Effects of Environment on Infection of Florists' Carnation by Gibberella zeae

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ABSTRACT

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Experiments were done to determine the effects of temperature, light, and humidity on infection of carnation by *Gibberella zeae,* causal agent of Fusarium stub dieback. The incidence of infection was the same at 13 or 18 C, but was significantly higher at 24 C. Severity of infection also was greater at 24 C than 18 C and was less at 13 C than 18 C. Incidence of infection was significantly lower at 50% relative humidity than at higher humidities. Intermittent wetting or presence of a saturated atmosphere for a short period following inoculation increased infection frequency. The combination of high temperature (24 C) and intermittent high humidity resulted in the greatest incidence and severity of infection. Growing plants at high light intensity prior to inoculation resulted in more disease than in plants grown at lower intensity. These results explain the common observation that Fusarium stem rot and stub dieback is frequently a problem in early summer in the eastern United States where conditions of temperature, humidity, and light are most favorable for infection and pathogenesis of carnation by *G. zeae.*

Fusarium stub dieback is part of a stem rotting disease complex of carnation, *Dianthus caryophyllus* L. The disease complex has been reported as being caused by *Fusarium culmorum* (W. G. Smith) Sacc., by *F. avenaceum* (Fr.) Sacc., and by *Gibberella zeae* (Schw.) Petch (imperfect stage = *F. graminearum* Schwabe) (3, 10). The occurrence of Fusarium stub dieback caused by *G. zeae* and the development of the disease under commercial greenhouse conditions has been described by Nelson et al. (10). Fusarium stem rot has long been observed to be a more serious problem on greenhouse carnations in the summer (6, 14, 15). In the eastern U.S., where summers are hot and humid, the high incidence of Fusarium stem rot is considered to be a principal factor limiting use of 2- or 3-yr culture of carnation.

Carnation cultivars examined to date are physiologically and horticulturally temperature-sensitive (8). Temperature affects the size, color, and keeping quality of flowers; the weight, length, and strength of stems; the size and number of leaves; and the size of internodes (7). Anatomical changes in the stem also occur if the temperature maintained during growth is changed (1).

Temperature affects development of other carnation diseases such as Fusarium wilt (caused by *F. oxysporum* f. sp. *dianthi*) and bacterial wilt (caused by *Pseudomonas caryophylli*); in these diseases the effect of temperature is partly on the host response to infection (2, 4). Several diseases of other crops caused by *G. zeae* are more severe at higher temperatures (5, 11, 12). The environmental factors which influence the development of Fusarium stub dieback disease of carnation have not been investigated thoroughly. Thus, the objective of this investigation was to determine their effect on disease development.

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MATERIALS AND METHODS

Carnation Culture.—Planting media consisted of equal parts of soil, washed sand, peat, and No. 2 Perlite mixed in a mechanical mixer. To each cubic meter of medium 0.24 kg N, 0.72 kg P, and 0.24 kg K was added. The mixture was autoclaved at 121 C for 4 hr and stored for several weeks prior to use. Plants were fertilized on alternate weeks with solutions containing 20-20-20 fertilizer at 2.5 g/liter or $Ca(NO_3)_2$ at 2.0 g/liter. Soil mixtures in benches were steamed at 85 C for 4 hr prior to use and plants were fertilized at every watering with 0.2 g/liter each of N and K.

Some experiments were done in a greenhouse maintained at a minimum temperature of 15 C. Other experiments were done in controlled environment growth chambers (Model M-1 or M-5 Environmental Growth Chambers; Integrated Development and Manufacturing Co., Chagrin Falls, OH 44022). Temperatures were controlled in the chambers to ± 1 C and relative humidity to ± 5%. Illumination was measured at plant height with a cosin-corrected light meter (Weston Model 756). Relative humidity was checked at intervals with a wet-bulb

psychrometer. Air speed at the edge of the plant canopy in all chambers was 0.9 ± 0.1 km/hr as measured by a nondirectional hot wire anemometer. Incandescent illumination was provided by 40W, 220V bulbs operated at 125v and was 8% of the total provided. The temperature, relative humidity, and light settings of the chambers used for the several experiments are described with the results of those experiments and are listed in Table 1.

Inoculum preparation and plant inoculation.—The original isolate of *G. zeae* used in these studies was #R-762 from the Fusarium Research Center (Dept. of Plant Pathology, The Pennsylvania State University, University Park, PA 16802). Voucher specimens of diseased carnation stems bearing both sporodochia and perithecia of *G. zeae* from several of the experiments reported herein are deposited in the Plant Pathology Herbarium at Cornell University (CUP #53528). Because this fungus may lose aggressiveness if maintained in pure culture (3), the pathogen was maintained in lesions on carnation plants. Each time inoculum was needed, the fungus was isolated from such an infected plant, cultured on Difco potato-dextrose agar (PDA), and incubated at room temperature (22 to 26 C) for 10 to 14 days, 15 cm from a 40W near-UV bulb (Sylvania Black Light Tube #F40-BLB). Conidia were washed from the plates with sterile distilled water.

Disease rating system.—To evaluate disease all plant stems were split lengthwise and presence and size of lesions noted. In preliminary studies, we found that environmental factors affect both incidence of infection and lesion size. Incidence of infection refers to the proportion of inoculated stems showing typical lesions, defined as visible discoloration exceeding 2 mm associated with a dead area in the stub. *Gibberella zeae* regularly was isolated from small lesions. "Severe infections" were defined as those in which the lesion had reached and passed the first node below the stem stub; frequently leaf and side shoot necrosis were associated with such lesions. Noninoculated stubs showed some drying out at the cut end but this was generally less than 2-3 mm and not discolored.

All counts of infections were square-root transformed and treated by analysis of variance unless otherwise noted.

RESULTS

Seasonal variation in infection.—Frequency of infection on carnation cultivar Improved White Sim included in several separate experiments previously reported (13), varied with the season even though inoculum and inoculation remained the same. The incidence of infection was highest in summer and lowest in winter. The incidence of infection for Improved White Sim in these experiments was significantly correlated ($r = 0.89$, $P = 0.01$) with average day temperature in the greenhouse (Fig. 1).

Spore germination.—Millipore filter disks (6 mm diameter, 0.3-μm pore size) were wetted in sterile distilled water and placed on freshly cut stubs. After excess moisture had disappeared, a 5-μliter aliquot of a

TABLE 1. Controlled-environment conditions used in experiments to investigate infection of florists' carnation by *Gibberella zeae*

	Pre-inoculation				Post-inoculation					
			Light		High-humidity chamber		Controlled-environment chamber			
									Light	
Expt.	Temp (C)[a]	RH[b] (%)	Period (hr)	Intens.[c] (klx)	Temp (C)	Time[d] at 100% (hr)	Temp (C)	RH (%)	Period (hr)	Intens. (klx)
A	16/22	70	14	16 ww	24	16	16/22	70	14	16 ww
					18	16				
					13	16				
B	18/24	70	14	18 dl	(not used)		18	50	14	16.5 ww
							18	70	14	16.5 ww
							18	90	14	16.5 ww
C	18/24	70	14	18 dl	(not used)		24	50	14	16.5 ww
							24	70	14	16.5 ww
							24	90	14	16.5 ww
D	15 minimum		(Greenhouse)		15	24	15 minimum		(Greenhouse)	
E	24 minimum		(Greenhouse)		24	24	24 minimum		(Greenhouse)	
F	16/21	70	14	21 ww	24	16	16/21	70	14	21 ww
G	15 minimum		(Greenhouse)		17	24	15 minimum		(Greenhouse)	
H	13	70	14	16.5 ww	(not used)		13	70	14	16.5 ww
	18	70 & 90	14	16.5 ww			18	70 & 90	14	16.5 ww
	24	70 & 90	14	16.5 ww			24	70 & 90	14	16.5 ww
I	18/24	70	14	22.5 ww	(not used)		18/24	70	14	22.5 ww

[a]Night temperature/day temperature, single value means constant day-night temperature.
[b]RH = relative humidity controlled to ± 5%.
[c]Light intensity measured at plant height. Light provided by daylight (dl) or warm-white (ww) fluorescent tubes + 8% incandescent (230 V, 40 W bulbs operated at 125V).
[d]High-humidity chamber (14) operated at 100% relative humidity for length of time per day, during remainder of day RH was approximately 80%.

suspension containing 100 macroconidia of *G. zeae* was placed on top of the filter. Plants were placed in a high-humidity chamber (9) at about 100% relative humidity at 17 ± 2 C for 7 or 24 hr. The disks were mounted in lactophenol cotton blue on a microslide and examined. Germination of macroconidia was 86% after 7 hr with germ tubes 10 to 30 μm long; in many macroconidia, several cells had germinated. After 24 hr, 98% had germinated and extensive mycelial growth had occurred on the surface of the disk.

Effect of temperature during the incubation period.—Rooted cuttings of Improved White Sim were planted and grown in a chamber under conditions 'A' (see Table 1).

Beginning 5 wk after planting, stems of 20% of the plants were cut each week and inoculated with *G. zeae,* placed in a high-humidity chamber for 1 wk, and then returned to the chamber. The high-humidity chamber was set to different temperatures each week. Disease was evaluated 4 wk after inoculation. The incidence of infection was essentially the same at incubation temperatures of 13 or 18 C, but was significantly greater at 24 C. Incidences of total infection and of severe infections were greater at 24 C; the relative increase for 18 to 24 C was greater for severe infections than for total infections (Fig. 2).

Effect of relative humidity.—In two experiments, cuttings of Improved White Sim were planted two per pot and grown for 4 wk in a chamber under conditions 'B' and 'C' (see Table 1). Following inoculations in both experiments 40 pots were placed in each of three chambers at different relative humidities. Disease incidence was evaluated 4 wk after inoculation. Infection occurred equally well at 70 or 90% relative humidity at both temperatures. Some infection occurred at 50% relative humidity, but significantly less than at the higher humidities (Table 2). The proportion of severe lesions was reduced at 50% relative humidity.

Effect of high humidity duration.—Four experiments were done to test the effect of prolonged high humidity (either immediately following inoculation or delayed for various intervals) on infection of cut carnation stems by *G. zeae.* Stems of plants grown in the greenhouse under conditions 'D' and 'E' (Table 1) were cut and inoculated with *G. zeae.* Some inoculated plants were placed in a high-humidity chamber (13) for several time intervals while others were left in the greenhouse. After incubation in the high-humidity chamber, plants were returned to the

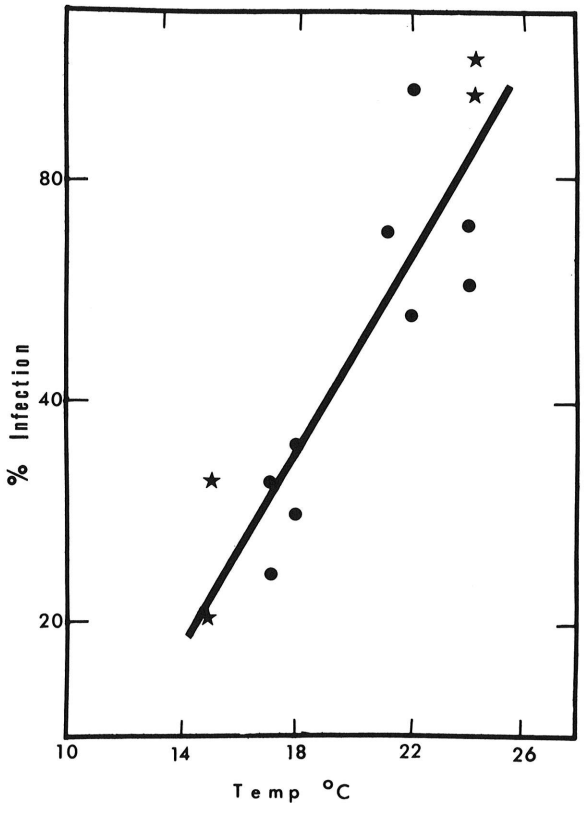

Fig. 1. Incidence of infection in carnation plants inoculated with *Gibberella zeae* and grown at several temperatures in the greenhouse. Each point represents the results of one replicated experiment. (•) = Carnation plants grown in pots. (★) = Carnation plants grown in benches. Temperature is average day temperature for the period between inoculation and recording measurements. The line is the best least-squares regression for the points plotted on a logarithmic scale (r = 0.89, $P = 0.01$).

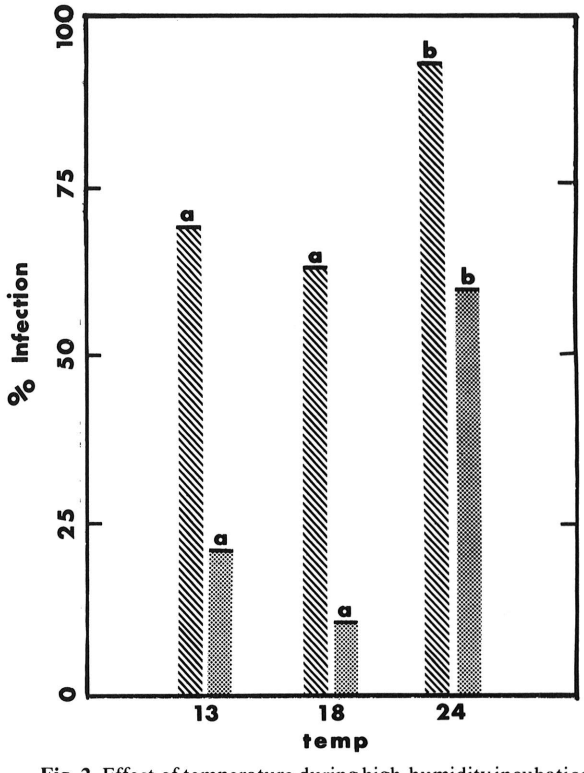

Fig. 2. Effect of temperature during high-humidity incubation on infection of carnation by *Gibberella zeae.* (▨) = incidence of infection (percent plants showing lesions); (▩) = infection severity (percent plants showing lesions through first node). Dissimilar letters over bars indicate significant differences, $P = 0.05$.

greenhouse. Disease was evaluated 5 wk after inoculation. Plants grown in a controlled environment chamber were treated similarly (Table 1, treatment 'F').

In the fourth experiment, (Table 1, treatment 'G') the period of incubation in the high-humidity chamber was delayed for 1, 2, or 4 wk after inoculation. Plants remained in the high-humidity chamber for 1 wk and then were returned to the greenhouse. Disease was evaluated 4 wk following the end of the high-humidity period.

High humidity favored infection when maintained only 16 hr/day. When high humidity was maintained constantly there were no differences for the time periods tested (Table 3). The incidences of total infections and severe infections for corresponding periods of high humidity were greater at 24 C than at 15 C.

When the high-humidity treatment was delayed 1 to 4 wk after inoculation a significantly greater number of infections occurred than when there was no high-humidity period (Fig. 3). The incidence of severe infections was also greatest when the imposition of the high-humidity period was delayed for one or more weeks after inoculation.

Effect of interaction of temperature and relative humidity on infection.—Five chambers were programmed to provide the combinations of temperature and relative humidity (shown in Table 1, treatment 'H'). The selection of treatment combinations was limited by the capabilities of the chambers.

Fifty plants of the cultivar, Colorado White Pike's Peak, were placed at each temperature-humidity combination and grown for 4 wk, then cut and inoculated with *G. zeae*. At the time of inoculation, 10 plants from each chamber were transferred to every other chamber so that all possible combinations (5^2) occurred; further, half of each group was covered with a plastic bag for 4 days following inoculation, and light intensity was reduced to about 6 klx. The temperature inside the bags was not

TABLE 2. Effect of relative humidity at two temperatures on infection of carnation by *Gibberella zeae*

Relative humidity (%)	Infection[a]			
	18 C (Exp. 1)		24 C (Exp. 2)	
	Incidence (%)	Severity (%)	Incidence (%)	Severity (%)
50	61 y	30 y	48 y	6 y
70	79 z	75 z	79 z	71 z
90	88 z	85 z	76 z	60 z

[a]Incidence of infection = percent of plants showing lesions; severity = percent of plants with lesions through the first node. Values within columns are not significantly different when followed by the same letter at $P = 0.05$ (Duncan's new multiple range test).

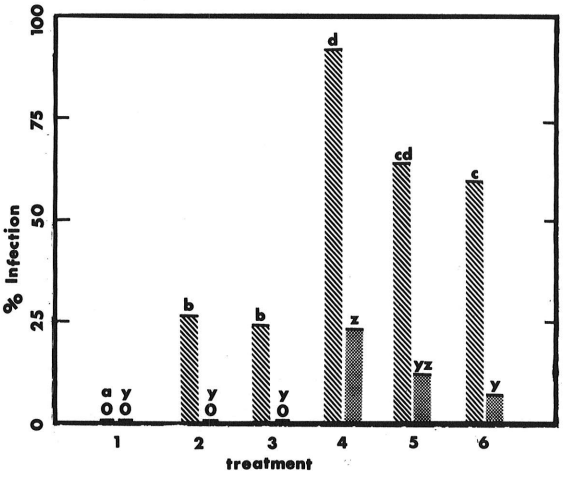

Fig. 3. Effect of delay of high-humidity period after inoculation on infection of carnation by *Gibberella zeae*. All stems were cut to three or four nodes and inoculated with *G. zeae*. *Treatments*: *1*) noninoculated; *2*) inoculated but not placed in high-humidity chamber; *3*) immediately placed in high humidity chamber for 1 wk after inoculation; *4*) placed in high humidity chamber 1 wk after inoculation for 1 wk duration; *5*) placed in high-humidity chamber 2 wk after inoculation for 1 wk; and *6*) placed in high-humidity chamber 4 wk after inoculation for 1 wk duration. Legend: (▨) = incidence of infection (percent plants showing lesions); and (▩) = infection severity (percent plants showing lesions through first node). Dissimilar letters over bars indicate significant differences, $P = 0.05$.

TABLE 3. Effect of duration of high relative humidity on infection of florists' carnation by *Gibberella zeae* at two temperatures

Time (days)	Temperature/hr per day high humidity[a]					
	15 C/16		24 C/24		24 C/16	
	Incidence[b]	Severity[c]	Incidence	Severity	Incidence	Severity
0	22 y	0	70	45	60 y	0 y
1	28 y	2			75 y	10 y
2	28 y	2	80	33	85 yz	5 y
4	35 y	7	70	40		
5					100 z	25 yz
6	55 z	7	80	40		
7					100 z	68 z

[a]Relative humidity near 100% provided in a high-humidity chamber.

[b]Incidence of infection = percent of inoculated plants showing lesions > 2 mm. Values followed by same letters within columns are not significantly different, $P = 0.05$; values in columns without letters show no significant differences.

[c]Severity of infection = percent of inoculated plants in which lesions extended through the first node.

more than 1.5 C higher than ambient and relative humidity was near saturation. Disease incidence was evaluated 4 wk after inoculation.

An analysis was made using chi-square (χ^2) comparisons of counts for the various treatment main effects and χ^2 contingency table analysis for the two-way and the three-way interactions of the treatment factors. From this analysis it was determined that the temperature/relative humidity condition at which the plants were grown prior to inoculation had no effect on subsequent infection, nor did this factor show significant interaction with the other treatment factors. An analysis of variance also was performed on the square-root-transformed counts of infection. Incidence of total and severe infections were greater at 18 or 24 C than at 13 C (Table 4) and both incidence and severity were greater where the plants had been bagged for 4 days following inoculation. There was no difference in infection of bagged plants between 70 and 90% relative humidity at either 18 or 24 C; however, there were fewer infections at 90% than at 70% at both temperatures where the plants had not been bagged. When plants had been bagged, there were more infections at 24 C than at 18 C. This was not the case in the nonbagged plants.

Effect of light on host plant susceptibility.—Plants for this experiment were grown in a chamber 0.2 m from the 0.7-cm-thick Plexiglas barrier that separated the lights from the chamber proper. The chamber was divided into quarters (each 2.15 m^2) and two diagonally opposite quarters were shaded by attaching a heavy translucent paper to the barrier. A significant change in light quality did not result from the use of this paper shade. Light intensity at plant height was 22.5 klx in the nonshaded portions of the chamber and about 6.5 klx in the shaded parts. By growing plants only 0.2 m from the Plexiglas barrier to which the shade was attached, edge effects between lighted and shaded portions were minimized. Air movement within the chamber was not affected. Temperatures in all parts of the chamber were monitored continuously by use of copper-constantan thermocouples and recorded on a multipoint (Honeywell Electronik 16) recorder at about 3-min intervals. Air temperature was measured with gold ball probes placed in the canopy and stub temperatures were monitored by needle probes placed in the stubs.

Improved White Sim carnation plants in pots were placed in this chamber; half of the plants were in full light and half under shade. After 4 wk, the stems on all plants were cut and inoculated with *G. zeae*. At this time half of the high-light plants were moved to the shaded sections and half of the plants grown under the shade were moved to the high-light parts of the chamber. Disease was evaluated after 2 wk.

Plants grown at a high light level before inoculation showed more infections than those grown at a low light level for the same period. However, there was no significant effect of light level during the postinoculation period. Changing the light level at the time of inoculation also significantly affected the incidence of infection ($P = .01$); plants that remained at the same light level after inoculation as before showed more infection than those which were moved to the other light level.

DISCUSSION

Of the factors that were studied, temperature had the greatest effect on infection of carnation by *G. zeae*. The incidences of total and of severe infections both were greater at higher temperatures. The duration of the period of temperature favorable (or unfavorable) to infection also affected how many stem stubs became infected. When the incidence of infection of nonbagged plants and that of bagged plants at three temperatures is compared, the relative increase in incidence of infection is about the same from 18 C to 24 C, but the reduction occurring between 18 C and 13 C is quite different for bagged versus nonbagged plants. Perhaps where 13 C occurred for only 1 wk and was followed by 3 wk at higher temperatures, most of the infections that had been initiated during the 13-C week were able to develop, whereas when 13 C was maintained for the whole period, fewer infected stem stubs developed lesions.

We could not determine whether the lack of decrease at low temperature was due to reduction in growth of the pathogen, to a better wound-healing response by the plant, or some interaction although the latter seems most likely. If one compares the occurrence only of severe infections, one sees a similar response pattern. We suggest that establishment of a severe infection involves three processes: (i) germination of the spores, (ii) initial growth of the mycelium, and (iii) colonization of host tissues. The rates at which these processes occur varies with temperature and relative humidity and may not be the same for all three processes.

TABLE 4. Effect of interaction of temperature and relative humidity (RH) on infection of florists' carnation by *Gibberella zeae*

Relative humidity	Infection[a]					
	13 C		18 C		24 C	
(%)	Incidence	Severity	Incidence	Severity	Incidence	Severity
70	8 u	0	44 x	20	28 w	8
90			12 v	4	16 v	4
100/70[b]	16 v	0	48 xy	24	60 z	40
100/90			36 wx	20	56 yz	40

[a]Incidence of infection = percent of plants showing lesions. Severity of infection = percent of plants with lesions through the first node. Values not followed by the same letters are significantly different, $P = 0.01$ (hsd). All columns and rows with letters may be compared.

[b]100/70, 100/90. Plants enclosed in plastic bags (100% RH) for 4 days following inoculation then grown at 70 or 90% RH.

Increased duration of high humidity (99%+) increased the number of infections which developed. Lengthening of the high-humidity period beyond 1 day probably influenced infection by some means other than promoting spore germination; it possibly enabled the pathogen to grow superficially on the surface of the tissue, as observed by Nelson et al. (10) and by us in our experiments in the high-humidity chamber.

One unexpected finding was that plants inoculated and placed immediately into a high-humidity chamber which maintains 99%+ relative humidity for 24 hr/day had incidences of infection similar to those for plants not given any high-humidity treatment. An intervening period of lower humidity increased the incidence of infection. Because *G. zeae* germinated readily in water or on the wet stub, one may surmise that this drying interval somehow affects the plant, possibly by allowing the tissues at the end of the stub to dry out, thus providing the fungus with an initial colonization site. If noninoculated plants are kept longer than 5-8 wk, these dried-out ends frequently are colonized even by weakly pathogenic or nonpathogenic organisms. When noninoculated stubs are maintained for some time in a saturated atmosphere, this drying-out occurrs less often and many stubs show a wound-healing response at the very end of the stub, similar to the corking-over of cut potato tubers.

Several explanations may account for infection of stubs at low relative humidities. Spores may lodge in cracks which develop in the end of the stub as it dries out and such spores would be in a more favorable microenvironment. It is likely that a vapor pressure gradient exists at the surface of the cut stub similar to that which occurs on leaves. Such a region would easily be deep enough to provide a humid atmosphere in the inner 50 μm, where the spore resides and surface mycelium grows.

That high-light growing conditions should precondition the plants to higher infection rates was surprising. The high light level provided a total daily light energy of about 250 gram-calories/cm^2/day (equivalent to that in a glass greenhouse in the northeastern United States during April or August-September); the low light level provided about 66 gram-calories/cm^2/day (equal to greenhouse light energy in November-December). One may suppose the reason for this preinoculation light response to involve levels of photosynthates or other substances. Alternatively, free-hand sections of stems from the high-level light treatment taken at the time of inoculation and mounted in toluidine blue showed that the ring of fibers which surrounded the vascular cylinder was much thicker and composed of more layers of cells than similar tissue from low-light plants. This morphological difference may account for the stiffer stems which are known to be associated with high light levels (8); whether this sort of morphological change affects susceptibility is unclear.

The occurrence of a reduction in infection rate when plants were changed to a different light level after inoculation may be associated with some sort of stress on the plants with the altered light conditions. It is interesting that whereas light level after inoculation had no effect on total number of infections, nearly twice as many severe lesions appeared in the low light treatment as in the high. Perhaps the high light induced more drying of the stub.

It appears that practical modifications of commercial greenhouse conditions have limited potential to aid in prevention of Fusarium stub dieback. Temperature modification may be helpful to reduce disease, because disease is less severe at lower temperatures and such temperatures are most desirable for carnation production. The ability to maintain cooler temperatures during the summer in Colorado or California may be one reason why Fusarium stub dieback is less of a problem there than in the east where maintaining cool greenhouse temperatures in summer is difficult. The light and humidity levels required for production of quality cut flowers are precisely those favorable for disease development.

The simultaneous occurrence (in early summer in the eastern United States) of temperature, light, and humidity conditions most favorable for infection and pathogenesis by *G. zeae* are sufficient to explain the observed occurrences of the disease at this season.

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