# Effect of Irrigation and Soil Water Stress on Densities of *Macrophomina phaseolina* in Soil and Roots of Two Soybean Cultivars

**S. R. Kendig,** Former Graduate Student, and **J. C. Rupe,** Associate Professor, Department of Plant Pathology; and **H. D. Scott,** Professor, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville 72701

**ABSTRACT**

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The effects of irrigation and soil water stress on *Macrophomina phaseolina* microsclerotial (MS) densities in the soil and roots of soybean were studied in 1988, 1989, and 1990. Soybean cvs. Davis and Lloyd received irrigation until flowering (TAR2), after flowering (IAR2), full season (FSI), or not at all (NI). Soil water matric potentials at 15- and 30-cm depths were recorded throughout the growing season and used to schedule irrigation. Soil MS densities were determined at the beginning of each season. Root MS densities were determined periodically throughout the growing season. Microsclerotia were present in the roots of irrigated as well as nonirrigated soybean within 6 weeks after planting. By vegetative growth stage $V_{13}$, these densities reached relatively stable levels in the NI and FSI treatments (2.23 to 2.35 and 1.35 to 1.63 log [microsclerotia per gram of dry root], respectively) through reproductive growth stage $R_6$. After $R_6$, irrigation was discontinued and root densities of microsclerotia increased in all treatments. Initiation (IAR2) or termination (TAR2) of irrigation at $R_2$ resulted in significant changes in root MS densities, with densities reaching levels intermediate between those of FSI and NI treatments. Year to year differences in root colonization reflected differences in soil moisture due to rainfall. The rate of root colonization in response to soil moisture stress decreased with plant age. Root colonization was significantly greater in Davis than Lloyd at $R_5$ and $R_8$. This was reflected in a trend toward higher soil densities of *M. phaseolina* at planting in plots planted with Davis than in plots planted with Lloyd. Although no charcoal rot symptoms in the plant were observed in this study, these results indicated that water management can limit, but not prevent, colonization of soybean by *M. phaseolina,* that cultivars differ in colonization, and that these differences may affect soil densities of the fungus.

*Macrophomina phaseolina* (Tassi) Goidanich is an important soilborne pathogen of soybean (*Glycine max* (L.) Merr.) (43). The disease it causes, charcoal rot, is most evident during the reproductive phases of plant growth, although the fungus can be isolated from plant roots throughout the growing season (8,31,37,43). Visible symptoms of the disease in the field are most apparent under conditions that reduce plant vigor, such as poor soil fertility (43), high seeding rates (37,43), low soil water (17,21), high temperatures (17,32), and root injury (9). The fungus infects plants over a wide range of temperatures (20 to 35°C) and is greatly influenced by soil water conditions (1,16,17,21,22,28,29,33–35,53).

Corresponding author: J. C. Rupe
E-mail: jrupe@comp.uark.edu

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Once in the roots, the fungus moves into the cortical tissue intercellularly and then intracellularly, finally invading the vascular system (2). The infected seedlings can continue to develop with no visible symptoms of the disease. Older plants infected with *M. phaseolina* have reduced leaf and seed size and senesce early (43). Severe infection results in yellowing and death of the leaves that remain attached to the plant. Pods, petioles, stems, and roots develop a gray or silver coloration due to the formation of microsclerotia in those tissues (50).

After harvest, the microsclerotia are released into the soil as the crop stubble decomposes (14,15,42). The microsclerotia can remain viable in the soil and debris for as long as 4 years (46). The microsclerotia in the soil and in crop debris (14,50,52) are the major sources of inoculum of *M. phaseolina*.

In an attempt to control *M. phaseolina,* soil fumigation (28,37) and solarization (30) have been tried with minimal success. Resistant cultivars have been reported (9,24,44), but few cultivars have more than moderate levels of resistance and their effectiveness in the field is uncertain. Cultural practices that help to reduce damage by the fungus include: (i) increasing soil fertility (43), (ii), decreasing the seeding rate (6,37,43), (iii), planting later-maturing cultivars (37,48), (iv), crop rotation (14,19,36,47,49,53), and (v), irrigation (5,16,35). Of these cultural practices, applying irrigation water is the most effective.

In Arkansas, approximately 600,000 of the 1,380,000 ha planted to soybeans are irrigated (3). Although irrigation recommendations for optimum soybean yields are available (38–40,48), information concerning the effects of irrigation on *M. phaseolina* root colonization or soil microsclerotial (MS) densities is lacking. The objectives of this research were to determine if irrigation would reduce *M. phaseolina* root colonization and reduce soil MS densities. In addition, the irrigation regimes were used to obtain a range of soil matric potentials to determine how timing of soil water stress affects *M. phaseolina* root colonization. Preliminary reports have been published (25–27).

## MATERIALS AND METHODS

The relationship between *M. phaseolina*, soil water, and soybean cultivar were determined in 1988, 1989, and 1990 at the University of Arkansas Agricultural and Research Station located at Fayetteville, AR. The soil was a Captina silt loam (fine-silty, mixed, mesic, Typic Fragiudult). Soil characteristics in the Ap horizon at the study initiation was 5.9 pH, 1.4% organic matter, 47% exchangeable base cations, P at 67 kg/ha, K at 192 kg/ha, Ca at 1,141 kg/ha, Mg at 118 kg/ha, Na at 30 kg/ha, Fe at 235 kg/ha, Mn at 373 kg/ha, Zn at 1.6 kg/ha, and Cu at 0.7 kg/ha. The field had been planted to soybean the previous two years and had an average initial population of 29 $\pm$ 8 microsclerotia of *M. phaseolina* per gram of dry soil.

**Experimental design.** Irrigation treatments were designed to simulate a range of possible field irrigation-management practices. The treatments included: no irrigation (NI), full-season irrigation as needed (FSI), irrigation terminated at flowering (TAR2), and irrigation initiated at flowering (IAR2). Two maturity group VI soybean cultivars were used in the study: Davis, a widely grown soybean with some tolerance to poorly drained soils (12), and Lloyd, a cultivar with some tolerance to nonproductive environments (10,11). The design was a split-split-split plot with four

replications. Main plots (irrigation) consisted of twelve rows, 1 m apart and 13 m long, with two border rows separating plots. Subplots (cultivars) consisted of six rows for each cultivar. The third split consisted of data collected from each of the subplots at various soybean growth stages during the year. Treatments were located in the same plot for each of the three years to determine the effect of cultivar and irrigation treatment on soil MS densities.

**Environmental data.** Soil water information was collected until reproductive growth stage $R_6$ in 1988, $R_7$ in 1989, and $R_8$ in 1990. Soil water status was monitored at the subplot level in 1988 and at the whole plot level in 1989 and 1990. Soil water matric potentials (J/kg) were determined by porous cup tensiometers placed at 15- and 30-cm soil depths. These depths were chosen based on previous studies (39), which reported that the majority of soybean roots were found in the top 30 cm of the soil profile in similar soils. The tensiometers were constructed of 1.28-cm-diameter polyvinyl chloride pipe, a 100-kPa standard porous cup (Soilmoisture Equipment Corp, Santa Barbara, CA), epoxy cement, and a rubber septum. The tensiometers were read biweekly with a tensiometer (Soil Measurement Systems, Tucson, AZ). The maximum soil water matric potentials (SWMP) measured with the system is approximately –85 J/kg. For statistical analysis, soils drier than the maximum were marked as an unknown value and recorded as –90 J/kg, although they were probably much drier. Irrigation water was applied with an overhead sprinkler system (Keeling Co, Springdale, AR) that ran parallel to each side of the whole plots. Water was applied to all plots in the treatment when the SWMP at the 30-cm depth approached –50 J/kg in at least two plots. Approximately 2.5 cm of water was applied at each irrigation event.

Climatic data were recorded during the experiment with a Campbell Scientific weather station equipped with a 21X micrologger (Campbell Scientific, Inc, Logan, UT). The station, located approximately 0.8 km from the field, measured air temperature, precipitation, and solar radiation hourly. The data were summarized into daily precipitation and maximum, minimum, and mean air temperatures. Long-term climatic data for air temperature and precipitation were obtained from data collected at the official National Oceanic and Atmospheric Administration reporting station located approximately 0.5 km from the field. Data from this site were used to calculate long-term monthly averages (1959 to 1980) for air temperature and precipitation (45).

**Plant growth.** Soybean seeds were planted 25, 28, and 29 May in 1988, 1989, and 1990, respectively, at a seeding rate of eight seeds per 30 cm of row. Weed control for each year included preplant incorporation of 0.42 kg a.i./ha metribuzin (Sencor, Bayer Chemical Corporation, Kansas City, Mo.) and 0.84 kg a.i./ha trifluralin (Treflan, Dow/Elanco, Indianapolis, IN). Later-emerging weeds were controlled by hoeing as needed.

Soybean growth stages were determined by the methods of Fehr et al. (18). Growth stages sampled in 1988 included: vegetative growth stages $V_3$, $V_7$, $V_9$, and $V_{13}$ (number of nodes above the cotyledonary node) and reproductive growth stages $R_2$ (full bloom, flowering), $R_4$ (full pod), $R_5$ (beginning seed), $R_6$ (full seed), and $R_8$ (full maturity). Plants were sampled at $V_9$ through $R_8$ in 1989 and $V_{13}$ through $R_8$ in 1990.

Harvest seed yields were determined from a 6-m length of the two center rows of each subplot at plant maturity. Plants were harvested on 11, 8, and 4 November in 1988, 1989, and 1990, respectively.

**Soil assays for *M. phaseolina*.** Each year at planting, soil MS densities of *M. phaseolina* were estimated from a bulk soil sample that consisted of 20 randomly collected cores (0.3 by 15 cm) removed from within the row of the four center rows of each subplot. MS soil estimates were made by a modification of the procedure described by Short et al. (41). Soil samples were air dried and then passed through a 20-mesh sieve. A 5-g portion of the sieved soil was suspended in a 500-ml flask containing 250 ml of 0.5% NaOCl. The flask containing the suspension was placed on a rotating shaker for 10 min. The suspension was then poured onto a 325-mesh sieve and the debris was rinsed under tap water for 1 min. The residue on the sieve was transferred to a 250-ml flask and 100 ml of the selective medium, Chloroneb-Mercury-Rose Bengal agar (CMRB), was added (41). The suspension was gently swirled and then poured into 7 to 10 petri plates. The petri plates were incubated in the dark at 33°C for 7 days. MS densities were calculated from the number of CFU on the plates and adjusted to a per gram of dry soil basis.

**Root assay for *M. phaseolina*.** The Short et al. (37) CMRB medium procedure was used to determine MS densities of *M. phaseolina* in the root tissue. Root collections were made with methods similar to those by Jones et al. (23). Roots were col-

**Table 1.** Monthly precipitation, average air temperature, and departure of each from the 30-year average, during the 1988, 1989, and 1990 soybean growing seasons at Fayetteville, AR[y]

| | | Precipitation | | Temperature (°C) | |
|---|---|---|---|---|---|
| Year, month | Growth stage[z] | Total (cm) | Percent 30-year average | Average | Departure |
| 1988 | | | | | |
| May | Planting | 3.41 | 25 | 18.89 | –2.7 |
| June | $V_1$–$V_9$ | 6.49 | 56 | 24.44 | –0.5 |
| July | $V_9$–$V_{13}$ | 9.67 | 106 | 26.11 | 1.7 |
| August | $V_{13}$–$R_4$ | 6.03 | 68 | 26.67 | –0.1 |
| September | $R_4$–$R_5$ | 7.74 | 74 | 22.00 | 2.3 |
| October | $R_5$–$R_8$ | 5.62 | 68 | 12.72 | –5.2 |
| 1989 | | | | | |
| May | Planting | 14.67 | 111 | 18.28 | –1.6 |
| June | $V_1$–$V_9$ | 21.41 | 184 | 21.56 | –3.5 |
| July | $V_9$–$V_{13}$ | 4.33 | 47 | 24.50 | –3.0 |
| August | $V_{13}$–$R_4$ | 4.31 | 48 | 24.94 | –0.8 |
| September | $R_4$–$R_5$ | 11.23 | 109 | 19.17 | –4.3 |
| October | $R_5$–$R_8$ | 1.59 | 19 | 16.44 | 1.5 |
| 1990 | | | | | |
| May | Planting | 30.92 | 234 | 17.28 | –3.4 |
| June | $V_1$–$V_9$ | 14.21 | 112 | 24.33 | 1.5 |
| July | $V_9$–$V_{13}$ | 1.72 | 19 | 25.61 | –1.0 |
| August | $V_{13}$–$R_4$ | 5.03 | 56 | 26.11 | 1.3 |
| September | $R_4$–$R_5$ | 16.69 | 159 | 23.72 | 3.9 |
| October | $R_5$–$R_8$ | 6.21 | 75 | 13.83 | –3.2 |

[y] Precipitation and temperature 30-year averages from the National Oceanic and Atmospheric Administration for the period of 1951 to 1980.
[z] Soybean vegetative and reproductive growth stages determined from Fehr et al. (16).

lected from the outer two rows of each subplot. A sample consisted of all the roots in a 61-cm section of row to a depth of 15 cm. The roots were washed and surface disinfested with a 0.5% solution of NaOCl. The roots were dried for 24 h at 28°C to eliminate further tissue colonization by the fungus (41). Once dried, the roots were ground with a Wiley mill equipped with a 0.2-mm screen. A weighed portion (0.2 to 1 g) of the root tissue was transferred to a 250-ml flask and 100 ml of the CMRB agar was added. The flask was incubated in a 45°C water bath for 20 min, to kill any viable mycelial fragments (41), before its contents were poured into the 7 to 10 petri plates. The petri plates were incubated in the dark at 33°C for 7 days before the colonies of *M. phaseolina* were counted.

A second portion of root tissue was dried at 60°C for 24 h and used to determine the percentage of moisture in the root tissue. MS densities were calculated from the CFU on the plates and reported on a per gram of root dry weight basis.

**Relationships between root colonization by *M. phaseolina* and soil water stress.** To further investigate the effect of SWMP on microsclerotia in root tissue, soil water stress days (SWSD) were calculated for each plot based on SWMP at the 15-cm depth. A SWSD was defined as a day when the SWMP was <–50 J/kg. The days between measurements were classified as SWSD if the last reading was a SWSD and no water event (precipitation or irrigation) had occurred. After a water event, new readings were made after 24 h to determine the current SWMP. Total SWSD, from one plant collection to the next, and cumulative SWSD (CSWSD), the total SWSD that had occurred from planting to a particular growth stage, were calculated.

**Statistical analysis.** The data was analyzed using the SAS statistical package (SAS, Inc., Cary, NC) for a split-split-split plot design. Analysis of variance (ANOVA) was conducted on each variable and the significant main effects and interactions are reported. Mean separations were determined by least significant difference (LSD; $P \leq 0.05$) (13). The relationships between CSWSD and MS density at each growth stage with each cultivar were determined using linear regression.

## RESULTS

**Environment.** Mean monthly precipitation was below average during the first two years and slightly above average during the third year (Table 1). The average air temperatures were below normal, but only slightly below in the third year. Rainfall was below the 30-year average in 1988 for May, June, August, September, and October. In 1989 and 1990, rainfall was below the 30-year average for July, August, and October. Average air temperatures were near or above the 30-year average for June through September in 1988, well below the 30-year average from May through September in 1989, and above the 30-year average in August and September in 1990.

Because soil matric potential was similar at both 15 and 30 cm, only the results from 15 cm will be presented. The growth stage by irrigation interaction for soil matric potential was highly significant ($P < 0.0001$) each year (*data not shown*). In 1989, there were not significant effects due to cultivar. Soil matric potential reflected both irrigation treatment and rainfall. In all three years, soil matric potentials at $V_{13}$

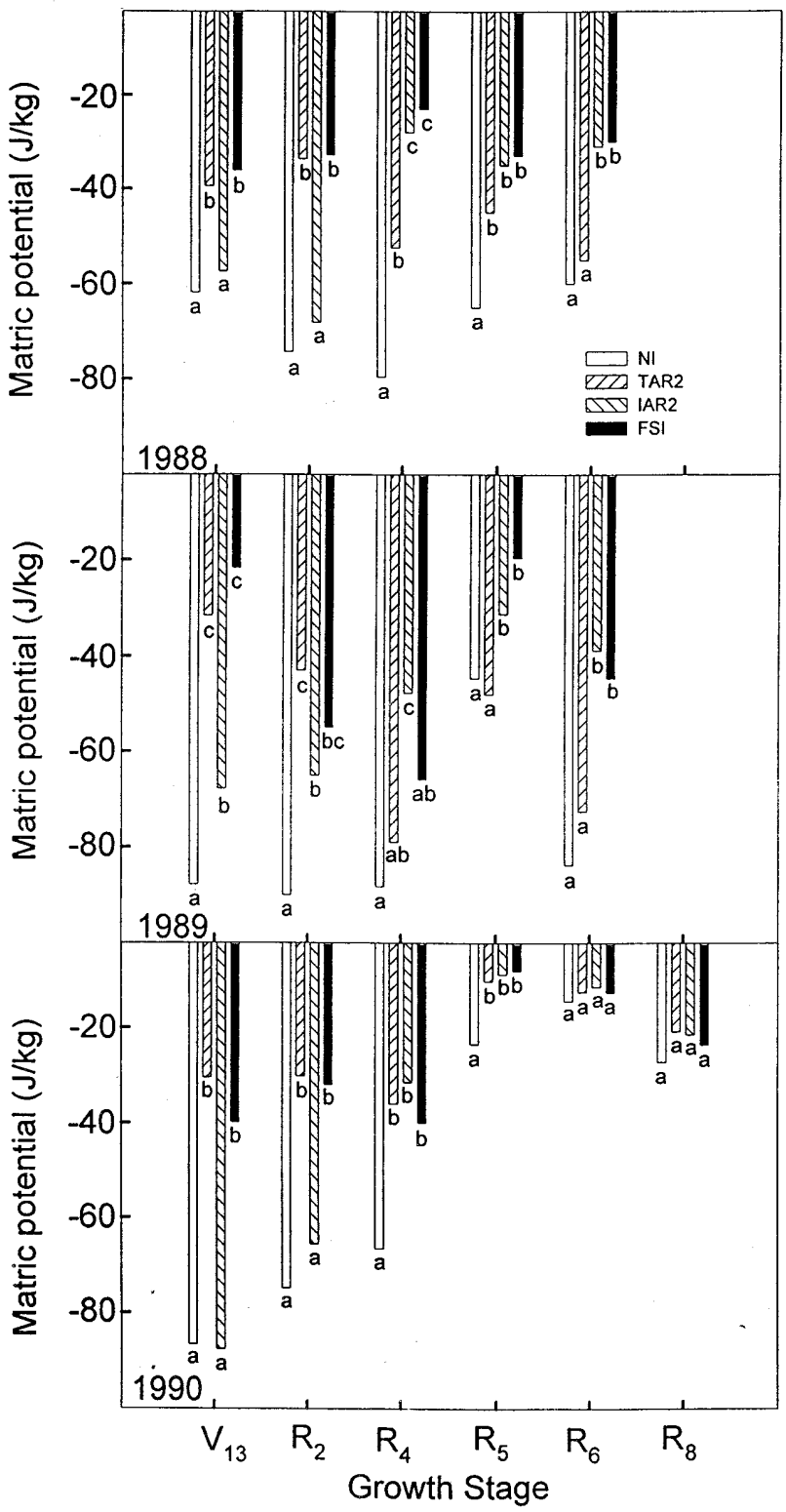


**Fig. 1.** Soil matric potential (J/kg) at various growth stages in 1988, 1989, and 1990 under four irrigation treatments: no irrigation (NI), irrigated until reproductive growth stage $R_2$ (TAR2), irrigated after $R_2$ (IAR2), or irrigated all season (FSI). Bars within a growth stage with the same letter are not significantly different ($P \geq 0.05$) by the least significant difference test.

and $R_2$ were lowest for the NI and the TAR2 treatments and highest for the IAR2 and FSI treatments (Fig. 1). Terminating (TAR2) or initiating (IAR2) irrigation at $R_2$ resulted in significant changes in soil matric potential for those treatments. A breakdown in the irrigation system at $R_4$ in 1989 resulted in temporary reductions in soil matric potential for all treatments. Once irrigation was resumed, the expected increases in soil moisture were observed between treatments. High rainfall in 1990 at and after $R_5$ raised SWMPs in all plots.

**Plant growth.** ANOVA indicated that only irrigation had a significant effect on yield ($P < 0.0001$). Yields were highest in FSI followed by IAR2, TAR2, and NI, in that order (Table 2).

**Soil fungal population.** Soil MS densities at planting were significantly lower ($P < 0.05$) in 1989 (29 microsclerotia/g) than in the same soils sampled at planting in 1988, 1990, and 1991 (35, 34, and 32 microsclerotia/g, respectively). MS densities in soils removed at planting each year were not influenced by irrigation or cultivar the previous year. There was a trend ($P = 0.08$) toward lower MS densities in those soils that were planted with Lloyd compared to those planted with Davis (*data not shown*). No significant differences in soil MS densities were observed with the different irrigation treatments.

**Fungal root infection.** ANOVA of the root colonization data for the three years indicated significant ($P < 0.001$) irrigation–growth stage, cultivar–growth stage, and year–growth stage interactions (*data not shown*). When averaged over year and cultivar, MS densities were greatest in the NI and least in the FSI treatments all season (Fig. 2A). MS densities in the NI treatment did not significantly differ from $V_{13}$ through $R_6$ ($LSD_{P=0.05} = 0.278$). Densities of microsclerotia in roots of the FSI treatment did not significantly increase through $R_6$. Densities of microsclerotia in plants under the TAR2 treatment did not differ from the FSI treatment and densities of microsclerotia in the IAR2 treatment did not differ from the NI treatment through $R_2$. Termination and initiation of irrigation at $R_2$ significantly increased microsclerotia in the TAR2 treatment through $R_6$ and decreased microsclerotia in the IAR2 treatment, respectively. In all treatments, MS densities in the roots were greater at $R_8$ than at all other growth stages.

When averaged over the three years and irrigation treatments, microsclerotia in the roots of the Davis soybean were significantly ($P < 0.05$) greater than those in

**Table 2.** Effect of irrigation regime on soybean yields averaged over three years (1988 to 1990) and two cultivars (Davis and Lloyd) in Fayetteville, AR

| Irrigation regime[y] | Yield (kg/ha)[z] |
|---|---|
| FSI | 2,294 a |
| IAR2 | 2,093 b |
| TAR2 | 1,280 c |
| NI | 1,078 d |

[y] Irrigated plots were maintained at a soil moisture above –50 J/kg either throughout the growing season (FSI), irrigated after reproductive growth stage $R_2$ (flowering; IAR2), irrigated until $R_2$ (TAR2), or not irrigated (NI).

[z] Numbers followed by the same letter are not significantly different ($P \geq 0.05$) by the least significant difference test.

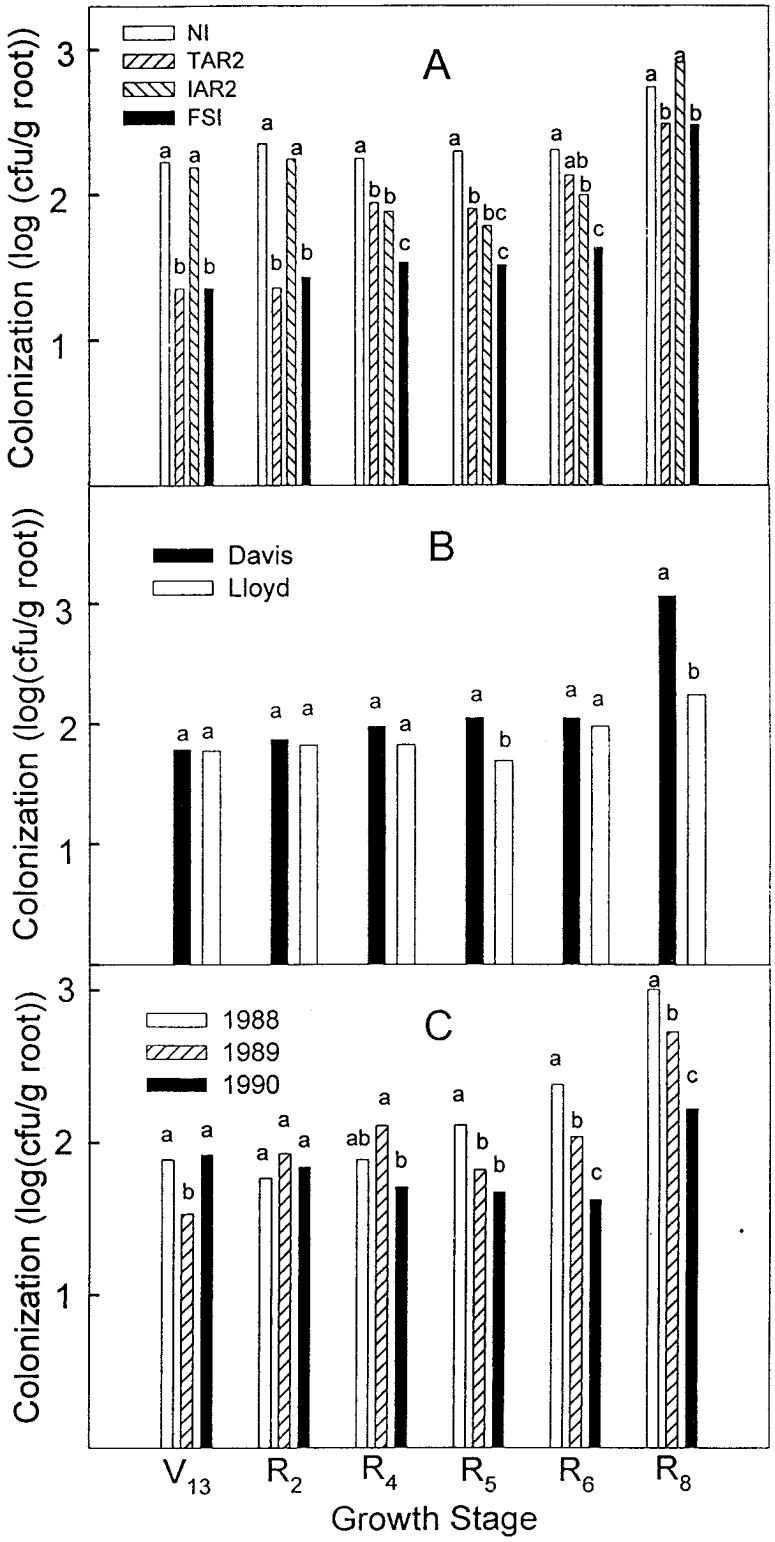


**Fig. 2.** Densities of *Macrophomina phaseolina* microsclerotia ($log_{CFU/g\ root}$) at various growth stages in response to **(A)** four irrigation treatments: no irrigation (NI), irrigated until reproductive growth stage $R_2$ (TAR2), irrigated after $R_2$ (IAR2), or irrigated all season (FSI); **(B)** cvs. Davis and Lloyd; and **(C)** year. Bars within a growth stage with the same letter are not significantly different ($P \geq 0.05$) by the least significant difference test.

Lloyd at $R_5$ and $R_8$ (Fig. 2B). MS means, averaged over irrigation and cultivar, indicate that MS densities in root tissue were greater in 1988 and least in 1990 after $R_4$ (Fig. 2C).

**Relationships between root colonization by *M. phaseolina* and soil water stress.** The relationships between CSWSD and MS densities as related by linear regression revealed a general decrease in the rate of colonization with growth stage (Table 3). Intercepts increased during the season, reaching a maximum at $R_8$. Intercepts were higher for Davis than Lloyd, especially at the $R_8$ growth stage.

## DISCUSSION

Soil moisture and irrigation treatment strongly affected soybean root colonization by *M. phaseolina*. Root colonization by *M. phaseolina* was greatest and least each year in roots of NI and FSI treatments, respectively. In 1988, differences in MS densities between irrigated and nonirrigated treatments (1.04 to 1.86 $\log_{10}$ microsclerotia/g root, respectively) were evident 6 weeks after seedling emergence and well before reproductive development. Microsclerotia developed in root tissue earlier than previous reports that link MS development to reproductive development (51).

Densities of microsclerotia in the roots remained relatively constant through $R_6$ for the FSI and NI treatments. These levels for FSI and NI treatments may represent minimum and maximum root MS densities resulting from nonstressed and stressed growing conditions, respectively. It should be noted that charcoal rot symptoms did not develop in any year even though the roots of both cultivars were colonized by *M. phaseolina*. These levels of colonization were not as great as those reported by Pearson et al. (37) in a test where charcoal rot symptoms were observed. It is likely that MS densities in our test would have been greater if charcoal rot symptoms had developed.

Even though no charcoal rot symptoms were observed during the growing season, the nonirrigated plants were stressed, as shown in the yield data. This was also observed in other plant growth parameters (*data not shown*) and agrees with previous studies on the effects of irrigation on plant growth and yield (4,7,20,38,39,48).

Exposure to drought stress at $R_2$ resulted in changes in MS densities in the soybean roots. When irrigation was terminated in well-watered plots (TAR2), MS densities in the roots increased, becoming significantly greater than densities in the roots of the FSI treatment, indicating increased root colonization. Likewise, the initiation of irrigation (IAR2) resulted in a decrease in root MS densities. This decrease was associated with an increase in root growth without an increase in root colonization by the fungus. Termination of irrigation at $R_6$ resulted in increases in MS densities in all treatments. The reason these levels reflected the preflowering differences between treatments is not known.

A few differences were observed between the two cultivars in this study, but these differences may be important where charcoal rot is a problem. Davis had significantly greater root colonization by *M. phaseolina* than Lloyd at $R_5$ and, more importantly, at $R_8$. These differences in root colonization were reflected in MS densities in soils. Plots planted with Lloyd had MS densities 98, 90, 84, and 82% of those soils planted with Davis in 1988, 1989, 1990, and 1991, respectively. These differences approached statistical significance, reaching $P = 0.08$ in 1991. Greater differences in soil densities might have been observed with continued cropping of these cultivars. Studies which included a greater number of cultivars in a wider range of maturity groups should give more insight into the effect of soybean cultivar on soil MS densities.

The results of this study indicate that water management can have a significant effect on root colonization by *M. phaseolina*. The strong effect of water stress on colonization early in the season suggests that early infection may be more important than previously thought. In addition, differences between cultivars at $R_8$ appeared to affect soil densities of *M. phaseolina*. Future studies are needed to screen soybean cultivars for the influence of MS densities on plant dry matter partitioning under drought conditions. Cultivars that vary in MS densities will be useful in separating the effects of drought from the ef-

**Table 3.** Linear regression intercepts and rates of colonization by *Macrophomina phaseolina* at different growth stages in response to accumulated soil water stress days (CSWSD) in two soybean cultivars grown in naturally infested soil at Fayetteville, AR in 1988, 1989, and 1990[w]

| | Davis | | | | Lloyd | | | |
|---|---|---|---|---|---|---|---|---|
| Year, stage[x] | Intercept[y] | Rate[z] | $R^2$ | $P > F$ | Intercept | Rate | $R^2$ | $P > F$ |
| 1988 | | | | | | | | |
| $V_3$ | 1.0469 | 0.1439 | 0.3244 | 0.0213 | 1.3905 | –0.0113 | 0.0022 | 0.8642 |
| $V_7$ | 0.8202 | 0.0980 | 0.4491 | 0.0045 | 1.0020 | 0.1033 | 0.4423 | 0.0049 |
| $V_9$ | 0.8702 | 0.0355 | 0.7517 | 0.0001 | 0.5830 | 0.0488 | 0.8253 | 0.0001 |
| $V_{13}$ | 1.2914 | 0.0254 | 0.3875 | 0.0100 | 1.2829 | 0.0241 | 0.4099 | 0.0075 |
| $R_2$ | 0.8459 | 0.0307 | 0.4386 | 0.0052 | 0.8630 | 0.0274 | 0.5615 | 0.0008 |
| $R_4$ | 1.3991 | 0.0133 | 0.3455 | 0.0167 | 1.5493 | 0.0042 | 0.1451 | 0.1455 |
| $R_5$ | 1.9396 | 0.0078 | 0.2479 | 0.0497 | 1.7593 | 0.0013 | 0.0315 | 0.5110 |
| $R_6$ | 2.0265 | 0.0069 | 0.2561 | 0.0455 | 1.9218 | 0.0050 | 0.2483 | 0.0495 |
| $R_8$ | 3.2602 | 0.0034 | 0.3594 | 0.0141 | 2.2280 | 0.0019 | 0.0276 | 0.5383 |
| 1989 | | | | | | | | |
| $V_9$ | 1.1326 | 0.0325 | 0.1883 | 0.1061 | 0.7869 | 0.0770 | 0.6830 | 0.0001 |
| $V_{13}$ | 1.2136 | 0.0207 | 0.4648 | 0.0036 | 1.1492 | 0.0224 | 0.3162 | 0.0234 |
| $R_2$ | 1.4128 | 0.0188 | 0.5854 | 0.0006 | 1.6156 | 0.0126 | 0.4549 | 0.0042 |
| $R_4$ | 1.8472 | 0.0062 | 0.1350 | 0.1615 | 1.4648 | 0.0118 | 0.5021 | 0.0021 |
| $R_5$ | 1.5283 | 0.0066 | 0.1821 | 0.9930 | 0.9772 | 0.0131 | 0.5211 | 0.0016 |
| $R_6$ | 1.4614 | 0.0078 | 0.1491 | 0.1397 | 1.5511 | 0.0065 | 0.1908 | 0.0907 |
| $R_8$ | 2.9810 | 0.0020 | 0.0126 | 0.6784 | 1.8683 | 0.0032 | 0.0907 | 0.2569 |
| 1990 | | | | | | | | |
| $V_{13}$ | 1.3075 | 0.0341 | 0.8390 | 0.0001 | 1.2200 | 0.0352 | 0.7084 | 0.0001 |
| $R_2$ | 1.2343 | 0.0227 | 0.6284 | 0.0002 | 1.1524 | 0.0249 | 0.5984 | 0.0004 |
| $R_4$ | 1.2589 | 0.0124 | 0.4588 | 0.0039 | 1.1981 | 0.0089 | 0.1489 | 0.1554 |
| $R_5$ | 1.3324 | 0.0113 | 0.3026 | 0.0273 | 1.0953 | 0.0084 | 0.1473 | 0.1578 |
| $R_6$ | 1.0285 | 0.0131 | 0.4243 | 0.0063 | 1.4591 | 0.0035 | 0.5069 | 0.3738 |
| $R_8$ | 1.9674 | 0.0050 | 0.0585 | 0.3668 | 1.8050 | 0.0016 | 0.0054 | 0.7944 |

[w] Cumulated water stress days defined as the number of days with soil matric potentials at a depth of 15 cm <–50 J/kg from emergence until the plants were sampled.
[x] Soybean growth stages as described by Fehr et al. (16).
[y] Intercept = $\log_{10}$ of microsclerotia per gram of root (LCFU).
[z] Rate = LCFU/CSWSD.

fects of drought and charcoal rot on soybean growth and yield.

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**LITERATURE CITED**

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