The Influence of Light on Relationships Between Sclerotinia Stem Rot of Soybean in Field and Controlled Environments

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ABSTRACT

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Interaction phenotypes between soybean and *Sclerotinia sclerotiorum* observed in controlled and field environments often do not correlate. Resistant and susceptible accessions were selected to study light intensity as a variable that influences interaction phenotype. Objectives were to investigate whether light intensity within a controlled environment influences the ability to: i) distinguish resistant and susceptible accessions; ii) predict field interaction phenotypes; and iii) determine whether the method used for disease assessment influences the outcome of results. Six accessions were evaluated in growth chamber and field disease nursery trials. Five environments ranging from 146 to 434 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetically active radiation were established in the growth chamber. Inoculum was delivered to cut petioles at the R1 growth stage and interaction phenotypes were assessed for 11 days. For field trials, individual plants were rated at growth stage R7. The breeding line W04.1002 had less disease than NK S19-90 in field environments. Rank correlations of field and light environment interaction phenotypes indicate that light intensity affected the prediction of field performance. Evaluations conducted at 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of light were most predictive of field interaction phenotypes ($r_s = 0.83$ to 0.94 ; $P = 0.05$ to < 0.005). Controlling light intensity is critical to facilitate the identification of resistance to *S. sclerotiorum* in soybean.

Additional keywords: white mold

Sclerotinia stem rot, caused by *Sclerotinia sclerotiorum* (Lib.) de Bary, is an economically important disease of soybean (*Glycine max* (L.) Merr.) in the north-central United States and other temperate regions of the world. An early planting date, narrow row width, and high plant populations are key agronomic practices that maximize yield potential (19). However, these cultural practices contribute to more disease and yield loss in growing seasons conducive to disease development (19,30). Thus, host resistance to *S. sclerotiorum* is needed to continue the use of these management practices in infested fields.

Although no complete resistance to *S. sclerotiorum* has been identified in soybean, partial resistance has been found in cultivars and plant introductions (2,13,15). Regardless of cultivar reaction, the occurrence and severity of Sclerotinia stem rot in the field is highly dependent on prevailing environmental conditions, which can prove problematic when evaluating soybean accessions for resistance (1,18,26).

Inoculation and evaluation of plants in controlled environments are therefore used to facilitate the evaluation of germplasm to identify new sources of partial resistance.

Controlled environment inoculations are only useful if the observed interaction phenotypes relate to those observed in the field. Previous experiments have often yielded inconsistent relationships between data from field and controlled environments (7,16,20,29). As of today, no isolate by soybean genotype interaction has been observed (17). Thus, variation in virulence among isolates of *S. sclerotiorum* is not considered a cause of inconsistent correlation between field and controlled environment data. We hypothesize that growth chamber environmental conditions may be a cause of inconsistencies between growth chamber and field Sclerotinia stem rot interaction phenotypes. We also hypothesize that the phenotypic variable assessed may influence the outcome of results.

The importance of environment in the development of plant disease has long been recognized. Many workers have studied the effect of light intensity on plant-pathogen interactions. Disease severity decreases with increasing light intensity in many plant-fungal pathosystems such as watermelon-*Verticillium dahliae* (4), corn-*Colletotrichum graminicola* (12), *Rhododendron-Erysiphe* spp. (14), tall fescue-*Rhizoctonia solani* (31), barley and wheat-*Puccinia striiformis* (3,27), carnation-

Fusarium oxysporum f. sp. *dianthi* (5), and alfalfa-*Verticillium albo-atrum* (24).

Light intensity, although understudied in the soybean-*S. sclerotiorum* pathosystem, is regarded as important to the outcome of the interaction and as a potential source of variation among experiments. Pennypacker and Risius (25) found that soybean accessions challenged with *S. sclerotiorum* were sensitive or insensitive to varying levels of photosynthetically active radiation (PAR). The sensitivity of soybean cultivar response to *S. sclerotiorum* was explained by the photon flux density during the 48-h period after inoculation. This study did not report information about the relative susceptibility of the soybean accessions they evaluated nor did it attempt to relate these results to field performance.

Objectives of our research were to investigate whether light intensity within a controlled environment influences the: i) ability to distinguish resistant and susceptible accessions; ii) ability to predict field interaction phenotype; and iii) to determine whether the method used for disease assessment influences the outcome of results.

MATERIALS AND METHODS

Soybean germplasm. Two susceptible and four partially resistant soybean accessions were common to all experiments. The susceptible accessions were BSR-101 and W01.1305. W01.1305 is an F6:8 progeny line derived from a cross between cv. Dwight (21) and PI 567.323A. The partially resistant accessions were NK S19-90, W04.1000, W04.1001, and W04.1002. The latter three lines were derived from progeny of single plants selected for partial resistance to *S. sclerotiorum* from the plant introductions 561.285B, 561.367, and 567.157A, respectively. BSR-101 and NK S19-90 are commonly used in Sclerotinia stem rot resistance evaluations as susceptible and resistant checks, respectively.

Pathogen isolate and growing conditions. Inoculum was prepared 3 days prior to inoculation by placing a mycelial plug of isolate 105HT on potato dextrose agar (PDA) plates. Isolate 105HT originated from soybean seed collected near Story City, IA in 1996 and was provided by G. Hartman, USDA-Agricultural Research Services, Urbana, IL (28,32). The cultures were placed for 72 h under two 40W 'Sun Stick' mercury bulbs (OSRAM Sylvania, Danvers, MA) (12-h photoperiod) at 24°C.

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Field environments. Soybeans were planted on 5 May 2004 and 2006 in a nursery infested with *S. sclerotiorum*. Metribuzin (Sencor; 0.42 kg a.i. ha⁻¹) and pendimethalin (Prowl; 1.39 kg a.i. ha⁻¹) were incorporated with a soil groomer for weed control prior to planting. Soybean seeds were planted to a density of one plant per 2.5 cm of row. Soybean accessions were planted in a randomized complete block design with four and three replications in 2004 and 2006, respectively. Plots were planted to 6.1 m lengths and trimmed to 4.9 m after emergence. In 2006, each plot had four equally spaced (76 cm) rows, while in 2004, each plot consisted of five rows (two border rows and three experimental rows). In 2004, border rows were planted to the Sclerotinia stem rot susceptible H2627RR (Golden Harvest Seeds, Pekin, IL) and row spacing was 76 cm between border and experimental accessions and 38 cm between experimental rows to encourage a dense canopy.

Controlled light environments and plant growth conditions. A growth chamber was illuminated for a 16-h photoperiod with 30 400W metalarc lamps (OSRAM, Sylva, IN). Temperatures were maintained at 27°C (±0.2°C) until inoculation to accelerate growth and 24°C (±0.2°C) after inoculation to provide an optimal environment for disease development. Relative humidity was maintained at 50% (±5%) for the duration of the experiment.

Soybeans were planted at the rate of three seeds per 12.7-cm pot with four pots per accession per light environment. The growth medium consisted of one part peat moss and one part Scott's Metro-mix 336P (Scott's-Sierra Horticultural Products Co., Marysville, OH). A light dusting of a commercial preparation of *Bradyrhizobium japonicum* (Lipatch Inc., Milwaukee, WI) was watered into each pot. Plants were thinned to one per pot at the unifoliate growth stage; plants were watered as needed and fertilized weekly with a 20:18:18 soluble fertilizer.

When plants reached the VC growth stage, environments that differed in PAR were constructed within the growth chamber using white shade cloth to cover custom-made carts. PAR is the photon flux density between 400 and 700 nm. White shade cloths providing 22, 40, or 50% shade (EnviroCept Greenhouses, Etc., Benton, WA) were used in various combinations to achieve different PAR intensities. White shade cloth provided temperature and relative humidity uniformity under and outside shade cloths and was confirmed by periodic measurements. The mean PAR intensity for the five environments was 146 (128-163), 282 (255-309), 310 (271-348), 337 (316-357), and 443 (412-473) µmol·m⁻²·s⁻¹. White shade cloth remained on carts until the completion of the experiment.

Petiole inoculation procedure. The petiole inoculation technique was similar to that described by del Rio et al. (9) and Hoffman et al. (13). Standard 1,000-µl pipette tips were used as core borers to cut plugs from the leading edge of 3-day-old colonies of 105HT to obtain 8 mm thick plugs of mycelium and PDA. At the R1 growth stage (22), the third trifoliate leaf of each plant was selected as the infection court and excised to leave a 2.5-cm petiole for inoculation. The petiole was pushed through the open end of the pipette tip into the center of the agar plug until the tip of the petiole was flush with the end of the agar plug.

Host response scoring. Interaction phenotypes in the disease nursery were assessed as described by Grau et al. (11). A section of each plot with a uniform plant stand was evaluated at the R7 growth stage. Ten consecutive plants from each of the three experimental rows were rated using a 0-3 scale in which 0 = no symptoms, 1 = lesions on lateral branches only, 2 = lesions on main stem, no wilt, and normal pod development, and 3 = lesions on main stem resulting in plant death and poor pod fill. A disease severity index (DSI) was calculated for each field plot using the following formula:

$$DSI = 100 \times \sum \frac{x}{yz}$$

in which x is the ratings, y is the maximum rating, and z is the number of plants rated.

Days to wilt and lesion length were used to evaluate plants included in each controlled environment experiment. For days to wilt, plants were examined daily for irreversible wilt symptoms for 11 days post inoculation (dpi). Plants that had not wilted by day 11 were given a score of 12 according to Zhao et al. (32). The lesion length (cm) on each plant was measured on the eleventh dpi.

Data analysis. PROC GLM in SAS was used to analyze 2004 and 2006 field data. For the controlled environment experiments, since four plants of each accession were included in each environment, the mean lesion length and day to wilt was calculated for each accession. Experiments were combined and data was analyzed in a split-plot model using PROC MIXED in SAS, with time as the blocking factor and a total of four individual replications (in time). Light environments, accessions, and light × accession were considered fixed effects and time, time × light, and time × accession were considered random effects. Time and light were the whole-plot factors with time × light as the whole-plot error term. Split-plot factors were accession, accession × time, and accession × light. Differences in least squares means were calculated using the diff option in SAS and differences in means among terms were compared using the t test. To determine relationships between interaction pheno-

types observed in field and controlled environments, Spearman's rank correlation coefficients (r_s) were computed using PROC CORR in SAS.

RESULTS

Field environment. Although both years were conducive for Sclerotinia stem rot development, disease severity was higher in 2004 than in 2006. In 2004, disease severity indices ranged from 17 to 29 for resistant accessions and 47 to 52 for susceptible accessions. In 2006, disease severity indices for resistant accessions ranged from 0 to 12 and 26 to 34 for susceptible accessions. Soybean accessions expressed strikingly different interaction phenotypes in the Sclerotinia stem rot nursery in 2004 and 2006. Differences among accessions were detected (DSI [2004: $F = 9.23$, $P = 0.0004$; 2006: $F = 46.84$, $P < 0.0001$]) (Table 1). NK S19-90 and BSR-101, the resistant and susceptible checks, respectively, differed in both years. Accession disease severity differed more strikingly in 2006. The partially resistant accession W04.1002 had no disease and was significantly more resistant than the partially resistant check (NK S19-90) and W04.1000 and W04.1001.

Controlled environment. Least squares means of lesion length and days to wilt data are presented in Table 2. There were no accession × PAR environment interactions for either the days to wilt or the lesion length disease assessment ($F = 1.13$ and 0.59 , $P = 0.3178$ and 0.9233 , for days to wilt and lesion length, respectively). For the lesion length disease assessment, the interactions between time and light ($Z = 1.93$, $P = 0.0268$) and time and accession ($Z = 2.51$, $P = 0.0061$) were significant, whereas the time factor was not ($Z = 1.05$, $P = 0.1474$). These factors were accounted for as they were designated as random effects in our model. For the subplots, light ($F = 1.88$, $P = 0.1793$) and light × acces-

Table 1. Sclerotinia stem rot of soybeans in a natural epidemic at the West Madison Agricultural Research Station in 2004 and 2006

Accession	Disease severity index ^y (DSI)	
	2004	2006
BSR-101	47 a ^z	26 b
W01.1305	52 a	34 a
NK S19-90	29 b	12 c
W04.1000	25 b	3 c
W04.1001	29 b	3 c
W04.1002	17 b	0 d

^y DSI = $100 \times \sum \frac{x}{yz}$ in which x is the ratings,

y is the maximum rating, and z is the number of plants rated. Ratings: 0 = no symptoms; 1 = lesion on a lateral branch; 2 = lesion on main stem, no wilt and normal pod development; and 3 = lesion on main stem, plant death, and poor pod fill (11).

^z Values within columns followed by the same letter are not significantly different at $P \leq 0.05$.

sion ($F = 0.59$, $P = 0.9233$) were not significant, while differences were detected among accessions ($F = 3.80$, $P = 0.0202$). Differences of least squares means revealed that for the lesion length disease assessment, W01.1305 had 61, 57, 55, and 67 mm greater lesion lengths than NK S19-90 ($P = 0.0058$), W04.1000 ($P = 0.0094$), W04.1001 ($P = 0.0118$), and W04.1002 ($P = 0.0032$), respectively. W01.1305 did not differ from BSR-101 ($P = 0.2348$). Also, BSR-101 had 38 mm longer lesions than NK S19-90 ($P = 0.0662$).

For the days to wilt disease assessment, the random effect of time was not significant ($Z = 0$, $P = \text{NA}$), whereas time $\times$ light environment ($Z = 1.63$, $P = 0.0515$) and time $\times$ accession ($Z = 1.59$, $P = 0.0561$) were. Again, these random effects were accounted for in our statistical model. For the subplot effects, differences were detected among light environments ($F = 3.25$, $P = 0.0504$) and among accessions ($F = 22.09$, $P < 0.0001$), but not for the light $\times$ accession interaction ($F = 1.13$, $P = 0.3178$). Differences in least squares means revealed that plants took the longest to wilt in the light environment of 434 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and plants took 0.9, 1.4, and 1.5 fewer days to wilt than plants grown under 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($P = 0.0848$), 146 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($P = 0.0119$), and 310 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($P = 0.0075$), respectively. The susceptible accession, W01.1305, wilted an average of 1.8 days faster than the susceptible BSR-101 ($P = 0.0019$) and 3.8, 0.7, and 4.4 days faster than resistant accessions NK S19-90 ($P < 0.0001$), W04.1000 ($P < 0.0001$), W04.1001 ($P < 0.0001$), and W04.1002 ($P < 0.0001$), respectively. The susceptible check BSR-101 wilted 2, 1.8, 1.1, and 2.5 days faster than the resistant NK S19-90 ($P = 0.0010$), W04.1000 ($P = 0.0017$), W04.1001 ($P = 0.0430$), and W04.1002 ($P < 0.0001$), respectively. W04.1001 wilted 1.5 days faster than W04.1002 ($P = 0.0084$).

Controlling light intensity improved correlations between phenotypic data collected in controlled and field environments. Rankings based on lesion length and days to wilt for plants grown in 434 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of PAR did not correlate to rankings of field-grown plants (Table 3). Environments

with 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of PAR were consistently most predictive ($r_s = 0.83$ to 0.94; $P = 0.05$ to 0.005) of field performance of soybean accessions in *Sclerotinia* stem rot disease nurseries in 2004 and 2006 (Table 3). Good relationships were also observed between accession disease reactions in the field and the controlled environment with 310 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($r_s = 0.75$ to 0.94; $P = 0.09$ to 0.005).

The type of disease assessment influenced accession differentiation. More accessions differed for the lesion length disease assessment (10 pairings) than for the days to wilt disease assessment (six pairings). The type of disease assessment also influenced the relationship between disease nursery and controlled environment data. In general, better relationships with field data were observed for the days to wilt than the lesion length disease assessment, regardless of the PAR environment (Table 3).

DISCUSSION

Light intensity of the environment in which the soybean-*S. sclerotiorum* interaction was observed was the focus of this study. Light intensity was observed to modify the severity of disease caused by *S. sclerotiorum*. Light intensity also influenced the ability to relate phenotypes observed in controlled environments to those observed in a natural epidemic in a disease nursery.

Previous investigations on soybean and *S. sclerotiorum* focused on methods of inoculation and disease assessment (7,16,20,29), but did not investigate how

the incubation light environment may influence the outcome and utility of data from greenhouse trials. The numerous studies on methods to inoculate soybean with *S. sclerotiorum* have provided a solid foundation of knowledge for this current study. Beginning in 1974 (10), workers have attempted to relate greenhouse inoculation and field data, often with variable results. Light intensity was not reported in previous studies, and therefore, there is no way of determining whether light was a factor in the variability of host response observed within and among experiments. In the current study, control of light intensity improved the ability to correlate phenotypic data collected in controlled and field environments. In general, data gathered in growth environments with 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of PAR exhibited strong relationships with disease nursery data. Correlation coefficients (r_s) ranged from 0.83 to 0.94 for this PAR environment and varied slightly according to the method of disease assessment and growing year. In a similar experiment in which vegetative soybeans were inoculated in a series of PAR environments that included 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, correlation coefficients between field and PAR environment data ranged from 0.94 to 1.00 ($P = 0.005$ to < 0.0001) under 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Appendix 2.1; 23).

In our study, the method of disease assessment affected the ability to detect differences among accessions for reaction to *S. sclerotiorum*, with more differences detected with the lesion length disease assessment. This phenomenon was also reported in a study of *Alternaria solani*

Table 3. Coefficients of rank correlation (r_s) of interaction phenotype data from a *Sclerotinia* stem rot disease nursery and a petiole inoculation conducted in controlled light environments ($n = 6$)

Year	Controlled environment (IP) ^a	Photosynthetically active radiation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)				
		146	282	310	337	443
2004	Lesion length ^v	0.72	0.75 ^w	0.75 ^w	0.93 ^x	0.70
	Days to wilt ^y	-0.87 ^z	-0.84 ^z	-0.93 ^x	-0.84 ^z	-0.55
2006	Lesion length	0.71	0.77 ^w	0.77 ^w	0.94 ^x	0.66
	Days to wilt	-0.89 ^z	-0.83 ^z	-0.94 ^x	-0.83 ^z	-0.54

^a IP = interaction phenotype.

^v Lesion length: measured in centimeters on the eleventh day post inoculation (dpi).

^w Denotes significance at less than the 0.10 probability level.

^x Significant at less than the 0.01 probability level.

^y Days to wilt: plants were assessed daily for wilt until the eleventh dpi (33).

^z Significant at less than the 0.05 probability level.

Table 2. Interaction phenotypes of soybean accessions challenged with *Sclerotinia sclerotiorum* in controlled environments that differ in light intensity

Accession	Photosynthetically active radiation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)									
	Lesion length ^y					Days to wilt ^z				
	146	282	310	337	434	146	282	310	337	434
W01.1305	9.6	8.1	9.0	7.3	4.5	6.6	7.0	6.9	7.4	9.0
BSR-101	7.4	5.3	6.0	5.4	3.2	8.0	9.3	9.1	8.6	11.1
NK S19-90	2.6	1.6	2.7	1.9	0.6	10.8	11.7	9.7	11.4	12.0
W04.1000	2.6	2.2	4.4	1.7	0.7	11.2	11.0	10.3	11.3	11.4
W04.1001	4.3	2.0	3.2	1.9	1.1	10.3	10.6	9.2	10.3	10.7
W04.1002	3.2	1.3	0.7	0.7	0.7	11.1	11.8	11.8	12.0	12.0

^y Lesion length: measured in centimeters on the eleventh day post inoculation (dpi).

^z Days to wilt: plants were assessed daily for wilt until the eleventh dpi (33).

and potato in which the method of disease assessment influenced cultivar ranking (6). For two of three rating days, percent symptomatic leaves per stem resulted in more detectable differences among cultivars than percent symptomatic stems per plot. In a study in which six different methods of assessment were used to characterize the quinoa-*Peronospora farinosa* f. sp. *chenopodii* interaction, differences among accessions were detected for each method of assessment, but cultivar ranking differed according to assessment method (8).

Linear correlation is frequently used to compare soybean-*S. sclerotiorum* interaction phenotype data obtained in controlled and field environments (7,13,16,20). As previously stated, Sclerotinia stem rot incidence and severity is largely influenced by environmental conditions, and as of today, no isolate $\times$ host interactions have been observed. Because we were more interested in trends than in quantitative similarities, Spearman's rank correlations were used to compare disease data from multiple growing seasons with controlled environment data. To compare or contrast our data with published comparisons of field and controlled environment data, we analyzed accession means from several publications using Spearman's rank correlations.

After observing no linear relationship between their field and greenhouse data, Nelson et al. (20) suggested that Sclerotinia stem rot evaluations should not be undertaken in a greenhouse environment (20). We applied rank correlation analyses to their data and found a good relationship between data from one controlled environment and field environments ($r_s = 0.65$, 0.82 , $P = 0.0093$, 0.0002). Kim et al. (16) found weak linear relationships between field and controlled environment data. Our rank correlations of their data yielded coefficients between 0.36 and 0.57 with probabilities ranging from 0.14 to 0.01. In Chun et al. (7), linear correlation coefficients ranged from 0.25 to 0.61, while rank correlation coefficients ranged from 0.27 to 0.29. In one study in which rank correlations were conducted, coefficients between -0.20 and 0.55 were found (29). Hoffman et al. (13), found a linear relationship between field and controlled environment data ($P < 0.01$). Rank correlation analysis of their data yielded a similar relationship ($r_s = -0.67$, $P = 0.0007$). Our results suggest that suboptimal lighting conditions may partly be responsible for the weak relationships previously reported. Nelson et al. (20) said that Sclerotinia stem rot evaluations should not be undertaken in a greenhouse. We are in agreement with this statement and pose that unless light intensity can be sufficiently and uniformly controlled throughout the growing facility, resistance evaluations should only be conducted in field environments.

One can speculate about the factor or factors that may account for the influence

of PAR intensity upon the plant-pathogen interaction phenotype. Because the photosynthetic rate of a plant is related to the quantity of PAR intercepted by the leaves, plants under low PAR conditions are under photosynthetic stress, and therefore, may be more vulnerable to pathogen infection (14). Metabolism, specifically the metabolism of phenolic compounds and secondary metabolites produced through the phenylpropanoid pathway, is also affected by the level of PAR intercepted by leaves (12,24,25). Others have claimed that polygenic resistance is photosensitive (24,25).

In summary, light intensity in controlled environments influenced the ability to relate interaction phenotype data collected in controlled environments to data from a disease nursery. For the purpose of predicting the field performance of soybean accessions, evaluations for reaction to *S. sclerotiorum* should be conducted in environments with PAR intensities between 310 and 337 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Light intensity also affected the ability to statistically distinguish resistant and susceptible accessions. In addition to predicting field performance, PAR environment 337 allowed statistical separation between susceptible and resistant accessions. The type of disease assessment also influenced the statistical distinction between resistant and susceptible accessions in controlled environments. The methodologies developed and tested in these studies can be used to identify higher forms of resistance to *S. sclerotiorum*.

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