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Density-Dependent Yield of *Heterodera glycines*-Resistant and -Susceptible Cultivars[1]

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Abstract: Yield of the soybean (*Glycine max*) cultivar Hartwig with resistance to all races of *Heterodera glycines* was compared to that of the susceptible cultivar, Deltapine 105, in a field infested with race 2 of this pathogen. The field had previously been in a cropping sequence experiment that provided a range of *H. glycines* population densities affording the opportunity to evaluate yield potential of resistant and susceptible cultivars in the presence of different levels of soybean cyst nematode in 1992. Plots were planted again in 1993 with the two cultivars in sequences that included Hartwig following Hartwig or Deltapine 105, and Deltapine 105 following Hartwig or Deltapine 105. The yield of Hartwig was inferior to Deltapine 105 at low population densities of *H. glycines,* but Hartwig yielded more than Deltapine 105 at high population densities. Hartwig was effective in suppressing *H. glycines* population density compared to susceptible Deltapine 105. The seed yield of Hartwig following Deltapine 105 or Hartwig, and Deltapine 105 following Hartwig yielded more than Deltapine 105 grown for 2 years.

Key words: crop loss, damage function, *Glycine max, Heterodera glycines,* host plant resistance, nematode, plant disease loss, soybean, soybean cyst nematode.

The most damaging pathogen of soybean *Glycine max* worldwide is the soybean cyst nematode, *Heterodera glycines*. This nematode is distributed throughout most soybean-growing areas in the United States and has been found in South America, causing significant soybean yield suppression in Brazil (Wrather et al., 1997). Resistant cultivars and cultural practices are the primary means for alleviating yield losses caused by this nematode (Kinloch, 1998; Koenning et al., 1998; Young, 1996a, 1996b). Surveys conducted in North Carolina indicate that as much as 60% of the soybean hectarage may be infested with *H. glycines*. The majority of *H. glycines* populations in North Carolina are classified as races 2 or 4, and these populations cannot be adequately controlled by most resistant cultivars available (Koenning and Barker, 1998).

The soybean cultivar, Hartwig, released in 1991, possesses resistance to most populations of *H. glycines* (Anand, 1992; Young, 1998). This cultivar has limited yield potential, and efforts to develop high-yielding cultivars with this type of resistance have met with only limited success. Young (1996a) reported that cv. Hartwig did not yield as well as a susceptible cultivar when grown in an infested field. However, this cultivar may be useful in areas where rotation options are limited. Proposed rotation schemes that limit yield suppression caused by *H. glycines* and prevent the development of resistance-breaking biotypes or races typically call for the inclusion of resistant and susceptible soybean cultivars alternated with a non-host crop (Young, 1984, 1998). Ideally, the resistant cultivar should limit reproduction of *H. glycines* as well as a non-host crop. Limited nematode reproduction on the resistant cultivar serves to minimize damage to the susceptible cultivar when it is included in the rotation. The lack of high levels of resistance to the predominant *H. glycines* populations in North Carolina makes the use of such rotation schemes questionable from an economic standpoint. The cultivar Hartwig, with its high level of resistance, could be integrated into such sequences, but the extent to which cv. Hartwig limits soybean cyst nematode reproduction in the field and its yield potential in the presence of varying levels of this pathogen have not been investigated.

A rotation experiment that included continuous soybean culture, rotation with non-

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hosts for 1 or 2 years, different soybean maturity groups, and different soybean planting dates with or without a winter wheat crop in a field infested with *H. glycines* (race 2) was terminated in 1991 (Koenning et al., 1993). A unique opportunity was presented to use this field to evaluate the level of resistance of cv. Hartwig and its yield potential in the presence of *H. glycines*. The objectives of this study were to: (i) determine the effectiveness of resistance in cv. Hartwig for suppressing population densities of soybean cyst nematode in the field compared to a susceptible cultivar, (ii) compare the yield of resistant and susceptible cultivars at varying population densities of this nematode, and (iii) develop damage functions for the respective cultivars.

Materials and Methods

The cropping sequence upon which the current experiments were superimposed was initiated in 1986 in a grower's field in Washington County, North Carolina, after a uniform planting of *H. glycines*-susceptible soybean in 1985. Rotations included soybean monoculture, 1-year non-host (corn-soybean), and 2-year non-host (corn-corn-soybean or corn-grain sorghum-soybean). Soybean cultivars of different maturity (maturity group V Deltapine 105 and maturity group VII Deltapine 417) were superimposed on rotations. Also, each combination of rotation and maturity group had two planting dates that correspond to full-season soybean and short-season soybean following a winter wheat crop. Late-planted soybean crops always followed a winter wheat crop planted in November of the previous year (Table 1). Maturity group and planting date effects were maintained because the plots received the same planting date and maturity group each time soybean was planted. Treatment sequences were repeated so that every combination of cropping system would appear in the rotation on a yearly basis from 1988 to 1991.

Initially, plots were 15.2 m long and eight rows wide, with rows spaced 0.96 m apart; 7.6-m-wide alleys were placed between ends of plots to prevent the distribution of nematodes with tillage equipment. Plots were arranged in a randomized complete-block design with four replications. In 1992, 8-row plots were divided into 4-row sub-plots and randomly assigned to either cv. Hartwig or cv. Deltapine 105. Sub-plots were divided again in 1993 into 2-row plots.

The soil type was Arapaho Sand (88% sand, 9% silt, 3% clay; 4.5% organic matter; pH 5.4). Standard management practices for North Carolina soybean production were followed for each crop with regard to weed control and fertilization. Soybean cultivars Hartwig and Deltapine 105 (maturity group V) were planted in late May each year. Soybean yield was calculated from the center two rows of each 4-row plot in 1992 and from the entire 2-row plot in 1993. Soil samples for nematode assays were collected from all plots at planting in May and at soybean harvest in November of each year.

Table 1. Rotation sequences of soybeans with nonhosts, soybean maturity group, and planting date used to evaluate management of *Heterodera glycines* in 1986–1991 in Washington County, North Carolina.

Soy(V,E)	Soy(V,E)	Soy(V,E)	Soy(V,E)
Soy(VII,E)	Soy(VII,E)	Soy(VII,E)	Soy(VII,E)
Soy(V,L)-W	Soy(V,L)-W	Soy(V,L)-W	Soy(V,L)
Soy(VII,L)-W	Soy(VII,L)-W	Soy(VII,L)-W	Soy(VII,L)
Corn	Soy(V,E)	Corn	Soy(V,E)
Soy(V,E)	Corn	Soy(V,E)	Corn
Corn	Soy(VII,E)	Corn	Soy(VII,E)
Soy(VII,E)	Corn	Soy(VII,E)	Corn
Corn-W	Soy(V,L)	Corn-W	Soy(V,L)
Soy(V,L)-W	Corn-W	Soy(V,L)-W	Corn
Corn-W	Soy(VII,L)	Corn-W	Soy(VII,L)
Soy(VII,L)	Corn-W	Soy(VII,L)	Corn
Soy(V,E)	Sorg	Corn	Soy(V,E)
Corn	Corn	Soy(V,E)	Corn
Sorg	Soy(V,E)	Sorg	Sorg
Soy(VII,E)	Sorg	Corn	Soy(VII,E)
Corn	Corn	Soy(VII,E)	Sorg
Sorg	Soy(VII,E)	Sorg	Corn
Soy(V,L)	Sorg	Corn-W	Soy(V,L)
Corn	Corn-W	Soy(V,L)	Sorg
Sorg-W	Soy(V,L)	Sorg	Corn
Soy(VII,L)	Sorg	Corn-W	Soy(VII,L)
Corn	Corn-W	Soy(VII,L)	Sorg
Sorg-W	Soy(VII,L)	Sorg	Corn

Soy, soybean: Sorg, grain sorghum. Soybean cultivars of maturity group V (early maturing) or VII (late maturing) were planted early (E) (mid-May to early June) or late (L) (mid-June to late June). W, wheat was planted in the rotation (Koenning et al., 1993).

Soil samples taken for nematode assays consisted of 8 to 12 cores, each 15 cm deep and 2.5 cm in diameter. Cores were composited, and a 500-cm^3 subsample was processed by elutriation and centrifugation (Barker et al., 1986) to collect cysts and second-stage juveniles. Cysts were crushed in a Ten Broeck homogenizer (Corning Inc., Corning, NY), and the eggs were extracted.

Data from 1992 were analyzed as a factorial split-plot design with three levels of rotation × two maturity groups × two planting dates × two cultivars (sub-plots). In 1993, the analysis was for a split-plot design with the previous year's cultivar as whole plots and the current year's planting as sub-plots. Reproductive factors (Rf = final population density/initial population density) were computed for the four sequences of resistant and susceptible cultivars using the mean preplant density in 1993 (mean preplant density following Hartwig vs. Deltapine 105). Nematode numbers were transformed with $\log_{10}(x + 1)$ before analyses to normalize the variance. Yield was regressed vs. preplant densities of *H. glycines* eggs plus second-stage juveniles, and a test for heterogeneity of slopes was performed for combined 1992 and 1993 data.

Results

The largest differences ($P < 0.05$) in preplant *H. glycines* population densities in 1992 were the result of the previous rotational sequence (Table 2). Nematode population densities were greatest when soybean followed a non-host crop the previous year and lowest with 2 years of non-host culture. Final soybean cyst nematode egg population densities in 1992 were significantly greater for Deltapine 105 than for Hartwig ($P < 0.001$) and unaffected by the other treatments of the preceding year. Mean egg densities per 500 cm^3 soil at soybean harvest for cv. Hartwig were 381 (SD 1,419) and 3,927 (SD 3,259) for cv. Deltapine 105. The rotational sequence and cultivar × rotational sequence interactions were both significant ($P = 0.01$) for soybean yield in 1992. The previous year's planting date and soybean maturity group had statistically significant effects when tested with the error-mean square for whole plots ($P < 0.10$), but not when tested with error B (replication × maturity group × planting × rotation). Seed yield of the resistant cultivar was not influenced by rotational sequence, whereas the yield of susceptible Deltapine 105 was related to initial population densities of *H. glycines* as a result of the previous year's rotational sequences (Table 2). The yield of Hartwig was only 89% of the yield of the susceptible Deltapine 105 when comparing the two cultivars grown after 2 years of a non-host crop.

Seed yield in 1993 of susceptible Deltapine 105 following Deltapine 105 was lower

TABLE 2. Influence of rotation sequences on mean numbers of eggs and juveniles of *Heterodera glycines* per 500 cm^3 soil in May 1992 and on soybean yield of two soybean cultivars (Hartwig and Deltapine 105).

Rotation sequence[a]	Number of observations in mean	Preplant egg[b] density/500 cm^3 soil		Soybean yield[c] (kg/ha) Hartwig		Soybean yield[c] (kg/ha) Deltapine 105	
		Mean	S.D.[d]	Mean	S.D.[d]	Mean	S.D.[d]
S-S-S	16	5,175	3,558	933	407	948	352
N-N-S	16	10,018	7,249	919	471	542	309
S-N-S	16	9,010	6,256	1,094	606	726	389
N-S-N	32	2,109	1,836	1,215	390	1,291	367
S-N-N	16	866	1,485	1,350	428	1,512	346
LSD $P = 0.05$		2,211		725		484	

[a] Rotational sequences: S-S-S denotes continuous soybean; N-N-S signifies 2 years of a non-host crop (corn or grain sorghum) followed by soybean in 1991; S-N-S denotes soybean-non-host-soybean (1989, 1990, 1991); N-S-N denotes non-host-soybean-non-host; S-N-N signifies soybean in 1989 followed by 2 years of non-host.

[b] Preplant nematode data were analyzed as a factorial with counts for sub-plots pooled.

[c] Data analyzed as a split split-plot design with cultivars as sub-plots.

[d] S.D. is the standard deviation of the mean.

than this cultivar grown after resistant Hartwig, and Hartwig grown following either Hartwig or Deltapine 105 at a significance level $P < 0.10$ (Table 3). Regression analysis of the yields for the two cultivars from both 1992 and 1993 vs. the transformed *H. glycines* Pi indicates that although yield declined for both cultivars with increasing Pi, the gradient for susceptible Deltapine 105 was much greater than that for Hartwig ($P = 0.02$). Varieties were significantly different ($P < 0.019$), and the slopes differed ($P < 0.02$) (Fig. 1).

Numbers of *H. glycines* cysts, eggs, and eggs per cyst were lower ($P \leq 0.10$) for resistant Hartwig than for susceptible Deltapine 105 in 1993 (Table 3). Deltapine 105 grown after Hartwig had greater ($P \leq 0.10$) numbers of eggs and a higher Rf than Deltapine 105 grown after itself.

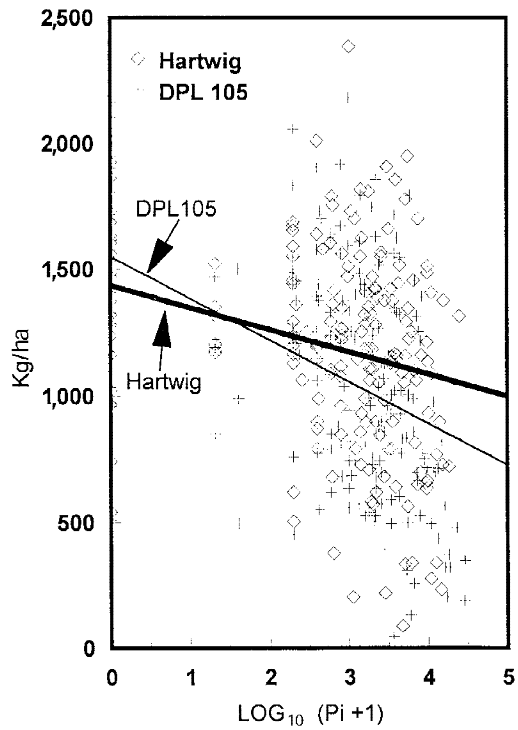

Fig. 1. Soybean seed yield of *Heterodera glycines*-susceptible Deltapine 105 (DP105) and -resistant Hartwig related to the initial soybean cyst nematode population density of eggs plus second-stage juveniles (Pi) transformed to $\log_{10}x + 1$ combined for the years 1992 and 1993. Regression equations: Deltapine 105, y = 1,549 − 164 $\log_{10}$ (Pi + 1), ($P < 0.0001$, $R^2 = 0.20$); Hartwig, y = 1436 − 87 $\log_{10}$ (Pi + 1), ($P < 0.0002$, $R^2 = 0.07$).

Discussion

The low population densities of *H. glycines* following the culture of Hartwig indicate that this cultivar is highly resistant and may suppress the population density of this nematode to the same degree as the culture of a non-host. The difference in *H. glycines* egg population density at harvest and Rf on Deltapine 105 grown after Hartwig, compared to Deltapine 105 grown after a susceptible cultivar, can be attributed to the low Pi following Hartwig, which resulted in less damage. The Rf for *H. glycines* on Hartwig was not different in the two sequences, yet there was a 10-fold difference when comparing continuous Hartwig to Hartwig after Deltapine 105. This is probably an artifact

Table 3. Influence of previous year's and current year's cultivar (resistant Hartwig and susceptible Deltapine 105 [DP105]) on soybean yield, cysts, and eggs/500 cm^3 soil, numbers of eggs per cyst, and reproductive factors in 1993.

Year/Sequence		Yield (kg/ha)		Cysts per 500 cm^3 soil		Eggs per 500 cm^3 soil		Eggs per cyst		Reproductive factor[c]	
92	93	Mean[a]	S.D.[b]	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Hartwig	Hartwig	1,346 A	312	5 A	3.1	192 A	738	10 A	30	0.49 A	1.84
DP105	Hartwig	1,326 A	314	2 A	2.6	67 A	262	9 A	29	0.04 A	0.14
Hartwig	DP105	1,294 A	474	60 B	40.1	4,579 C	4,532	72 B	56	11.75 C	11.4 B
DP105	DP105	1,057 B	405	57 B	41.9	3,100 B	2,454	60 B	62	1.65 B	1.31

All data are means of 48 observations.

[a] Means followed by the same letter are not significantly different according to the Waller Duncan K-ratio *t*-test (K-ratio = 50).

[b] S.D. is the standard deviation.

[c] The reproductive factor was calculated from mean initial population (Pi) densities at planting from plots according to the previous year's cultivar. Mean Pi for Hartwig was 400 (S.D. 1,397) and for Deltapine 105 was 1,907 (S.D. 3,323).

associated with calculation of reproductive factors because the Pi for the Hartwig-Hartwig sequence was 400, whereas the Pi for the Deltapine 105-Hartwig sequence was 1,907. Also, more cysts and eggs may have been left from the previous season with the Deltapine 105-Hartwig rotation compared to continuous Hartwig. Evidence for this assumption is found in the lower numbers of eggs per cyst following Hartwig than Deltapine 105.

Both resistant Hartwig and susceptible Deltapine 105 show predictable yield suppression related to the preplant density of *H. glycines*. Density-dependent yield suppression of cultivars resistant to this nematode has been noted by other researchers (Francl and Dropkin, 1986; MacGuidwin et al., 1995). The poor yield of Hartwig at low population densities of *H. glycines* makes decisions concerning the use of this cultivar difficult. Hartwig would be the appropriate choice of cultivars in those situations when soybean cyst nematode densities are high, or if a grower intends to plant soybean in the subsequent year. Considering overlap of the 99% confidence limits, the yield of a susceptible cultivar is likely to be greater than or equivalent to that of Hartwig at preplant densities from about 100 to 7,500 eggs and juveniles per 500 cm^3 soil. At *H. glycines* population densities greater than this level, Hartwig would be the logical choice for a grower. With high numbers of *H. glycines,* cv. Hartwig provides the highest yield in the current year and suppresses the nematode population density. However, growers and farm advisers may be reluctant to select a cultivar based on potential benefits in future years (Young, 1996b).

More research is needed to determine circumstances under which low-yielding cultivars with resistance might be useful. Studies using various cropping sequences that integrate resistant and susceptible cultivars with different yield potentials may reveal the value of such highly resistant cultivars. The gain in yield of a susceptible cultivar following a resistant cultivar may offset the yield penalty associated with a low-yielding yet highly resistant cultivar. An additional value of cultivars such as Hartwig, with resistance to the majority of *H. glycines* populations, is that the race of the nematode need not be known in order to select a cultivar although, if a cultivar with resistance to the specific race were available, its yield potential would likely be greater than Hartwig. New cultivars with some or all of the resistance found in Hartwig have been released recently (Anand, 2000; Nickell et al., 1999), but their yield potential and adaptability have yet to be evaluated thoroughly.

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