illuminance for 48 hr prior to inoculation than on those exposed to high illuminance. The limitations of studies on the behavior of *Alternaria* spp. in vitro and in vivo in which the effect of light has been overlooked are discussed.

Although the effect of light on sporulation of *Alternaria* spp. is well documented (28), little information is available on how light affects other aspects of life cycles of *Alternaria* and their interactions with plants. Experiments designed to elucidate the effect of humidity on disease induction by *Alternaria* spp. have frequently been performed in the dark or under unregulated and/or unmeasured low light conditions (1,5,17,18). Similarly, light often has not been considered and/or strictly monitored in studies dealing with toxin production by *Alternaria* spp. Consequently, much of our current knowledge of plant pathogenic *Alternaria* spp. is based on the results of experiments in which light was not regarded. The need for studies on the effects of light on disease development (7) and toxin production (24) has been emphasized.

We have studied the effect of light on susceptibility of marigold (*Tagetes erecta*) to *A. tagetica*. We have also investigated the influence of light on the growth, sporulation, and spore germination of the fungus, and in vitro production of zinniol, a phytotoxin of possible importance in diseases caused by a number of *Alternaria* spp. (3,8,9,31).

MATERIALS AND METHODS

Cultures. Isolate 23, a pathogenic isolate of *A. tagetica* already known to produce zinniol (9), was used in these studies. The fungus was maintained in the dark at 27 C on a modified V-8 juice medium (5/2) containing 5% V-8 vegetable juice (v/v) and 2% agar (w/v). When sporulating cultures were required, subcultures were placed under fluorescent lights (5,200 lux) on a 12-hr diurnal cycle at 27 C. Illuminance was measured with a model 756 Weston sunlight illumination meter (Weston Instruments, Inc., Newark, NJ).

Effect of light on fungus growth. The fungus was grown under various light regimes on the following three solid media: potato-dextrose agar (PDA) (Difco Laboratories, Detroit, MI), the casamino acids-enriched medium (TOX) used for zinniol production (8,9,31) solidified with 2% agar, and the 5/2 medium described above. Fungal disks, 4 mm in diameter, taken from the edge of advancing fungal colonies on medium 5/2, were placed in the center of 9-cm-diameter plastic petri plates containing various media. Cultures were incubated in either the light or the dark by placing seeded culture plates either inside 14-cm-diameter clear plastic petri plates or inside identical 14-cm-diameter plates painted on the outer surfaces with a flat black enamel paint. The 14-cm-diameter plates were then placed under appropriate illumination. This method permitted free exchange of gases in both light and dark treatments and thus was superior to wrapping plates with various materials (1,14,22).

Culture plates were maintained at 27–29 C under either 21,000 or 8,000 lux illuminance either continuously or on a 12-hr diurnal cycle. General Electric (General Electric, Cleveland, OH) F48T12 and Sylvania (Sylvania Electric Products, Inc., Danvers, MA) F20T12 cool-white fluorescent lights provided the 21,000 and 8,000 lux illuminances, respectively. Radial growth of the fungus was measured at the widest colony diameter daily for 7 days. The values were used to generate a regression line by the least squares method. To prevent the initial lag period from skewing the data, the zero-time points were not included in the calculations. The slopes of the regression lines were used as estimates of the fungus growth rates. Differences among rates within experiments were determined by analysis of variance. Values with statistically significant differences were separated by the least significant difference method (LSD).

The following experiment was conducted to determine if the observed responses of *A. tagetica* to light could be duplicated by changes caused in the media by exposure to light prior to seeding, as reported for other fungi (32). Nine-cm-diameter culture plates containing 5/2 medium, on which the greatest light responses occurred, were exposed to light or to darkness by placing them in either clear or blackened 14-cm plates under 8,000 lux continuous illuminance at 27–29 C for 72 hr. Light-treated and dark-treated culture plates were then seeded with the fungus as described earlier. Each group was split and incubated at 27–29 C, half in the light (8,000 lux) and half in the dark, as previously described. Fungus growth rate was measured and values were analyzed as described above.

Effect of light on germination. Spore suspensions (10 μl) were applied to microscope slides placed on moistened filter papers inside 9-cm-diameter plastic petri dishes. Spores were subjected to either continuous light (23,000 lux) or continuous dark at 27–29 C by placing petri dishes inside either clear or blackened 14-cm-diameter plastic plates as described earlier. The number of germ tubes per spore and the maximum germ tube length per spore were determined with a compound microscope after 4 hr.

Effect of light on lesion production. Marigold plants (*Tagetes erecta* L. 'Orangeade') were grown in sand in 200-ml (7-oz)

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Styrofoam cups under fluorescent lights with 8,000 lux illuminance (photosynthetically active radiation [PAR] at 400–700 nm = 96 $\mu E \cdot s^{-1} \cdot m^{-2}$) on a 12-hr diurnal cycle at 27–33 C. Cups were watered daily with distilled water and fertilized once every 10 days with 10 ml of a 4,000-ppm solution of Miracle-Gro (Stern's Nurseries, Inc., Geneva, NY). Five 6-wk-old plants at the 8- to 10-leaf stage were trimmed of senescent and damaged leaves and sprayed to runoff with spore suspensions containing 600–1,000 spores per milliliter and were immediately placed in humidity chambers. Similar individuals were paired and pairs were split between treatments. Inocula were prepared by flooding sporulating plates (prepared as described above) with sterile distilled water and by passing the suspensions through two layers of cheesecloth.

Humidity chambers were constructed from disposable plastic 16-oz beverage bottles that permitted illumination of plants during infection. These bottles, with the bottoms removed, fit over the individual marigold plants used in this experiment. For dark treatments, plastic chambers were covered with two layers of aluminum foil. Glass thin-layer chromatography tanks (30 × 27 × 10 cm) with clear glass lids containing 100 ml of distilled water also were used as humidity chambers to ensure that the observed responses were not due to factors unique to the plastic chambers. Identical chambers covered with aluminum foil were used for dark treatments. All humidity chambers containing plants were placed in growth chambers (Environmental Growth Chambers, Chagrin Falls, OH) under fluorescent lamps (General Electric cool-white, F48T12) in various illuminances for various periods as described below. Plants were removed from the humidity chambers after different periods and maintained at 27–29 C under 21,000 lux (PAR = 252 $\mu E \cdot s^{-1} \cdot m^{-2}$) illuminance on a 12-hr diurnal cycle. Lesions on the six oldest leaves of each plant were counted by illuminating the leaves with back lighting 48 hr after inoculation.

To compare the effect of light and dark on lesion production, inoculated plants were placed inside either plastic or glass chambers and exposed to 21,000 lux light for 12, 20, 24, and 48 hr following the above procedure.

Experiments on the effect of high versus low light intensity on lesion production were conducted within one environmental chamber, a portion of which was shaded with fiberglass screening to reduce the illuminance from 23,000 lux to 2,000 lux (PAR = 24 $\mu E \cdot s^{-1} \cdot m^{-2}$). Plants were subjected to either high (23,000 lux) or low (2,000 lux) illuminance inside plastic humidity chambers (as described above) for 20 hr and were examined for lesion production 48 hr after inoculation (also described above). Experiments were performed twice, each with six replications.

The effect of varying light intensity prior to infection on host susceptibility was tested by exposing plants for 48 hr prior to inoculation to either 23,000 lux or 2,000 lux illuminance on 12-hr diurnal cycles. Plants were then inoculated (as above) and placed in the same unilluminated humidity chamber for 16 hr after which they were removed and kept under 23,000 lux light for an additional 32 hr and then examined for lesion production. The experiment was performed twice with six replications.

Effect of light on zinniol production. Erlenmeyer flasks (125 ml) containing 25 ml of a casamino acids-enriched medium, used previously for zinniol production (8,9,31), were seeded with 2-cm-diameter disks from 2-wk-old sporulating cultures of *A. tagetica* on 5/2 medium. For dark treatment, flasks were wrapped with two layers of aluminum foil. Wrapped and unwrapped flasks were arranged in a complete block design and incubated without shaking under 23,000 lux continuous light at 27–29 C.

After 10, 20, and 30 days, culture filtrates were pooled in groups of five and passed through Whatman #1 filter paper. The fungus colonies were dried on preweighed filter papers at 106 C for 48 hr and weighed to the nearest 10 mg. The filtrate was extracted and analyzed for zinniol content as described earlier (9). Filtrates were adjusted to pH 10 and extracted three times with 50 ml of chloroform. The chloroform fraction was washed twice with 50 ml of 0.1 N NaOH, pH 13, and three times with 50 ml of 0.1 M KH_2PO_4, pH 4.5, and evaporated under reduced pressure. Zinniol was silylated and quantified by gas-liquid chromatography as previously described (9). Analyses were performed with a Varian series 1700 dual flame ionization gas chromatograph (Varian Associates, Inc., Palo Alto, CA) with a 100-cm long, 2.1-mm i.d. stainless steel column of 3.0% SE-52 on Gas Chrom Q. The column, detector, and injector were kept at 190, 220, and 250 C, respectively, and the carrier gas (N_2) flow rate was 30 ml/min. A standard curve (micrograms of zinniol per centimeter of peak height) was constructed with silylated synthetic zinniol (synthetic zinniol was supplied by J. A. Martin, Roche Products Ltd., Welwyn Garden City, England). Each of the two experiments consisted of six treatments replicated twice. Each replicate consisted of one analysis of five pooled filtrates.

To ascertain possible internal temperature differences, the temperatures within dark-treated and light-treated humidity chambers, petri plates, and Erlenmeyer flasks were measured with a TH-65 thermocouple thermometer (Wescor, Inc., Logan, UT). Constantan-copper thermocouple probes were placed in the appropriate containers either within the liquid medium, touching the solid medium, or in the plant canopy at 75 and 125 mm above the soil line. The containers were then placed in an environmental chamber under 23,000 lux illuminance at 27 C and the temperatures were recorded at 20- to 30-hr intervals for 7 days.

TABLE 1. Growth rates of *Alternaria tagetica* on solid media under various light regimes at 27–29 C

Experiment[w] number	Illuminance (lux)	Medium[x]	Diurnal light[y] period (hr)	Rate[z] (μm/hr)
1	23,000	PDA	24	293 ± 14 a
			0	373 ± 17 b
		5/2	24	292 ± 16 a
			0	369 ± 42 b
		TOX	24	177 ± 4 c
			0	212 ± 3 c
2	23,000	PDA	12	346 ± 2 a
			0	402 ± 3 b
		5/2	12	343 ± 9 a
			0	437 ± 9 c
		TOX	12	261 ± 6 d
			0	289 ± 7 e
3	8,500	5/2	24	202 ± 40 a
			0	416 ± 10 b
		TOX	24	154 ± 3 c
			0	214 ± 3 a
4	8,500	PDA	24	239 ± 61 a
			0	473 ± 3 b
		TOX	24	157 ± 1 c
			0	212 ± 3 d
5	8,500	5/2	12	447 ± 4 a
			0	467 ± 3 b
		TOX	12	211 ± 5 c
			0	260 ± 3 d
6	8,500	PDA	12	410 ± 14 a
			0	430 ± 6 b
		TOX	12	215 ± 2 c
			0	243 ± 4 d

[w] Treatments were replicated three times. Each replicate consisted of one culture; radial growth was measured seven times at 20–30-hr intervals. All experiments were repeated twice with similar results; data from one repetition is presented here.

[x] PDA = potato-dextrose agar; 5/2 = 5% V-8 vegetable juice and 2% agar; and TOX = the casamino acids enriched medium used for zinniol production plus 2% agar.

[y] The fungus was exposed to light at the indicated illuminance for 0, 12, or 24 hr daily.

[z] Growth rate ± standard deviation. Growth rate was determined by calculating the slope of the best fit line for the seven measured points with the least squares method. The initial point was not included to avoid slope skewing by the lag period. Statistical comparisons were made only within experiments. Values not followed by the same letter are significantly different ($P = 0.01$ except experiment 6 for which $P = 0.05$) by the LSD method.

RESULTS

Effect of light on the growth of the fungus. The growth of the fungus on the three tested media was inhibited by both continuous and alternating light (Table 1). Although the growth rates varied among experiments, the differences between the growth rates of light-grown and dark-grown cultures were in most cases statistically significant ($P = 0.01$ by the LSD method).

Exposure of media for 72 hr to either continuous 8,000 lux illuminance or dark prior to seeding did not result in statistically significant differences ($P = 0.2$ by the LSD method) in the rate of growth. This held for growth both in the dark and under 8,000 lux illuminance.

Effect of light on spore production and germination. Spores were not produced on TOX or PDA media. No spores were produced under continuous light or continuous dark on any medium. Abundant spores were produced on 5/2 medium under light (8,000 lux and 23,000 lux) on a 12-hr diurnal cycle at 27–29 C. The number of spores produced per plate was $1.6 \times 10^5 \pm 7.9 \times 10^3$ after 5 days under 23,000 lux. Light condition affected neither the number of germ tubes per spore nor the maximum germ tube length per spore.

Effect of light on lesion production. More lesions were produced on inoculated plants kept in the dark than on those kept in the light in both glass and plastic humidity chambers (Table 2). More lesions also developed on inoculated plants kept under low illuminance (2,000 lux) than on those kept under high illuminance (23,000 lux)(Table 3).

TABLE 2. Effect of light (23,000 lux) during high-humidity periods on the number of lesions produced by *Alternaria tagetica* on 30- to 40-day-old marigold plants

Experiment[a] number	Humidity[b] period	Number of lesions[c]	
		Light	Dark
1	12	0	2 ± 1
2	12	0	14 ± 11
3	20	0	11 ± 5
4	20	2 ± 2	58 ± 21
5	24	2 ± 2	25 ± 14
6	24	0	11 ± 7
7	48	6 ± 4	51 ± 22
8	48	34 ± 11	86 ± 45

[a] Light and dark treatments were replicated four times each in experiments 1 and 2 and 5 to 8, and three times in experiments 3 and 4.
[b] Duration of period immediately following inoculations during which plants were maintained in humidity chambers.
[c] Mean number of lesions on the six oldest leaves per plant. The differences between light and dark treatments were significant at $P = 0.05$ by analysis of variance in experiments 1 to 7 and at $P = 0.07$ in experiment 8.

The light intensity to which plants were exposed prior to inoculation also affected the number of lesions. More lesions developed on plants grown under low illuminance (2,000 lux on a 12-hr diurnal cycle) for 48 hr prior to inoculation than on plants grown under high illuminance (23,000 lux on a 12-hr diurnal cycle) (Table 3).

Effect of light on zinniol production. Zinniol production was greatly affected by light. The zinniol production pattern in the light and in the dark differed and probably followed the curves in Fig. 1 which were extrapolated from the data in Table 4. Zinniol production in the light coincided with the active growth of the fungus and stopped as the fungal growth ceased. In the dark, only small amounts of zinniol were produced during active fungus growth while large quantities were rapidly produced for a short period after cessation of growth. Zinniol production peaked after different growth periods in the two experiments (Table 4) apparently due to a more rapid growth rate in the second experiment. In both the light and the dark, the quantity of zinniol in filtrates rapidly declined once zinniol production ceased.

There were no detectable differences between the temperatures of the solid culture medium in the light and in the dark; the standard deviation was 0.45 C. The temperatures of the liquid in the Erlenmeyer flasks and of the air inside humidity chambers were 0.29 ± 0.18 C and 0.84 ± 0.29 C higher in the light than in the dark,

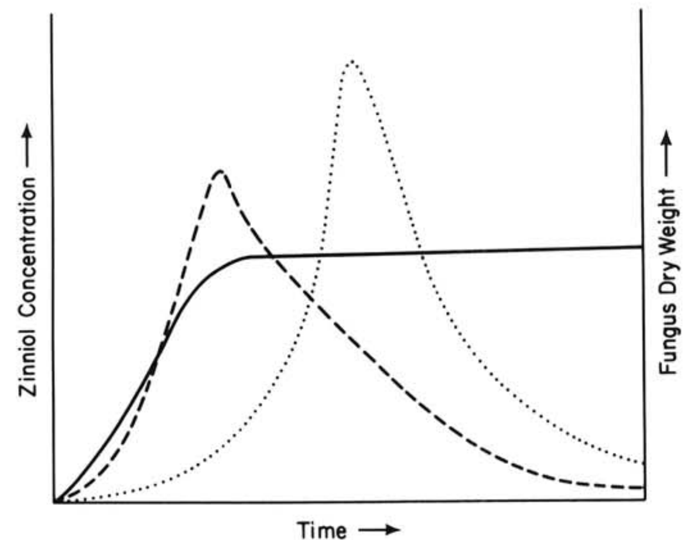

Fig. 1. Zinniol production by *Alternaria tagetica* under continuous light (dashed line) and continuous dark (dotted line) as a function of growth (solid line) extrapolated from data in Table 4.

TABLE 3. Number of lesions produced on 35-day-old marigold plants exposed to different light intensities prior to and after inoculation with *Alternaria tagetica*

Experiment[v] number	Illuminance (lux)[w] prior to inoculation	Humidity[x] period (hr)	Illuminance (lux)[y] during humidity period	Number[z] of lesions
1	8,000	20	23,000	9.5 ± 5.8 a
	8,000	20	2,000	50.7 ± 23.5 b
2	8,000	20	23,000	1.6 ± 1.6 a
	8,000	20	2,000	26.3 ± 16.0 b
3	23,000	16	0	12.7 ± 7.4 †
	2,000	16	0	23.3 ± 10.0 †
4	23,000	16	0	17.5 ± 4.4 a
	2,000	16	0	45.2 ± 14.7 b

[v] Experiments consisted of two treatments, each with six replicates.
[w] Light intensity on a 12-hr diurnal cycle under which plants were grown for 48 hr prior to inoculation.
[x] Duration of period immediately following inoculations during which plants were maintained in humidity chambers.
[y] Continuous illuminance.
[z] Mean number of lesions on the six oldest leaves per plant ± the standard deviation. Statistical comparisons were made only within experiments. Numbers not followed by the same letter are significantly different by analysis of variance, ($P = 0.01$). † = significantly different by analysis of variance ($P = 0.06$).

respectively. These differences were significant at the 5% level. Readings within individual humidity chambers varied 0.40 ± 0.20 C. The temperature differences became stable within two hours and did not increase thereafter.

DISCUSSION

Sporulation of many *Alternaria* spp. is influenced by light intensity and duration (28). Results of this study have shown that *A. tagetica* is not an exception and that a diurnal light cycle is required for sporulation. In addition, the growth rate of *A. tagetica* was decreased by exposure to light on all media and under all light regimes tested. The growth rates of *A. brassicicola* (29) and *A. brassicae* (14,22) are also decreased by light while that of *A. helianthi* is increased (1). Griffin (13) has pointed out that light modulation of in vitro fungus growth must be cautiously interpreted because preexposure of media to light can result in growth inhibition (32). In our study, no differences were found between the growth rates of *A. tagetica* on media preexposed to 8,000 lux for 3 days and on media preexposed to dark.

We found that light also influenced production of zinniol, a nonselective phytotoxin which may play a role in a number of diseases caused by *Alternaria* including that caused by *A. tagetica* on marigold (3,8,9,31). Results summarized in Table 4 show that zinniol is predominantly produced during the active growth phase of the fungus in the light and during the stationary growth phase in the dark. The relationships between growth phase and zinniol production in the light and in the dark are more clearly seen in the extrapolated curves in Fig. 1. The patterns of zinniol production by *A. tagetica* in the light and in the dark differ greatly from that reported for *A. dauci* (3). The quantity of zinniol present in filtrates of *A. dauci* increased with increases in fungus dry weight and remained unchanged once zinniol production ceased. In contrast, the quantity of zinniol in culture filtrates of *A. tagetica* rapidly declined once zinniol production stopped. *A. tagetica*, but not *A. dauci*, apparently is able to alter zinniol extracellularly.

Light-mediated inhibition of toxin production by *A. alternata* has been reported (15,23,25). The light-induced alterations in the zinniol production pattern of *A. tagetica* exemplify difficulties of evaluating toxin production data in studies where toxin levels are measured at one time (9,15,23) or during one growth phase (9,15,23,25) (exponential or stationary) of the fungus. A reevaluation of the earlier studies (9,15,23,25) may be of value.

Results presented here show that the number of lesions produced on marigold plants inoculated with *A. tagetica* is decreased by increased light intensity in the humidity chamber. Similarly, dark exposure increases lesion diameter on bean leaves (*Phaseolus vulgaris* 'Irene' and 'Corene') inoculated with *A. zinniae* (30). In that study, however, light intensity was neither measured nor carefully regulated and the effect of light on the number of lesions produced was not determined.

The observation that light modulates disease production by *A. tagetica* and a number of other pathogens (2,4,11,12,26,30) has profound implications on the interpretation of the results of studies on various aspects of diseases caused by *Alternaria*. For example, light-dependent resistance mechanisms may be overlooked in laboratory screenings conducted under inappropriate light conditions (17,20,21). Such studies may lead to an unrealistic assessment of relative resistance of cultivars and/or species to certain *Alternaria* spp. Moreover, incidence and severity of diseases caused by *Alternaria* and some other pathogens in the field may be expected to be influenced by factors such as canopy position, cloud cover, and shading which modulate the quality and the quantity of light that plant parts receive. Shading has been implicated in at least one disease caused by *Alternaria* (2) and canopy position may explain in part the higher susceptibility of older leaves to *Alternaria* spp. (19,27).

Light intensity in the field varies greatly depending on weather, altitude, latitude, and time of the year and the day. Thus, although the lighting used in these experiments was sufficient to demonstrate light modulation of lesion development, it is difficult to compare laboratory light intensities, which are relatively constant, with those in the field. The highest light intensity (23,000 lux) used in this study is far less than the maximum daily light intensity of clear days in the field.

In studies designed to assess the role of humidity on disease development, light condition has generally not been taken into account as an important parameter. Inoculated plants are often placed in humidity chambers under either no light or low light conditions, for periods longer than 12 hr (1,5,6,16,17). The observed influence of light on disease development underscores the need for considering the effect of light on disease development during exposure of plants to high humidity. Careful consideration of both light and humidity may help to separate the influences of these two variables on disease development.

The mechanism by which light intensity influences host susceptibility to *A. tagetica* is not known. Preliminary observations while using the tissue-clearing method of Diener (10) and staining with a fast green/clove oil mixture showed that *A. tagetica* penetrates marigold leaves predominantly by direct means. Therefore, a simple effect on stomata opening is inadequate to explain the light effect on the disease. The growth rate of the fungus in vitro is somewhat reduced in the presence of light. However, it is rather unlikely that the increased susceptibility of marigold to *A. tagetica* under low light intensity is conditioned solely by a concomitantly increased rate of colonization of the host by the fungus. The results indicate that the light response also is not due to inhibition of spore germination.

Zinniol production in vitro is modulated by both light and the growth phase of the fungus (Fig. 1). It is, therefore, tempting to ascribe a role for zinniol in the low light-high susceptibility equation. However, since zinniol production in vivo has not been demonstrated, the role(s) of this toxin in disease and in light-induced responses remains speculative.

Our demonstration that exposure of marigolds to low light intensity prior to inoculation leads to an increase in susceptibility suggests that the light-induced changes in susceptibility may be due to the effect of light on the host rather than on the pathogen. Changes in susceptibility to disease were observed in plants subjected to low light intensity for as little as 12 hr. Thus, alterations in susceptibility may indeed be a natural phenomenon because plants in the field are diurnally subjected to low light intensity for comparable periods.

It is unlikely that the minor temperature differences observed between light and dark treatments in liquid cultures and in humidity chambers contributed appreciably to the observed

TABLE 4. Effect of light on growth and zinniol production by *Alternaria tagetica* in a casamino-acids enriched liquid medium at 27–28 C

Experiment number[a]	Illuminance[b] (lux)	Growth period (days)	Growth (g)[c]	Zinniol (μg)[d]
1	0	10	2.5 ± 0.55	210 ± 142
	0	20	2.5 ± 0.02	9,856 ± 113
	0	30	2.6 ± 0.06	2,748 ± 573
	23,000	10	2.1 ± 0.16	1,827 ± 113
	23,000	20	2.5 ± 0.08	4,034 ± 956
	23,000	30	2.6 ± 0.13	418 ± 90
2	0	10	2.5 ± 0.17	2,179 ± 313
	0	20	2.6 ± 0.09	3,869 ± 1,047
	0	30	2.6 ± 0.08	402 ± 176
	23,000	10	2.4 ± 0.09	6,031 ± 81
	23,000	20	2.7 ± 0.14	784 ± 119
	23,000	30	2.7 ± 0.13	185 ± 6

[a] Each experiment consisted of six treatments replicated twice. Each replicate consisted of five filtrates (25 ml each) which were pooled and batch analyzed.

[b] Continuous illuminance.

[c] Dry weight ± standard deviation.

[d] Micrograms zinniol ± standard deviation. Quantities have been divided by 0.62 to compensate for the average percent recovery as previously described (9).

differences in lesion formation and zinniol production. Moreover, the increased susceptibility of plants subjected to low light intensity prior to inoculation compared to those subjected to higher light intensity in the same environmental chamber argues strongly against the involvement of temperature.

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