Source of Resistance Affect Soybean Yield, Yield Components, and Biomass Accumulation in *Heterodera glycines*-Infested Fields

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ABSTRACT

The soybean cyst nematode (*Heterodera glycines* Ichinohe) is the main yield limiting pathogen of soybean [*Glycine max* (L.) Merr.] in the USA. Resistant cultivars are the most efficient management tool today. Our research studied the physiological basis of yield differences between *H. glycines*-susceptible and *H. glycines*-resistant cultivars developed from the Hartwig, PI 88788, and Peking sources of resistance at two locations in Iowa during 2005 and 2006. Supplementing resistance with chemical control may improve soybean yield and/or nematode control, so nematicide application {aldicarb[2-methyl-2 (methylthio) propionaldehyde *O*-(methylcarbamoyl) oxime]} was included as an experimental factor. Aldicarb increased total plant biomass by 9% during R1–R5 soybean growth stages, but there was no increase in seed yield. Yields of the resistant cultivars were greater than those of the susceptible cultivars, except for the Peking source. Compared with the susceptible cultivars, cultivars with *H. glycines* resistance from PI 88788 had a 13% increase in yield associated with a 15% increase in growth during R1–R5. In cultivars with resistance from Hartwig, a 6% increase in yield was associated with a 4% increase in R1–R5 duration and increased seed-set efficiency. This work demonstrates that yield increases due to resistance to *H. glycines* can be attained by different physiological mechanisms associated with the different resistance sources and probably are controlled by different genes. This opens the possibility of pyramiding genes conferring resistance by different mechanisms.

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Abbreviations: CBA, crop biomass accumulation; CGR, crop growth rate; SCN, soybean cyst nematode; SFD, seed-filling duration.

Several biotic and abiotic factors limit soybean yield potential (Specht et al., 1999). Between 2003 and 2005, it was estimated that more than 10 million megagrams of soybean yield were lost to plant diseases (Wrather and Koenning, 2006). Thirty percent of this loss was attributed solely to *Heterodera glycines* (Wrather and Koenning, 2006), the soybean cyst nematode, which is an obligate endoparasitic nematode whose life cycle comprises four juvenile and an adult stage (Niblack et al., 2006). Several management practices have been investigated to control this pest, such as the use of *H. glycines*-resistant cultivars, chemical control (nematicides), and the rotation with nonhost crops. *Heterodera glycines*-resistant cultivars are, by far, the most effective and consistent strategy to control this pest, providing yield advantages in most situations (Chen et al., 2001b; De Bruin and Pedersen, 2008a, 2008c; Donald et al., 2006) and also improved yield stability (De Bruin and Pedersen, 2008c).

There is wide availability of soybean cultivars with *H. glycines* resistance, but most of these cultivars were derived from a few *H. glycines* resistance sources (Niblack et al., 2006). Resistance to *H. glycines* is not 100% effective in these soybean cultivars, so growers are advised to rotate sources of resistance to better manage highly diverse and virulent *H. glycines* populations and to avoid loss of effectiveness of the sources of *H. glycines* resistance (Niblack, 2005). However, this

Published in Crop Sci. 50:2565–2574 (2010).
doi: 10.2135/cropsci2009.12.0724
Published online 27 Sept. 2010.

Table 1. Field characteristics at Bancroft and Nevada locations in Iowa during 2005 and 2006.

Characteristic	Bancroft		Nevada	
Latitude	43°3' N		42°0' N	
Dominant soil series	Nicollet		Clarion	
Soil family	fine, montmorillonitic, mesic Cumulic Haplaquolls		fine-loamy, mixed, mesic Typic Hapludolls	
Soil fertility	2005	2006	2005	2006
Average pH	6.5	7.7	6.5	7.2
P (mg kg^{-1})	3	4	62	20
K (mg kg^{-1})	249	101	248	173
OM (g kg^{-1})	83	33	49	23
Planting date	2 June	8 May	6 May	8 May
Harvest date	15 October	10 October	1 October	10 October

recommendation often cannot be followed because of limited availability of *H. glycines*-resistant cultivars with resistance from sources other than PI 88788 (Niblack, 2005). In 2007, approximately 98% of the cultivars resistant to *H. glycines* in Iowa possessed resistance from PI 88788 (Tylka, 2007).

Nematicides in general are expensive and their effectiveness can be inconsistent, particularly under particular field conditions. Noel (1987) evaluated the efficacy of aldicarb applications on soybean yield in *H. glycines*-infested fields during 3 yr. An increase in yield was associated with the nematicide only in 1 yr, when rainfall was below average. This result suggests that the negative influence of *H. glycines* on crop water uptake was minimized in conditions of adequate soil moisture (Fallick et al., 2002; Johnson et al., 1994).

The physiological basis of yield differences between *H. glycines*-susceptible and *H. glycines*-resistant soybean cultivars has not been fully elucidated yet. Yield determination is a complex process that may be dissected into simpler, more tractable traits to determine the physiological causes of genotypic differences (Hammer et al., 2005; Yin et al., 2004). Numerically, soybean yield is the product of seed number per unit area and individual seed weight. De Bruin and Pedersen (2008a, 2008c, 2009) showed that differences in yield between modern *H. glycines*-susceptible and *H. glycines*-resistant soybean cultivars were due to a higher seed set per unit area. Differences in seeds per unit land area usually are determined by the amount of crop biomass accumulated during the critical R1–R5 growth period (Jiang and Egli, 1995; Kantolic and Slafer, 2001; Vega et al., 2001b). De Bruin and Pedersen (2009) demonstrated that differences in number of seeds per unit land between *H. glycines*-susceptible and *H. glycines*-resistant cultivars were determined by differences in crop growth rate during the critical period. Reduced growth in *H. glycines*-susceptible cultivars may be related to a reduction in water uptake from a smaller root system (Fallick et al., 2002; Johnson et al., 1994). There also is evidence that *H. glycines* may cause slight reductions in leaf photosynthesis that may be directly linked with reduced crop growth rates (Koenning and Barker, 1995).

Biomass accumulation is a key aspect of crop yield determination, but a detailed functional description of the effect of different *H. glycines*-resistance sources in combination with nematicide on the processes responsible of soybean biomass accumulation (i.e., crop growth rate and phase duration) and yield determination is currently lacking. Radcliffe et al. (1990) compared crop biomass accumulation of *H. glycines*-susceptible and *H. glycines*-resistant cultivars but did not study different sources of *H. glycines* resistance. Similarly, Wang et al. (2003) showed differences in biomass accumulation but did not assess differences among sources of *H. glycines* resistance. De Bruin and Pedersen (2009) presented a detailed analysis of crop growth rate and yield determination for *H. glycines*-susceptible and *H. glycines*-resistant cultivars derived only from PI 88788.

Soybean resistance to *H. glycines* is not 100% effective, and in-field selection of nematode populations with increased reproduction on resistant soybean cultivars can occur (Niblack 2005). The ability of an *H. glycines* population to reproduce on the sources of resistance is characterized by a greenhouse test called the HG type test (Niblack et al., 2002). In Iowa and the adjacent states Illinois and Missouri, *H. glycines* populations of HG types with increased ability to reproduce on *H. glycines*-resistant soybean cultivars are not uncommon (Mitchum et al., 2007; Niblack et al., 2008; Tylka, 2007). So use of a nematicide, like aldicarb, in conjunction with resistant cultivars, may be needed in Iowa fields infested with diverse and virulent populations of *H. glycines*. The main objective of this work was to study the physiological basis of differences in yield between *H. glycines*-susceptible and *H. glycines*-resistant soybean cultivars with different sources of resistance to *H. glycines*. Three different sources of resistance (two of them tested under different genetic backgrounds) were assessed for yield components and crop growth processes and compared with *H. glycines*-susceptible cultivars. This was done with and without aldicarb to test the effect on the physiological processes associated with the determination of yield.

MATERIALS AND METHODS

Experiments were conducted in 2005 and 2006 at two locations in Iowa: northern Iowa near Bancroft and central Iowa near Nevada (Table 1). Rainfall and temperatures during the growing season were obtained from a weather station near the experimental sites. For all experiments, the design was a randomized complete block in a split-plot arrangement with

Table 2. Sources of resistance to *H. glycines* and maturity groups of glyphosate-resistant varieties evaluated at Bancroft and Nevada, IA, during 2005 and 2006.

Bancroft			Nevada		
Variety	Reaction to *H. glycines* †	Maturity group	Variety	Reaction to *H. glycines*	Maturity group
E2201RX	R (Hartwig)	2.2	E2201RX	R (Hartwig)	2.2
E2620RX	R (Hartwig)	2.6	E2620RX	R (Hartwig)	2.6
FC2449RR	R (Hartwig)	2.4	E2811RX	R (Hartwig)	2.8
P91M90	R (Peking)	1.9	P91M90	R (Peking)	1.9
2038R	R (PI 88788)	2.0	PB2606NR	R (PI88788)	2.5
DG33X19	R (PI 88788)	1.9	SOI2642N	R (PI88788)	2.6
T-7193RR	R (PI 88788)	1.9	SOI2858N	R (PI88788)	2.8
Ag2106	Susceptible	2.1	FC2940RR	Susceptible	2.9
Ag2403	Susceptible	2.4	L-967	Susceptible	2.9
T-7234RR	Susceptible	2.3	NK-S32-G5	Susceptible	3.2

†R, resistant to *H. glycines* (source of resistance in parentheses).

four replications. Main plots were with and without aldicarb, applied in-furrow at 2.5 kg a.i. ha^{-1} at planting by a Smart-Box system (American Vanguard Corporation, Newport Beach, CA). Subplots were randomly assigned to 10 different soybean cultivars differing in source of resistance to *H. glycines* (Table 2). Only one cultivar having Peking source of resistance was available to use in the experiment. In both years and both locations, soybean was planted after corn (*Zea mays* L.) in a conventionally tilled seedbed. Fields were chisel plowed in the fall followed by two field cultivations in the spring. For each cultivar–nematicide treatment combination, two plots of 3 by 7.6 m (one assigned to biomass sampling and the other to yield) were seeded at a rate of 432,000 seeds ha^{-1} at 38-cm row spacing with an Almaco heavy duty drill (Almaco, Nevada, IA). Glyphosate [*N*-(phosphonomethyl)] was applied twice as a post-emergent herbicide at a rate of 865 g a.i. ha^{-1} for weed control.

Plots were harvested with an Almaco plot combine, and harvest weights were adjusted to 130 g kg^{-1} moisture. Individual seed weight was determined in a 300-seed sample and seed number m^{-2} was estimated (Board and Modali, 2005). Throughout the growing season, aboveground crop biomass was sampled every 3 wk from a 0.76 m^2 area of the remaining biomass sampling plots, and the plant tissue was dried to constant weight and weighed. Also, vegetative and reproductive stages of soybean crop development (Fehr and Caviness, 1977) were measured from three randomly selected plants in each biomass sampling plot. Total biomass accumulation was calculated for different phenological periods: emergence to beginning bloom (E–R1), beginning bloom to beginning seed (R1–R5), and beginning seed to physiological maturity (R5–R7). These three periods correspond to the vegetative phase, the critical period for seed set, and the seed-filling phase, respectively. Biomass sampling and phenological records conducted at fixed calendar days for practical reasons did not match the above mentioned growth stages. Therefore, we first estimated the exact calendar day of occurrence of R1, R3, R5, and R7 by regressing the R stage against calendar day for each replication. A quadratic model provided an adequate fitting of this data, with $R^2 > 90\%$ in all cases. Then, biomass at the R1, R3, R5, and R7 stages were estimated by means of a 3-degree polynomial function relating biomass and calendar days for each replication with $R^2 > 90\%$ in all cases. With this information, biomass accumulation (g m^{-2}), crop growth rate (g m^{-2} d^{-1}), and phase duration (days) were calculated for each of the above defined intervals.

Heterodera glycines egg population densities were determined in each plot at planting (initial population density) and at harvest (final population density). Ten soil cores 2.5-cm diameter and 15 to 20 cm deep were collected in a zigzag pattern from each plot and a composite sample was obtained. Cysts (dead, egg-filled *H. glycines* females) were extracted from a 100-cm^3 subsample of each sample by wet-sieving (Gerdemann, 1955) through a 840-μm-pore sieve nested over a 250-μm-pore sieve. Cysts were crushed with a rubber stopper on a 250-μm-pore sieve (Faghihi and Ferris, 2000), and eggs were recovered on a 25-μm-pore sieve. Eggs were then stained with acid fuchsin (Niblack et al., 1993) and counted with a dissecting microscope.

An HG type test (Niblack et al., 2002) was performed on the *H. glycines* population recovered from the initial soil samples collected from each experiment each year. HG types are determined on the basis of the percentage of females that develop on seven indicator lines, which are the different sources of *H. glycines* resistance (PI 548402, PI 88788, PI 90763, PI 437654, PI 209332, PI 89772, and PI 548316), compared with the number of females that develop on the *H. glycines*-susceptible cultivar Lee 74. The *H. glycines* population is considered virulent on an indicator line or source of resistance if the reproduction on the indicator line is >10% of what occurs on the susceptible cultivar in the HG type test (Niblack et al., 2002).

Data were analyzed by the PROC MIXED procedure of SAS (SAS Inst., 2003). Locations were analyzed separately because the same cultivars were not evaluated at each location. Within locations, the model included cultivar, nematicide treatment, and the interaction between both as fixed factors. Years and blocks were considered random factors. Data on egg counts were log transformed to improve normality. The log transformed egg count at planting was used as a covariate to control for initial differences between plots in *H. glycines* density. As expected, the initial egg counts were not different in the plots assigned to the different experimental factors. To test source of resistance effects, single degrees of freedom contrasts were conducted against susceptible cultivars.

RESULTS

Rainfall at Nevada was in general below the 20-yr average for both 2005 and 2006 (Table 3). For Bancroft, both years differed when compared with the 20-yr average. In

Table 3. Rainfall and monthly air temperature at Bancroft and Nevada locations in Iowa during 2005 and 2006.

Year	Location	May		June		July		August	
					Rainfall (mm)				
2005	Bancroft	186	(73)†	110	(4)	135	(41)	0	(–77)
	Nevada	92	(–32)	115	(–6)	66	(–59)	172	(53)
2006	Bancroft	20	(–92)	91	(–15)	126	(32)	92	(14)
	Nevada	28	(–85)	35	(–71)	101	(7)	166	(89)
					Mean monthly average temperature (°C)				
2005	Bancroft	13.3	(–1.7)	21.7	(1.2)	22.8	(0.2)	20.6	(–0.1)
	Nevada	14.4	(–2.2)	22.8	(1.1)	23.3	(0.0)	21.1	(–0.6)
2006	Bancroft	15.6	(0.5)	20.6	(0.1)	23.3	(0.7)	21.1	(0.4)
	Nevada	16.7	(0.0)	21.7	(0.0)	23.9	(0.6)	22.2	(0.6)

†Numbers in parenthesis shows departure for 20-yr average.

2005, rainfall was above the historical average up to July. In 2006, the first part of the crop cycle was in general below the long-term average (Table 3). For both locations in 2005, monthly average temperatures were fairly close to the 20-yr average. In 2006, temperatures in both locations were warmer than the long-term average, mostly during July and August (Table 3).

Heterodera glycines Types, Virulence and Population Densities

The *H. glycines* populations in the experimental locations in the field at Nevada were of a more diverse and virulent HG type than the *H. glycines* populations in the experimental locations at Bancroft (Table 4).The *H. glycines* populations at Nevada had greater than 10% reproduction on the PI 88788 (indicator line 2), PI 209332 (indicator line 5), and PI 548316 (indicator line 7) sources of resistance and thus were of HG type 2.5.7. The *H. glycines* populations in the experimental sites at Bancroft had greater than 10% reproduction only on PI 548316, which is HG type indictor line 7, so the populations were HG type 7.

Initial *H. glycines* egg population densities at the Bancroft experimental sites were, on average, greater compared with those in the experimental sites at Nevada (Table 5). As expected, initial egg counts were not affected by source of *H. glycines* resistance or aldicarb treatment (Table 5).

Table 4. HG type test results for *H. glycines* populations in experimental locations at two locations in Iowa.

HG type indicator line number	Indicator line	FI (%)†			
		Bancroft		Nevada	
		2005	2006	2005	2006
1	PI 548402 (Peking)	0	0	1	7
2	PI 88788	1	7	12	18
3	PI 90763	0	0	0	0
4	PI 437654	0	0	0	0
5	PI 209332	1	9	22	16
6	PI 89772	0	1	0	0
7	PI 5483146 (Cloud)	19	11	90	34
HG type		7	7	2.5.7	2.5.7

†Female Index (FI) = (average number of females on indicator line)/(average number of females on Lee 74) ×100.

All three *H. glycines* resistance sources had reduced *H. glycines* egg population densities at harvest (final egg population densities) compared with the SCN-susceptible cultivars, and there were no significant differences among the sources of SCN resistance. Aldicarb had no effect on final egg population densities, and there was no interaction with *H. glycines* source of resistance (Table 5).

Seed Yield and Yield Components

The Hartwig and PI 88788 sources of resistance provided the highest seed yield when compared with the *H. glycines*-susceptible cultivars (Table 6). The *H. glycines*-resistance source Peking, tested in only one genetic background, did not increase yield compared with the susceptible cultivars (Table 6). Aldicarb did not increase seed yield (Table 6) and this lack of nematicide effect was similar for all three sources of *H. glycines* resistance evaluated. Seed yield increases due to *H. glycines* resistance were explained by increased seed numbers per area rather than by increased seed mass. Aldicarb reduced seed numbers in Nevada, but this reduction did not affect seed yield significantly (Table 6).

Vegetative Period Effects (Emergence to R1)

Differences in crop biomass accumulation (CBA) between *H. glycines*-resistant and *H. glycines*-susceptible cultivars were not evident during the vegetative period at any of the locations (Table 7). Aldicarb did not improve CBA during this period either. As expected from the lack of effect of *H. glycines* sources of resistance and aldicarb on CBA, crop growth rate was not affected by any of the experimental factors (Table 7). However, the duration of the vegetative period was increased for cultivars with the Hartwig source of resistance at Bancroft, but the magnitude of the effect was small and it did not affect CBA. At Nevada, the *H. glycines* sources of resistance reduced the duration of the vegetative period, but it did not affect CBA (Table 7). At both locations, aldicarb slightly reduced the duration, but again the magnitude of the effect was small, causing no significant impacts on CBA.

Early Reproductive (Critical Period) Effects (R1 to R5)

At Bancroft, soybean cultivars with the Hartwig and PI 88788 sources of *H. glycines* resistance had more CBA compared with the *H. glycines*-susceptible cultivars during the critical period for seed set (R1–R5) (Table 8). The increased CBA for PI 88788 was due to a faster CGR (Table 8). In contrast, the increased biomass in cultivars with the Hartwig source of *H. glycines* resistance was due to longer duration of the critical period R1–R5. Aldicarb increased CBA between R1–R5 at Bancroft because of marginal increases in CGR and a longer duration of critical period (Table 8).

At Nevada, only PI 88788 provided an advantage in terms of CBA between R1–R5 (Table 8). Peking had reduced CBA during the critical period compared with the *H. glycines*-susceptible cultivars because of marginal reductions in both CGR and duration of the phase R1–R5. Aldicarb increased CBA of all cultivars evaluated in Nevada because of an increase in CGR but not an increase in the duration of the critical period (Table 8).

Seed-Filling Effects (R5–R7)

At Bancroft, cultivars with the PI 88788 source of resistance had increased CBA during the seed-filling period (R5–R7) (Table 9). A faster CGR was responsible for this increase in biomass accumulation without changes in duration of the period. Cultivars with Hartwig and Peking sources of *H. glycines* resistance had larger and reduced durations of the seed-filling period, respectively, compared with the *H. glycines*-susceptible cultivars (Table 9). These changes in duration of the seed-filling period, however, were too small to affect biomass accumulation. Aldicarb increased duration of the seed-filling period only for Hartwig-derived source of *H. glycines* resistance, as indicated by a *H. glycines* resistance source by nematicide interaction (Table 9).

At Nevada, all three sources of *H. glycines* resistance had increased CBA during the seed-filling period (Table 9). The process responsible for more CBA in Hartwig and PI

Table 5. Initial and final *H. glycines* egg population densities for susceptible and resistant cultivar groups having different sources of resistance with and without nematicide treatment (aldicarb), at two locations in Iowa, 2005–2006.

	Initial egg density		Final egg density	
	Bancroft	Nevada	Bancroft	Nevada
	eggs 100 cm^{-3} soil			
Source of resistance				
Hartwig	2733ns†	1858ns	1420***	800***
PI 88788	3275ns	1977ns	1352***	1293**
Peking	2881ns	1837ns	875***	506***
Susceptible	2595	2067	6112	4185
Nematicide				
Control	2927	1926	2244	1813
Aldicarb (2.5 kg a.i. ha^{-1})	2815	1944	2635	1580
	$P > F$			
Hartwig vs. Susceptible	0.536	0.249	<0.0001	<0.0001
PI 88788 vs. Susceptible	0.500	0.865	<0.0001	0.006
Peking vs. Susceptible	0.522	0.297	<0.0001	<0.0001
Nematicide	0.543	0.785	0.518	0.469
Source × Nematicide	0.284	0.120	0.566	0.625

*** Significantly different from susceptible cultivars $P < 0.001$.

†ns, not significant.

Table 6. Seed yield, seed number, and seed weight of *H. glycines*-susceptible and resistant cultivar groups having different sources of resistance with and without nematicide treatment (aldicarb), evaluated at two locations in Iowa, 2005–2006.

	Yield		Seed number		Seed weight	
	Bancroft	Nevada	Bancroft	Nevada	Bancroft	Nevada
	kg ha^{-1}		seeds m^{-2}		g 100 seeds^{-1}	
Source of resistance						
Hartwig	3814**	3806*	2671***	2788***	14.3***	13.6ns†
PI 88788	4052***	4008***	2559***	3125***	15.8ns	12.8***
Peking	3711ns	3752ns	2300ns	2549ns	16.2ns	14.7**
Susceptible	3586	3543	2245	2542	16.0	13.8
Nematicide						
Control	3756	3832	2447	2818	15.4	13.6
Aldicarb (2.5 kg a.i. ha^{-1})	3825	3723	2440	2684	15.7	13.8
	$P > F$					
Hartwig vs. Susceptible	0.006	0.038	<0.0001	0.001	<0.0001	0.255
PI 88788 vs. Susceptible	<0.0001	0.000	<0.0001	<0.0001	0.398	<0.0001
Peking vs. Susceptible	0.281	0.243	0.472	0.948	0.342	0.002
Nematicide	0.342	0.345	0.886	0.031	0.146	0.362
Source × Nematicide	0.664	0.267	0.522	0.265	0.825	0.723
Pi‡	0.553	0.059	0.373	0.238	0.957	0.307

* Significantly different from susceptible cultivars at $P < 0.05$.

** Significantly different from susceptible cultivars $P < 0.01$.

*** Significantly different from susceptible cultivars $P < 0.001$.

†ns = not significant at $P < 0.05$.

‡P_i = Initial *H. glycines* egg density used as covariate.

Table 7. Biomass accumulation, crop growth rate, and duration of the vegetative period encompassing emergence and beginning bloom (R1) of *H. glycines*-susceptible and resistant cultivar groups having different sources of resistance with and without nematicide treatment (aldicarb), evaluated at two locations in Iowa, 2005–2006.

	Bancroft			Nevada		
	Emergence to R1					
	Biomass	CGR	Duration	Biomass	CGR	Duration
	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}
Source of resistance						
Hartwig	117.4ns†	2.7ns	41***	76.5ns	1.9ns	39**
PI 88788	84.5ns	2.5ns	36ns	72.4ns	1.8ns	38***
Peking	112.0ns	3.2ns	36ns	70.9ns	2.1ns	34***
Susceptible	99.3	2.7	37	89.1	2.1	41
Nematicide						
Control	100.3	2.6	38	73.8	1.9	39
Aldicarb (2.5 kg a.i. ha^{-1})	106.3	2.9	37	80.7	2.2	37
	$P > F$					
Hartwig vs. Susceptible	0.089	0.909	<0.0001	0.177	0.374	0.002
PI 88788 vs. Susceptible	0.154	0.291	0.097	0.076	0.194	<0.0001
Peking vs. Susceptible	0.406	0.112	0.527	0.170	0.992	<0.0001
Nematicide	0.529	0.081	0.034	0.406	0.112	0.041
Source × Nematicide	0.281	0.231	0.311	0.579	0.552	0.536
Pi‡	0.781	0.802	0.867	0.569	0.707	0.806

* Significantly different from susceptible cultivars at $P < 0.05$.

** Significantly different from susceptible cultivars $P < 0.01$.

*** Significantly different from susceptible cultivars $P < 0.001$.

†ns = not significant at $P < 0.05$.

‡Initial *H. glycines* egg population density used as covariate.

88788 sources was a faster CGR; in Peking, both the CGR rate and the seed-filling duration increased (Table 9). In this location, aldicarb did not affect any of the parameters evaluated at Nevada.

DISCUSSION

Heterodera glycines Population Management

The three sources of *H. glycines* resistance effectively managed *H. glycines* population densities at both locations. At Bancroft, the experimental location was infested with *H. glycines* HG type 7, a population that did not have elevated virulence (greater than 10% reproduction in the HG type test) on any of the sources of resistance present in the resistant cultivars used in the experiment. Egg population densities were reduced by 48 to 70% with resistant cultivars during the season at Bancroft, and there were no differences in final *H. glycines* egg population densities among the sources of resistance in the resistant cultivars. Egg population densities increased by 135% on the susceptible cultivars at Bancroft. At Nevada, the experimental location was infested with a more diverse and virulent HG type (2.5.7) than was present at Bancroft. The *H. glycines* populations at Nevada had elevated virulence on PI 88788, one of the sources of resistance in the resistant cultivars grown in the experiment, as well as on PI 209332 and PI 548316. So it might have been expected that there would be greater final SCN egg population densities at the Nevada experiments on resistant cultivars with the PI 88788 source of resistance than resistant cultivars with the Hartwig and Peking sources of resistance. Brucker et al. (2005) indicated that PI 88788 gives only partial resistance to a HG type 2.5.7. However, in our experiments there were no differences in final *H. glycines* egg population densities among the sources of resistance, and densities were reduced by 35 to 72% by the resistant cultivars. In contrast, SCN population densities increased by 102% on the susceptible cultivars.

Heterodera glycines Source of Resistance Effects on Biomass Accumulation and Yield

Vegetative Period (Emergence to R1)

There were no differences in CBA during the vegetative period between *H. glycines*-susceptible and *H. glycines*-resistant cultivars. Detrimental effects of *H. glycines* on plant growth are usually associated with root malfunction and limited water uptake (Fallick et al., 2002). This study was not conducted under drought conditions (Table 2) and, in general, chances of water stress in the Midwest during the spring are very low (Purcell et al., 2003). This may help to explain why there were no differences between the three *H. glycines* sources of resistance early during vegetative growth. Another possibility, however, may be related to the life cycle of *H. glycines*. After the winter, eggs hatch and the infective, second-stage juveniles (J2) enter the soybean roots. A full

Table 8. Biomass accumulation, crop growth rate, and duration of the early reproductive period encompassing beginning bloom (R1) to beginning seed (R5) of *H. glycines*-susceptible and resistant cultivar groups having different sources of resistance with and without nematicide treatment (aldicarb), evaluated at two locations in Iowa, 2005–2006.

	R1–R5					
	Bancroft			Nevada		
	Biomass	CGR	Duration	Biomass	CGR	Duration
	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}
Source of resistance						
Hartwig	616.0**	11.9ns†	52***	732.5*	13.4ns	55*
PI 88788	645.7***	12.9***	50ns	692.5ns	13.0ns	53ns
Peking	608.0ns	11.8ns	51ns	617.3*	11.9ns	52ns
Susceptible	556.8	11.2	50	681.2	12.7	54
Nematicide						
Control	586.3	11.7	50	646.4	12.2	53
Aldicarb (2.5 kg a.i. ha^{-1})	626.9	12.2	51	715.4	13.3	54
	P > F					
Hartwig vs. Susceptible	0.0081	0.1019	0.0075	0.024	0.091	0.029
PI 88788 vs. Susceptible	0.0001	<0.0001	0.9909	0.619	0.470	0.851
Peking vs. Susceptible	0.1049	0.2939	0.1767	0.045	0.144	0.137
Nematicide	0.009	0.056	0.059	<0.0001	<0.0001	0.008
Source × Nematicide	0.514	0.747	0.041	0.180	0.322	0.006
Pi‡	0.385	0.592	0.235	0.053	0.061	0.846

* Significantly different from susceptible cultivars at $P < 0.05$.

** Significantly different from susceptible cultivars $P < 0.01$.

*** Significantly different from susceptible cultivars $P < 0.001$.

†ns = not significant at $P < 0.05$.

‡Initial *H. glycines* egg population density used as covariate.

cycle from the J2 infective stage to eggs formed in the cyst takes approximately 22 d under optimal conditions (Lauritis et al., 1983). However, the maximum *H. glycines* densities are first reached around soybean flowering (Niblack et al., 2006). This may suggest that potential negative effects of *H. glycines* would first be expected after the R1 growth stage.

Early Reproductive Critical Period (R1–R5)

As the crop develops and enters the critical period of yield determination (R1–R5), the probability of water stress and a buildup of *H. glycines* increases. Under these kinds of stressful conditions, cultivars with Hartwig derived and PI 88788 sources of *H. glycines* resistance at Bancroft had increased CBA compared with the SCN-susceptible cultivars. Since *H. glycines* is known to accelerate crop development (Niblack et al., 2006), it is not clear whether the alleviation of *H. glycines* effects would increase CGR or the duration of the phase. Interestingly, the increase in CBA due to PI 88788 was explained by an increase in CGR while the increase in Hartwig was due to a longer R1–R5 duration. A prolonged critical period has been previously related with more seed set (Kantolic and Slafer, 2001; Kantolic et al., 2007). For both sources of *H. glycines* resistance at this location, higher CBA was associated with higher seed number and seed yield, as was previously observed for *H. glycines*-susceptible vs. *H. glycines*-resistant cultivars (De Bruin and Pedersen, 2009). Even though both PI 88788 and Hartwig derived sources of *H. glycines* resistance have the same genomic region associated with *H. glycines* resistance (Brucker et al., 2005), results from this experiment suggest that the physiological mechanism that explain the increase in yield differ between these two sources of resistance (increased CBA via increased CGR or via increased phase duration).

At Nevada, Hartwig consistently had higher CBA because of a longer duration of the critical period compared with susceptible cultivars, consistent with the findings at Bancroft. In this case, a higher CBA was related to a higher seed number and yield. On the contrary, PI 88788 at Nevada did not increase CBA during R1–R5 compared with the susceptible cultivars. This may be related to the elevated virulence of the HG type at this location on PI 88788. Still, PI 88788 source of resistance had an increased seed number and seed yield compared with the susceptible cultivars, even though both set of cultivars had equivalent CBA during the R1–R5 period. A higher seed-number set at a given CBA during the critical period indicates a higher seed-set efficiency in PI 88788 compared with *H. glycines*-susceptible cultivars at Nevada. This higher efficiency is usually related with a lower requirement of assimilate of each seed to be set (Vega et al., 2001a). This requirement has been associated with seed size; smaller seeds usually have less amounts of assimilates (C and N) required to be set and avoid abortion (Egli, 1998). Interestingly, PI 88788 at Nevada had the smallest seed size of all the cultivars compared, which agrees with a lower assimilate requirement per seed to be set in that source.

Table 9. Biomass accumulation, crop growth rate, and duration of the seed-filling period encompassed between beginning seed (R5) to physiological maturity (R7) of *H. glycines*-susceptible and resistant cultivar groups having different sources of resistance with and without nematicide treatment (aldicarb), evaluated at two locations in Iowa, 2005–2006.

	Seed-filling period (R5–R7)					
	Bancroft			Nevada		
	Biomass	CGR	Duration	Biomass	CGR	Duration
	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}	g m^{-2}	g $d^{-1}m^{-2}$	d^{-1}
Source of resistance						
Hartwig	94.9ns†	3.8ns	23***	105.0*	4.5*	22ns
PI 88788	129.6***	5.1***	25ns	109.2*	4.5*	23***
Peking	79.0ns	3.1ns	24*	142.0**	5.1*	27***
Susceptible	90.7	3.5	25	68.4	3.0	22
Nematicide						
Control	106.2	4.3	24	110.1	4.6	24
Aldicarb (2.5 kg a.i. ha^{-1})	90.9	3.5	25	102.2	4.0	24
	$P > F$					
Hartwig vs. Susceptible	0.606	0.312	<0.0001	0.038	0.047	0.422
PI 88788 vs. Susceptible	0.001	0.001	0.474	0.021	0.047	<0.0001
Peking vs. Susceptible	0.548	0.760	0.043	0.003	0.050	<0.0001
Nematicide	0.138	0.067	0.049	0.621	0.396	0.743
Source × Nematicide	0.545	0.676	0.039	0.424	0.544	0.714
Pi‡	0.895	0.945	0.405	0.222	0.160	0.863

* Significantly different from susceptible cultivars at $P < 0.05$.

** Significantly different from susceptible cultivars $P < 0.01$.

*** Significantly different from susceptible cultivars $P < 0.001$.

†ns = not significant at $P < 0.05$.

‡Initial *H. glycines* egg population density used as covariate.

The lack of positive effect of the Peking source of resistance when compared with the susceptible cultivars at the Nevada location may be related with an actual lack of source effect or with the confounding effect of maturity group. At this site, all susceptible cultivars were a maturity group (MG) ~3, while the cultivar carrying the Peking source of resistance was MG 1.9. However, the Peking source was not different from the susceptible at the Bancroft location. At this location, MGs of Peking and the susceptible cultivars were not that different (1.9 vs. and average of 2.2 for the susceptible cultivars). This suggests that the Peking source of resistance may indeed not be better than the susceptible counterparts.

Seed Filling (R5–R7)

Seed biomass at maturity has two sources of carbon: concurrent net photosynthesis (estimated as CBA during R5–R7) and remobilization of carbon previously stored in roots, leaves, and stems (Gallagher et al., 1976). At Bancroft, only PI 88788 had increased CBA during R5–R7 compared with the *H. glycines*-susceptible cultivars. The mechanism that explained this increase is a faster CGR rather than a longer seed-filling duration that would have been likely since *H. glycines* is known to accelerate senescence (Niblack et al., 2006).

In contrast, all sources of resistance had increased CBA during the seed-filling period compared with susceptible cultivars at Nevada. Seed filling of *H. glycines*-susceptible cultivars relies highly on remobilization of carbon previously stored since it is well documented that water stress during seed filling (likely caused by a *H. glycines* infection) increase the relative participation of remobilization for seed filling (Egli et al., 1983). On the contrary, healthier root systems of the resistant cultivars may keep pace with crop water demand, increasing both the rate of crop growth and the duration of the seed-filling phase.

Effects of Aldicarb

There were only limited effects of aldicarb on the crop parameters measured at both experimental locations. Nematicide only increased CBA during the early reproductive period (R1–R5), but it occurred at both locations. Increases in CBA without reductions in *H. glycines* population densities have been attributed to direct a physiological effect of aldicarb rather than to an effect mediated by *H. glycines* control. For example, experiments under controlled conditions in the absence of *H. glycines* showed increases in soybean growth, denoting a direct physiological effect (Barker et al., 1988). Similarly, results with cotton (*Gossypium hirsutum* L.) indicated stimulatory effects of aldicarb in the absence of nematode pressure (Reddy et al., 1997). Surprisingly, the positive effect observed on CBA during the critical period for seed set was not translated into more seed yield, which may suggest that the increased growth has been counterbalanced by a reduced seed-set efficiency.

Contrasting evidence about the efficacy of aldicarb in protecting soybean yield against *H. glycines* exists. Koenning et al. (1998) found positive effects at low rates (0.84 kg a.i. ha^{-1}) of aldicarb on plant height and crop cover that translated into limited yield increases (100–200 kg ha^{-1}) in one out of 3 yr. Noel (1987) showed slight aldicarb effects with doses up to 3.6 kg a.i. ha^{-1} on yield of *H. glycines*-susceptible cultivar in Illinois, showing increases in yield in one out of three locations evaluated. Trevathan and Robbins (1995) indicated small yield increases (i.e., 100 kg ha^{-1}) with aldicarb rates of 0.84 kg a.i. ha^{-1}. Conversely, experiments conducted in sandy soils in Alabama indicated yield benefits of approximately 400 kg ha^{-1} with 3.6 kg a.i. ha^{-1} (Weaver et al., 1995). Minton (1992) reported yields increases between 800 and 1200 kg due to applications of aldicarb at 3.6 kg a.i. ha^{-1} in a similar soil type in Georgia. Discrepancies in yield responses to aldicarb seem to be related to soil type, weather pattern, initial *H. glycines* densities, rate, and cultivar interactions (Smith et al., 1991).

The positive effect of nematicide was expected to be more likely observed in *H. glycines* susceptible cultivars. But in most cases, aldicarb affected the various resistant and susceptible cultivars used in our experiments similarly. However, aldicarb increased the duration of the R1–R5 phase at both locations only in the *H. glycines*-resistant cultivars derived from Hartwig. This effect was small and did not determine a differential effect on CBA for this source compared with the other ones. The result suggests that the physiological effect, potentially associated with aldicarb, is source-dependent. De Bruin and Pedersen (2008b) found that fumigation with Telone C-35 (Dow Agroscience, Indianapolis, IN) eliminated yield differences among cultivars with the same sources of resistance, suggesting a similar effect of the fumigant across sources in locations that included fields with high virulence of *H. glycines*.

CONCLUSIONS

The results of this research show that soybean cultivars with different sources of resistance to *H. glycines* had different physiological mechanisms that explain yield increases compared with susceptible cultivars. The mechanisms involved increased growth during the critical period for some of the sources of resistance but also differences in critical period duration and seed-set efficiency in other sources. The different sources of *H. glycines* resistance (with the exception of Peking) were tested under three different backgrounds, providing true replications to test the effect of the sources and to provide confidence on the conclusions brought up in this paper. However, the development of isolines carrying the sources of resistance is needed to obtain the most definitive conclusion and to avoid possible limitations related with confounding factors such as the identity of the cultivar. Our work also showed that aldicarb did not increase yield of *H. glycines*-resistant cultivars in the years and at the locations that the experiments were conducted. The nematicide only increased CBA during the R1–R5 period, probably because of a direct physiological effect of aldicarb rather than to an effect on *H. glycines* population densities, and there was no effect on yield for any of the three sources of *H. glycines* resistance studied.

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