Soybean Response to *Rhizobium japonicum* Strain, Row Orientation, and Irrigation[1]

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ABSTRACT

Stresses or environmental differences associated with soybean [*Glycine max* (L.) Merr.] row configuration and drought could affect selection and symbiotic performance of *Rhizobium japonicum* strains and subsequent growth and yield of soybean. The present field studies were conducted in 1981, 1982, and 1983 to assess the response of soybean nodulation, growth, and yield to *R. japonicum* strains, row orientation, and irrigation. Strains USDA3I1b110 (110), NC1004 (04), and B587 (587) of *R. japonicum* were compared to indigenous populations in a Norfolk loamy sand (fine loamy, siliceous, thermic, Typic Paleudult). Soybean cultivars 'Davis,' 'Braxton,' and 'Coker 338' were grown with and without irrigation, with east/west and north/south row orientations, and with inoculation variables. The seasonal weather was different for air temperature, rainfall, and solar radiation; and soil temperatures were generally 1 to 5 °C lower for north/south-oriented than east/west-oriented rows at depths of 5 and 15 cm. Nodular occupancies of inoculated strains were increased by inoculation in 1981 and 1982, but not in 1983. No significant differences in N concentration or total N of soybean shoots were found in any year. Yet, a strain × row orientation interaction occurred for seed yield in all 3 yr, and a strain by irrigation interaction occurred in 1983. Seed yield of soybean inoculated with strain 04 or 110 were significantly different for row orientation; differences ranged from 0.24 to 0.43 Mg ha^{-1} for irrigated soybean. Soybean inoculated with 587 was not significantly different in seed yield for row orientation. It was concluded that environmental differences induced by row orientation influence some *R. japonicum* strains in soybean more than others, particularly under irrigated conditions.

Additional index words: ***Glycine max*** **(L.) Merr., Soil temperature, Seasonal weather pattern, Irrigation, Canopy light spectral quality.**

DINITROGEN fixation is important to the growth and yield of soybean [*Glycine max* (L.) Merr.]. This is particularly true for soybean grown on low N content soils; in the southeastern USA, generally greater than half of the accumulated N in determinate soybean is from dinitrogen fixation (Matheny and Hunt, 1983). Inoculation with more efficient *Rhizobium japonicum* strains has increased soybean N accumulation and yield in some soils (Weber et al., 1971; Bezdicek et al., 1978). Unfortunately, the inoculation and infection of soybean with more efficient strains of *R. japonicum* does not consistently increase soybean yield (Williams and Phillips, 1983; Morris and Weaver, 1984). The interaction of growth and/or yield responses to various *R. japonicum* strains with different management and environmental conditions may be of significant importance.

Rhizobium japonicum strains react differently under varying environmental conditions in field, greenhouse, and laboratory studies. Munevar and Wollum (1981a, 1981b, 1982) demonstrated the differential responses of *R. japonicum* strains to temperature in both the free-living and symbiotic state. Optimum free-living growth temperatures for a 96-h period ranged from 27.4 to 35.2 °C for various strains, while maximum survival temperatures ranged from 33.7 to 48.7 °C. Temperature changes as small as 1.5 °C had noticeable effects on some strains. Nitrogen accumulation in soybean cultivars also varied depending on *R. japonicum* symbionts and root temperatures. Lindemann and Ham (1979) also documented differences in the responses of the soybean symbiosis to temperature. Hunt et al. (1981, 1983) demonstrated the effect of soil water status on the yield and growth responses of several determinate soybean cultivars to *R. japonicum* strain 3I1b110 (110). Under good soil-water conditions, strain 110 generally increased total plant N and N concentration. Yet, under soil-water excess or deficit, strain 110 generally did not elicit host growth and yield as well as the indigenous strains. Mahler and Wollum (1980) have shown differences in *R. japonicum* survival with varying soil-water conditions.

Spacing within and between rows are among the most variable aspects of soybean culture. They have been studied since the 1930s (Wiggans, 1939), and row widths < 1 m are accepted as good management for indeterminate soybean. Yet, there is little agreement concerning the best spacing and arrangement for determinate soybean in the southeastern USA. Parks and Manning (1980) reported very high soybean yields with narrow rows and high populations in Tennessee. Nelson and Weaver (1980) found no difference in yield of 'Lee' soybean with plant populations ranging from 48 500 to 194 000 ha^{-1} in Texas. Ramseur et al. (1984) found no difference among intrarow spacings of 6, 8, 10, 15, 30, and 46 cm for yield of 'Braxton' soybean planted in 91-cm rows in South Carolina. Different results among such investigations are commonly attributed to differences in seasonal weather patterns, planting dates, cultivars, and soils. Most likely, all of these factors contributed to differences in soybean growth and yield.

An understanding of the interaction of yield responses to inoculation with *R. japonicum* strains, under various management practices and the environments they create, might illuminate some new aspects of soybean growth and yield. The objective of the present study was to determine if soybean growth and yield responses to inoculation with *R. japonicum* strains interacted with row orientation under irrigated or nonirrigated conditions on a loamy sand.

MATERIALS AND METHODS[3]

A 3-yr field study was initiated in 1981 on a Norfolk loamy sand (fine-loamy, siliceous, thermic, Typic Paleudult) at the Coastal Plains Soil and Water Conservation Research Center, Florence, SC. A split-split-plot design with water application (irrigation vs. no irrigation) and row orientation (east/west vs. north/south) as the main treatment was used in 1981

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and 1982. Row spacing (50 cm vs. 100 cm) split-plot data were pooled for analysis. Each subplot contained eight rows 6.1 m in length. Inoculation with *R. japonicum* [USDA 3I1b110 (110), NC1004 (04), or B 587 (587)] or no inoculation was the split-split-plot treatment. Four replications were used in both years. *Rhizobium japonicum* strains 110 and 04 were used in 1981; strains 04, 110, and 587 were used in 1982. Soybean cultivar 'Coker 338' was planted in both 1981 and 1982. The most probable number (MPN) of indigenous rhizobia for the field used in 1981 was approximately 10^4 g^{-1}, and the indigenous rhizobial MPN for the field used in 1982 was 10 g^{-1}.

In 1983, water treatment (irrigation vs. no irrigation) and row orientation (east/west vs. north/south) were the main plot treatments, and soybean cultivar ('Davis,' 'Braxton,' and Coker 338; maturity groups VI, VII, and VIII, respectively) was the split plot treatment. Rows were 75 cm wide, and MPN of indigenous rhizobia was approximately 10^3 rhizobia g^{-1}. Inoculation with *R. japonicum* (110 vs. 587) was a split-split-plot treatment. Rhizobia were applied in an aqueous form directly to the furrow and seed at planting at the rate of 10^8 cells cm^{-1} of row in all 3 yr.

Treflan (trifluralin-α,α,α-trifluoro-2,6-dinitro-*N*,*N*-dipropyl-*p*-toluidine) and Lexone [metribuzin-4-amino-6-(1,1-diemethethyl)-3-(methylthio)-1,2,4-triazin-5(4*H*)-one] were applied prior to planting at the rate of 1.2 and 0.6 L ha^{-1}, respectively. Fertilization in 1981 was 25, 46, and 8 kg ha^{-1} for P, K, and S, respectively; it was 15, 85, and 10 kg ha^{-1} for P, K, and S, respectively, in 1982 and 1983. Dolomitic lime was applied at a rate of 1500 kg ha^{-1} in all 3 yr. Planting dates were 12 May, 2 June, and 10 June for 1981, 1982, and 1983, respectively. Plant populations averaged about 20 plants m^{-2}.

Water was applied to the interrow area by trickle irrigation tubing when the soil matric potential exceeded 0.025 MPa at the 30-cm depth as measured with tensiometers. Soil temperatures were measured with thermocouples at depths of 5-, 15-, and 30-cm depths in the row and row middle. Measurements were taken daily before canopy closure in two replicates in June 1981 and in four replicates in July 1982 and 1983. Midday and afternoon soil temperature values were similar, and the irrigation treatment was not started until July 1981. Therefore, mean soil temperatures for June 1981 were pooled for the midday and afternoon measurements as well as for irrigated and nonirrigated plots.

Plant tops and roots were sampled from 30 cm of row during the early pod development stage (R3). Top samples were dried at 70 °C, weighed, ground to pass a 0.4-mm screen, and digested with 3 mL of 30% H_2O_2 and 7 mL H_2SO_4 and analyzed for total Kjeldahl N on a Technicon Auto Analyzer using industrial method 334-74 W/B (Technicon Industrial Systems, 1977). Rhizobia strain identification in soybean nodules was determined by the indirect enzyme-linked immunosorbent assay (ELISA) technique on 20 nodules per plot (Berger et al., 1978; Kishinevsky and Barr-Joseph, 1978; Kishinevsky and Gurfel, 1980). Twenty nodules per plot were used. Antiserum protein concentrations used in this analysis were 18-, 12-, and 9-μg mL^{-1} for 04, 110, and 587, respectively. Conjugate concentration ranged from 0.1 to 0.2 μg mL^{-1}. Plots were trimmed, and yields were taken from 18 m of row in 1981 and 1982 and from 27 m of row in 1983. Data were analyzed by analysis of variance and least significance difference (LSD) as outlined by Steel and Torrie (1960).

Air temperature, solar radiation, and rainfall were measured at a weather station located < 200 m from the field studies. Seasonal air temperature patterns of 1981, 1982, and 1983 are shown in Fig. 1. June air temperatures in 1981 were higher than those of 1982 or 1983; most of the daily minima were > 20 °C, and 11 of the daily maxima were > 35 °C. June and July of 1983 were much cooler; 10 of the daily

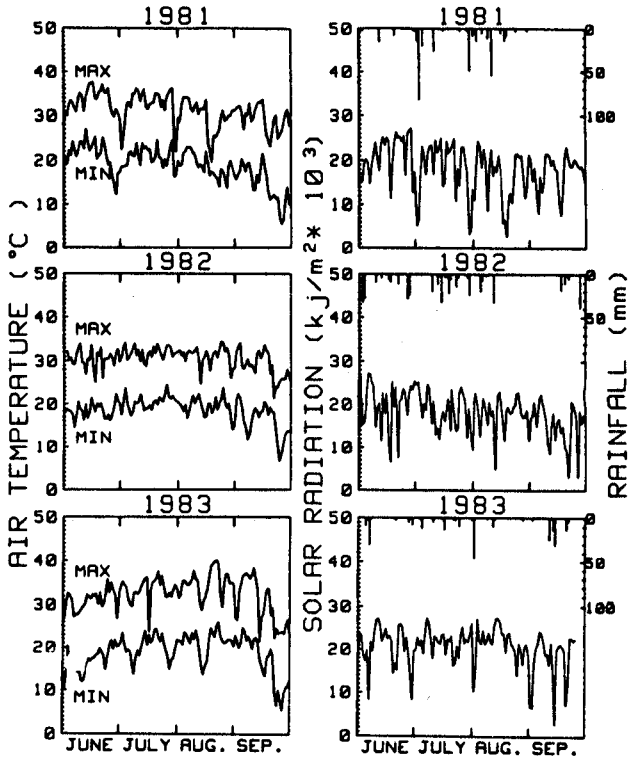

Fig. 1. Seasonal weather patterns during the study.

minima were < 15 °C, and only 23 minima were > 20 °C. Late-season temperatures were relatively cooler in 1981 and relatively hotter in 1983. Temperatures were fairly stable across the season in 1982.

June solar radiation patterns were similar for the 3 yr (Fig. 1). There were approximately 6 days > 25 mJ m^{-2} day^{-1} and 6 days > 17 mJ m^{-2} day^{-1} in each year. July 1983, however, was distinctly brighter than July 1981 or 1982. There were 13 days > 23 mJ m^{-2} day^{-1} and only one day < 17 mJ m^{-2} day^{-1} in July 1983.

Rainfall patterns were different among growing seasons (Fig. 1). In 1981, no major drought occurred, although there were periods of low rainfall and plant stress. There was adequate rainfall with no water stress until after flowering in 1982. After that time, a major drought occurred. Similarly, in 1983, a signficant drought occurred after flowering. Total irrigation water applied was 20, 20, and 18 cm in 1981, 1982, and 1983, respectively.

RESULTS AND DISCUSSION

Soil Temperature

In June 1981 before canopy closure, temperatures in both mid-row and in-row positions at 5-, 15-, and 30-cm soil depths were all numerically higher for east/west- than for north/south-oriented rows (Fig. 2). The mean temperature for all depth and row position were 32.7 and 29.5 °C for east/west and north/south-oriented rows, respectively; and the observed level of significance for row orientation was 0.09 by the *F* test. Mid-row, 5-cm depth soil temperatures were most different, but even 15-cm depth soil temperatures were significantly different. These differences would be large enough to cause differential *R. japonicum* free-living growth and host response (Munever and Wollum, 1981a, 1981b). Soil temperature differences associated with row orientation in 1982 and 1983 were smaller,

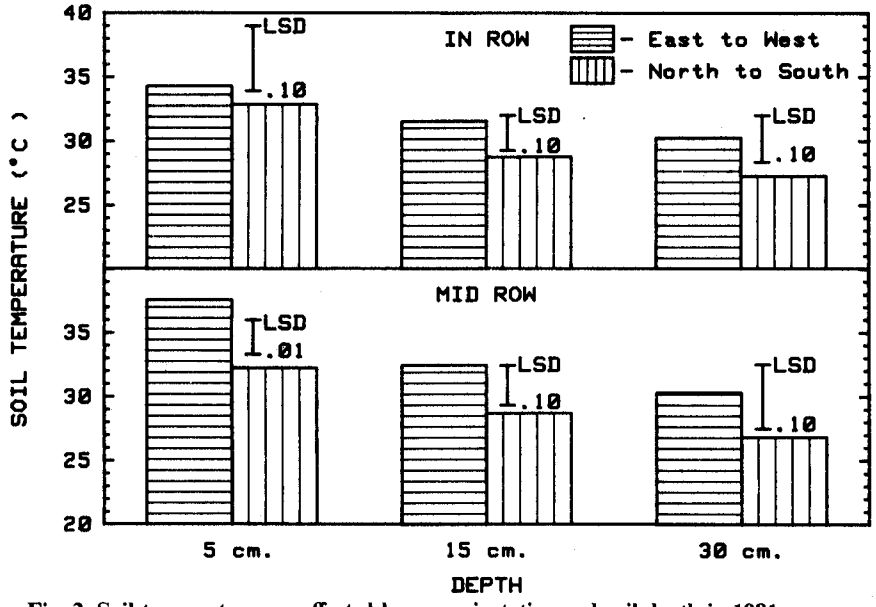

Fig. 2. Soil temperatures as affected by row orientation and soil depth in 1981.

Table 1. Nodular occupancy of *R. japonicum* strains in Coker 338 soybean.

	Strain occupancy†‡						
	04§		110			587§	
Inoculant	1981	1982	1981	1982	1983	1982	1983
	%						
04	5	66	3	3	--	7	--
110	2	3	10	61	7	8	35
587	--	2	--	2	6	67	37
Control	3	-	2	--	--	--	--
LSD (0.01)	NS¶	8.6	6.7	9.3	NS	11.0	NS

† Nodule occupancy was not significantly different for treatment interactions.
‡ Means are pooled across irrigation, orientation, and cultivar treatments.
§ Strain 587 was not used in 1981 and strain 04 was not used in 1983.
¶ NS = not significant at the 0.10 level.

generally < 2°C, but they were measured later in the season.

Nodule Occupancy

Rhizobium japonicum strain occupancies of Coker 338 root nodules are presented in Table 1. Inoculation with strain 110 increased the occupancy of strain 110 in 1981 and 1982. Strain 04 inoculation increased the 04 occupancy only in 1982. The occupancy of strain 587 was also increased by inoculation in 1982. Neither strain 110 nor 587 occupancy was increased by inoculation in 1983. The field used in 1981 had a high indigenous population of rhizobia, but a low population of strains 110 and 04. The field used in 1982 had a very low rhizobial population. The lack of nodular occupancy increase from inoculation of 110 or 587 in 1983 was likely due to high indigenous populations of both strain 110 and 587 in the soil. Since nodules were obtained near the R3 stage of growth in all years, it is possible that nodule occupancy could have changed before or after samples were obtained. Nodular occupancy was not significantly ($P \leq 0.05$) affected by orientation, irrigation, or cultivar in these experiments.

Seed Yield

In 1981, irrigation significantly increased yield, but the rainfall pattern was such that nonirrigated yields were generally good. Yields were 2873 and 2414 Mg ha^{-1} for irrigated and nonirrigated soybean, respectively. Inoculation alone did not cause overall differences, and the lack of severe drought stress eliminated any inoculation by irrigation interaction. Therefore, data on soybean seed yield for row orientation and *R. japonicum* strain inoculation were pooled for irrigated and nonirrigated treatments. Inoculation greatly accentuated the impact of row orientation (Fig. 3). Yields of inoculated soybean were significantly higher for the north/south orientation, but the noninoculated control treatment was not different for orientation. These findings are consistent with earlier reports that introduced *R. japonicum* strain 110 caused different responses to soil and water management practices (Hunt et al., 1983). As previously discussed, the soil temperature of east/west-oriented rows was hotter than that of the north/south-oriented rows, and it is possible that the introduced strains were more sensitive than the indigenous strains to this higher soil temperature. Munevar and Wollum (1981a, 1982) reported differences in *R. japonicum* strain performance with similar differences in soil temperature. However, no significant differences in total N per plant or N concentration in the plant were found in 1981, 1982, or 1983. These findings suggest an effect of *R. japonicum* on growth partitioning or reproduction. The possibility of different partitioning of N is supported by recent evidence that soil-extracted N and symbiotically fixed N are partitioned differently in soybean (Henson and Heichel, 1984). Additionally, the possibility that *R. japonicum* strains may be involved in the balance of nodular- or rhizoplane-produced growth regulators is supported by recent work that showed nodules of pea (*Pisum sativum* L.) to be involved in the cytokinin economy of the whole plant (Badenoch-Jones et al., 1984).

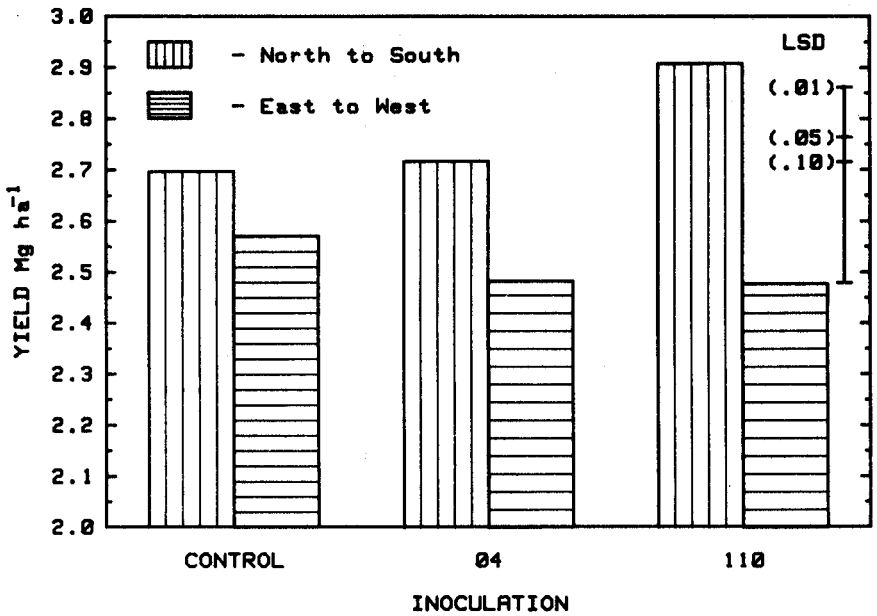

Fig. 3. Yield of Coker 338 soybean grown under different row orientations after inoculation with different *R. japonicum* strains in 1981.

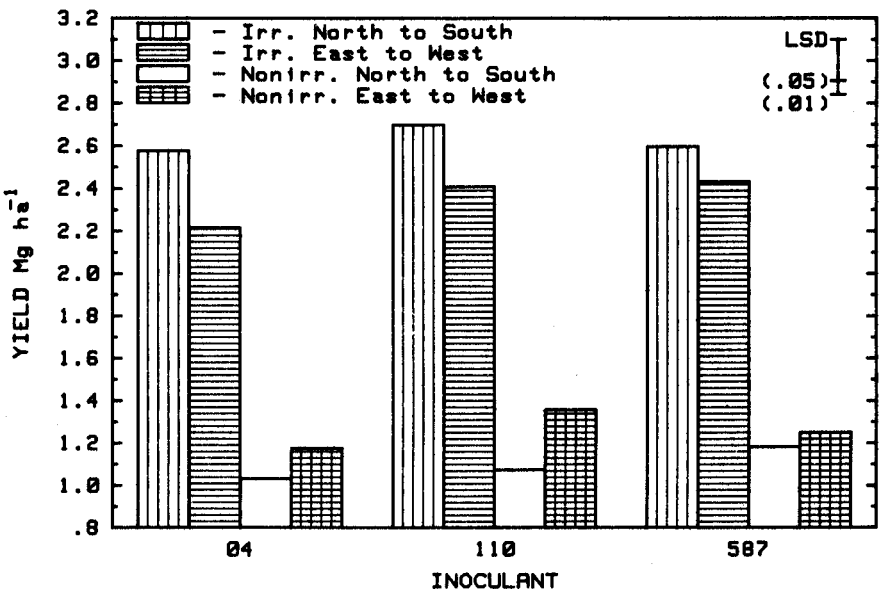

Fig. 4. Coker 338 soybean yield response to row orientation, inoculation, and irrigation in 1982.

Munevar and Wollum (1981a, 1981b, 1982) had shown strain 587 to be less sensitive to temperature differences than strain 110. Strain 587 was used along with strains 04 and 110 in 1982 to follow the interaction of yield responses to strain inoculation with orientation and irrigation. As expected, seed yields of soybean inoculated with strain 587 were not significantly ($P \leq 0.05$) affected by row orientation. Yields of soybean inoculated with either strain 04 or 110 were higher ($P \leq 0.01$) for north/south-oriented rows than east/west-oriented rows under irrigated conditions (Fig. 4). However, east/west-oriented rows yielded best under nonirrigated conditions for all strains, but soybean inoculated with strain 587 was least affected. Explanation of irrigated soybean yield results were consistent with the slightly cooler soil temperatures of the north/south-oriented rows. An explanation of higher yield for east/west-oriented soybean under drought is less clear, but it could be related to shoot/root growth and the spectral quality of canopy light as subsequently discussed. Additionally, it suggests that the seed yield sensitivity of 04 and 110 inoculated soybean to row orientation is a complex and interactive effect in which north/south-oriented rows may not necessarily be superior.

Since there was an interaction of *R. japonicum* strain and row orientation with the group VIII soybean, Coker 338, in 1981 and 1982; group VI and VII maturity soybean were also used in 1983 (Fig. 5). Since there was not a significant cultivar interaction, seed yield data for Davis, Braxton, and Coker 338 were combined. As expected, the mean seed yield of cultivars

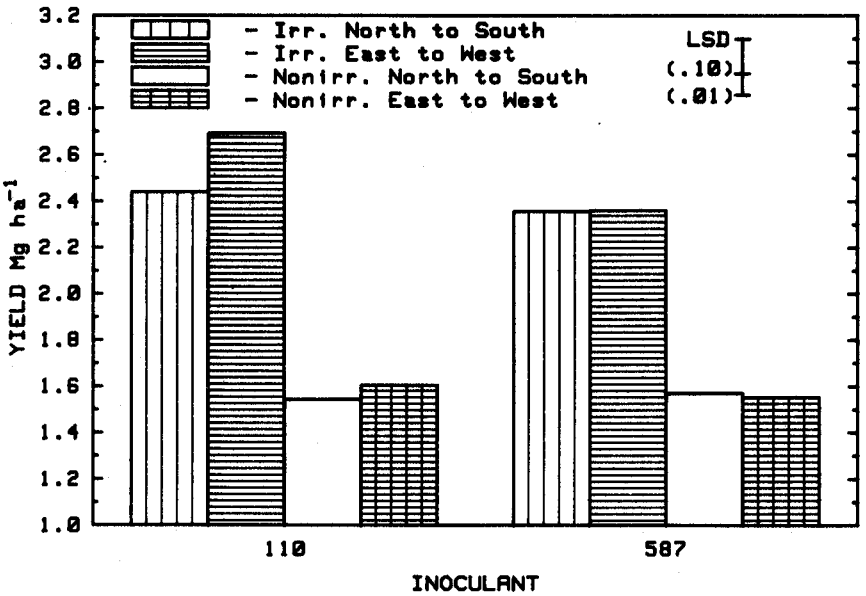

Fig. 5. Mean yield of Davis, Braxton, and Coker 338 soybean inoculated with two *R. japonicum* strains and grown under different row orientations and irrigation treatments in 1983.

inoculated with strain 110 was found to be more affected by row orientation than the mean seed yield of soybean inoculated with strain 587. Somewhat unexpectedly, the east/west, irrigated, 110-inoculated cultivars had the highest seed yield ($P<0.01$). The 110-inoculated, east/west and north/south-oriented soybean did not yield differently under nonirrigated conditions. However, there was a significant ($P\leq0.05$) strain × irrigation interaction for seed yield. Strain 110 was affected more by irrigation than strain 587.

As in 1981 and 1982, neither total N nor N concentration of the shoots were significantly different for any treatment in 1983. Hundred-seed weights were not different, so the increased yield came from increased seed numbers. Additionally, the lack of significant differences in nodular occupancy by strain 110- and 587-inoculated treatments suggest that a different rhizosphere or rhizoplane effect was induced by inoculation with the two strains of *R. japonicum*. Rhizoplane effects have recently been discussed by Elliott et al. (1984), and a very interesting rhizoplane effect on corn (*Zea mays* L.) has been reported for *Azosprillum brasilense* (Lin et al., 1983). Additionally, Kosslak and Bohlool (1984) have shown *R. japonicum* inoculation on one side of a split-root soybean to affect the nodulation of the other side prior to the development of nodules or nitrogenase on the inoculated side, and the effect was related to light intensities.

The variation in seed yield results among years could possibly be explained by a variation in seasonal solar radiation or temperature pattern. The relative growth advantage of east/west- or north/south-oriented rows could shift with monthly or yearly fluctuations of environmental parameters. June was much warmer in 1981 than in 1983. However, there does not seem to be as clear a difference in seasonal temperature patterns of 1982 and 1983. The relatively high solar radiation of July 1983 might also have been a factor. Spectral quality of canopy light was shown to be different for north/south- and east/west-oriented soybean rows in the reported experimental plots in 1983 (Kasperbauer et al., 1984). The red/far-red ratio was higher for the east/west-oriented rows. They also reported that the partition of dry matter differed with red to far-red spectral ratios for growth chamber–grown Coker 338 soybean. The far-red enriched light stimulated more shoot growth and a larger shoot/root ratio. The presence or absence of *R. japonicum*–infected nodules did not change these relations. Work is in progress to determine if light quality affects soybean differently when infected by different *R. japonicum* strains.

CONCLUSIONS

Row orientation and *R. japonicum* strains may interact to cause significant differences in soybean yield, particularly under irrigation conditions. However, these treatment responses are highly dependent on the climatic conditions during the growing season. It is suggested that row orientation and identity of *R. japonicum* strains be considered when effects of management practices on soybean yield are evaluated.

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[Note added in proof: *Rhizobium japonicum* used in this study is now classified as *Bradyrhizobium japonicum* in *Bergy's Manual of Systematic Bacteriology*.]