

# Influence of *Heterodera glycines* on Interspecific and Intraspecific Competition Associated with *Glycine max* and *Chenopodium album*

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**Abstract:** The influence of *Heterodera glycines* (soybean cyst nematode) on the interspecific and intraspecific competition associated with *Glycine max* (soybean) and *Chenopodium album* (common lambsquarters) was studied in 1988 and 1989 in three de Wit replacement series experiments in growth chambers and microplots. *Glycine max* was grown alone (1 plant/experimental unit), in intraspecific competition (2 plants/experimental unit), in interspecific competition with *C. album*, and in presence or absence of *H. glycines*. No significant effects of *H. glycines* and *C. album* on *G. max* growth were observed 14 days after planting. By 42 days after planting, both *H. glycines* and *C. album* had a negative ( $P = 0.05$ ) influence on the growth of *G. max*. Relative crowding coefficients for *G. max* were lower and deviated ( $P = 0.05$  and  $P = 0.001$ ) from 1.0 in the presence of *H. glycines*, compared to that of *C. album* and early emerged *C. album* in the absence of the nematode, respectively. *Glycine max*, therefore, became less competitive than *C. album*. There was a trend that the presence of *H. glycines* decreased the competitiveness of *G. max* on measures of the aggressivity and relative mixture response. *Heterodera glycines* decreased the aggressivity of *G. max* (ca. 150–350%) and increased the relative effects of intraspecific interference on *G. max* (ca. 10–50%) and interspecific interference (ca. 60–350%) after 42 days of plant growth, compared with plants grown in the absence of *H. glycines*. No *H. glycines* × *C. album* interactions were detected. Observations showed that *H. glycines* and early emerged *C. album* inhibited the growth of *G. max* 5–13%, as measured by plant dry weight.

**Key words:** aggressivity, *Chenopodium album*, common lambsquarters, competition, *Glycine max*, *Heterodera glycines*, interaction, interspecific competition, intraspecific competition, soybean, soybean cyst nematode.

*Chenopodium album* L., common lambsquarters, is one of the most widely distributed weed species in the United States and throughout the world. In Michigan, 32 *C. album* plants/10 m of row decreased soybean (*Glycine max* (L.) Merr.) yield 20% (4). *Heterodera glycines* Ichinohe (soybean cyst nematode) (SCN) is a major limiting factor in U.S. soybean production (3,13). This nematode was first detected in Michigan in 1987, and is currently known to be present in 12 counties (19). *Heterodera glycines* is also a problem in Michigan dry bean production (2).

Coexistence of *H. glycines* and *C. album* in soybean fields is not unusual. There is an extensive literature on interactions between *G. max* and *H. glycines*, including the effects of SCN and environmental factors

on the early growth of *G. max* (3,10,13,14, 16,17) and on competition between *G. max* and *C. album* (4). There are no previous reports, however, on the relationship between *G. max* and *C. album* in the presence of *H. glycines*.

Competition is defined as mutually adverse impacts among organisms that utilize common resources in short supply. Intraspecific competition results from negative interactions among organisms of the same species, whereas interspecific competition constitutes adverse interactions among different species (4). Competitive interactions among plants are complex, and require thorough investigation of each component to understand the competition component of the ecosystem (11). The objectives of this research were to determine the impact of *H. glycines* on interspecific and intraspecific competition associated with *G. max* and *C. album*.

## METHODS AND MATERIALS

*de Wit replacement series:* The de Wit method of substitution analysis was used to

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identify relationships among plants growing concomitantly, and to predict competitiveness among species (6,12). Using this procedure, total plant population density remains constant while the proportion of the *G. max* and *C. album* to each other are varied. The experimental treatments included two *G. max* per pot; one *G. max* and one *C. album* per pot; and two *C. album* per pot. The plants were grown in the presence or absence of *H. glycines*. *Glycines max* or *C. album* were also grown alone (one plant/experimental unit) in the presence or absence of *H. glycines*. The experimental variables ( $\pm G. max$ ;  $\pm C. album$ ;  $\pm H. glycines$ ;  $\pm$ intraspecific interference of *G. max*) were evaluated in three factorial experiments using the replacement series procedure.

*Experiments:* The first experiment (growth chamber experiment 1) with a  $2 \times 3$  factorial design was initiated on 19 November 1988. A growth chamber was programmed for a 16-hour day of photoperiod at 24 C, and 8-hour night at 16 C. Steam-sterilized (2 hours at 98 C) loamy sand (75.3% of sand, 13.7% of silt, 11.0% of clay, 1.1% of organic matter) was used. Manganese was added to the soil mix at the equivalent rate of broadcasting 111 kg/ha. *Glycine max* cv. Corsoy 79, susceptible to *H. glycines*, was used in all experiments. Seeds of *G. max* were inoculated with *Bradyrhizobium japonicum* (Kirchner) Jordan before planting. Seeds of *C. album*, a nonhost of *H. glycines* (1), were stored at 4 C before planting. Seeds of both plant species were germinated in vermiculite.

Plants were destructively sampled 14, 28, and 42 days after planting. Plants were dried at 90 C to a constant weight. Total dry weights of *G. max* and *C. album* were determined for the first, second, and third harvest. Roots of the first harvest were weighed separately. Duncan's multiple-range test was performed to determine LSD values at  $P = 0.05$ .

The *H. glycines* population was obtained from a SCN-infested field site in Gratiot County, Michigan. An inoculum rate of

300 eggs and second-stage juveniles (J2) of *H. glycines* per 100 cm<sup>3</sup> of soil was added to sterilized soil in ca. 1,600 cm<sup>3</sup> experimental units 2 days after *G. max* transplanting. Infection by *H. glycines* was determined 14 days after planting by staining four randomly selected root systems (7).

The second experiment (growth chamber experiment 2) with a  $2 \times 4$  factorial design was initiated on 30 June 1989. The methods were the same as described for the previous experiment. An inoculum rate of 600 eggs and J2 of *H. glycines* per 100 cm<sup>3</sup> of soil was added to sterilized soil in ca. 1,600 cm<sup>3</sup> experimental units 2 days after *G. max* transplanting.

The third experiment (microplot experiment) with a  $2 \times 4$  factorial design was initiated on 8 July 1989. The methods were the same as described for the previous experiment. Microplots were established 0.3 m apart in the middle of 1.0-m strips of soil fumigated with 558 kg/ha of 98% methyl bromide and 2% chloropicrin 14 days before planting. An inoculum rate of 150 eggs and J2 of *H. glycines* per 100 cm<sup>3</sup> of soil was added to the steam-sterilized loamy sand ca. 10,000 cm<sup>3</sup> experimental units 2 days after *G. max* transplanting.

*Factorial analysis:* The factorial treatments were arranged in a completely randomized design with four replications. Factorial analyses were used for each experiment. The factorial set of treatment combinations was the level of every factor that occurs together with each level of every other factor. The "A" factor was assigned to the effects of *H. glycines* (A1 = absence of *H. glycines* and A2 = presence of *H. glycines*). The "B" factor was assigned to the other experimental variables. In growth chamber experiment 1, the levels of factor B were as follows: B1 = without intra- and interspecific competition; B2 = with interspecific competition (*C. album* planted at same time with *G. max*); and B3 = with intraspecific competition. In growth chamber experiment 2 and the microplot experiment, the levels of factor

were as follows: B1 = without intra- and interspecific competition; B2 = with early emerged *C. album* interspecific competition (*C. album* was planted 7 days before *G. max*); B3 = with delay emerged *C. album* interspecific competition (*C. album* was planted 7 days after *G. max*); and B4 = with intraspecific competition.

If an interaction was nonsignificant, it was concluded that the "A" and "B" factors acted independently of each other. The main effect then was considered the best estimate of the differences (9). The main effects of *H. glycines*, intraspecific and interspecific competitions, on *G. max* dry weights were calculated (9) from the equations (1) to (3), given that  $\bar{x}_i$  = mean of factor A level *i*,  $\bar{x}_j$  = mean of factor B level *j*, and  $\bar{X}$  = grand mean. Results of the main effects were interpreted and discussed when the *P* value of the factor was 0.05 or less.

$$A_i = \bar{x}_i - \bar{X} \quad (i = 1, 2) \quad (1)$$

$$B_j = \bar{x}_j - \bar{X} \quad (j = 1, 2, 3) \quad (2)$$

$$B_j = \bar{x}_j - \bar{X} \quad (j = 1, 2, 3, 4) \quad (3)$$

*Competition parameters:* Replacement series studies enabled the determination of competition parameters for growth of *G. max* with respect to *C. album*. Aggressivity (a) was used to evaluate the relative success of two species using resources, interference, and hierarchy of competitiveness (12,15,18). Relative monoculture response (Rm) and relative mixture response (Rx) are the relative effects of intraspecific and interspecific interference, respectively, on the biomass of a species. They are calculated as quantitative measures of plant interference; since it is often more suitable to assess the effects of interference on a relative rather than absolute basis (8). The relative crowding coefficient (RCC) was described by Harper as a way to measure the competitiveness of one species on another (6).

Competitive relationships were quantitatively represented in equation (4)–(7), given that Ax and Bx are the biomass of species A and B in mixture, respectively;

Am and Bm are the biomass of species A and B in pure stand, respectively; and A is the biomass of only one plant per experimental unit.

$$a = Ax/Am - Bx/Bm \quad (4)$$

$$Rm = (A - Am)/A \quad (5)$$

$$Rx = (Am - Ax)/Am \quad (6)$$

$$RCC = (Ax/Am)/(Bx/Bm) \quad (7)$$

The nature of interactions between component species in a mixture is indicated by *a*, Rx, or RCC. When *a* = 0, Rx = 0, or RCC = 1.0, the interspecific competition by each component of the system is equally severe. When *a* > 0, Rx < 0, or RCC > 1.0, *G. max* competition is more severe than *C. album*. When *a* < 0, Rx > 0, or RCC < 1.0, *G. max* competition is less severe than *C. album*. A Student's *t*-test analysis was performed to determine the deviation (*P* = 0.05) of each *G. max* RCC value from 1 using an MSTAT-C Software Program (MSTAT/Crop and Soil Science, Michigan State University, East Lansing, Michigan).

## RESULTS

Second-stage juveniles of *H. glycines* were present in the roots of inoculated *G. max* 14 days after planting. Females of *H. glycines* were present in *G. max* roots 42 days after planting.

No effect of *H. glycines* on *G. max* was detectable 14 days after planting. Negative effects attributable to nematode parasitism, however, were evident after 42 days (Tables 1–3). *Chenopodium album* effects on *G. max* were observed after 28 days in all three experiments. No *H. glycines* × *C. album* interactions were detected in any of the experiments.

The presence of *H. glycines* resulted in a decrease in *G. max* dry weight of 0.07 g/plant after 28 days, an equivalent of a 3.4% loss in growth chamber experiment 2 (Table 2). The presence of *H. glycines* inhibited the growth of *G. max* 0.30, 0.29, and 0.47 g dry weight per plant, an equivalent of a 5–6% loss after 42 days, in growth chamber experiment 1 (Table 1), growth cham-

TABLE 1. Factorial analysis of *Glycine max* dry weights and *Chenopodium album* (0–42 days) competition in the presence or absence of *Heterodera glycines* in growth chamber experiment 1.

Factor A	Factor B	<i>G. max</i> dry weight (g/plant)		
		14 days	28 days	42 days
- <i>H. glycines</i> - interspecific/intraspecific competition		0.42	2.85	6.38
- <i>H. glycines</i> + interspecific competition with <i>C. album</i>		0.32	2.14	3.68
- <i>H. glycines</i> + intraspecific competition with <i>G. max</i>		0.31	1.81	4.38
+ <i>H. glycines</i> - interspecific and intraspecific competition		0.38	2.53	5.45
+ <i>H. glycines</i> + interspecific competition with <i>C. album</i>		0.24	1.78	3.25
+ <i>H. glycines</i> + intraspecific competition with <i>G. max</i>		0.39	1.72	3.95
LSD value at $P = 0.05$		0.11	0.50	1.06
Main effect of <i>H. glycines</i> absence (A1)		+0.01	+0.13	+0.30
Main effect of <i>H. glycines</i> presence (A2)		-0.01	-0.13	-0.30
Main effect of plant competition absence (B1)		+0.06	+0.55	+1.40
Main effect of <i>C. album</i> competition (B2)		-0.02	-0.18	-1.05
Main effect of <i>G. max</i> competition (B3)		-0.04	-0.37	-0.35

There were no A × B interaction ( $P = 0.05$ ) after 14, 28, and 42 days. Factor A was significant ( $P = 0.05$ ) after 42 days. Factor B was significant ( $P = 0.05$ ) after 28 and 42 days. The main effects of the presence or absence of *H. glycines* on *G. max* dry weights were calculated from the equation (1):  $A_i = \bar{x}_i - \bar{X}$  ( $i = 1, 2$ ) where  $\bar{x}_i$  = mean of factor A level  $i$  and  $\bar{X}$  = grand mean. The main effects of the presence or absence of intraspecific or interspecific competitions on *G. max* dry weights were calculated from the equation (2):  $B_j = \bar{x}_j - \bar{X}$  ( $j = 1, 2, 3$ ) where  $\bar{x}_j$  = mean of factor B level  $j$  and  $\bar{X}$  = grand mean.

ber experiment 2 (Table 2), and the microplot experiment (Table 3), respectively.

Competition from *C. album* planted at the same time as *G. max* resulted in 6.3% less dry weight per plant after 28 days of growth. The level of growth suppression almost tripled (16.5%) after 42 days (Table 1). Competition from early emerged *C. album* caused a 10–11% decrease in *G. max* dry weight after 28 days. The results were

similar (10–13%) after 42 days under both growth chamber and microplot conditions (Tables 2–3).

Forty-two days after planting, the relative crowding coefficients for *G. max* were

TABLE 2. Factorial analysis of *Glycine max* dry weights and *Chenopodium album* (0–42 days) competition in the presence or absence of *Heterodera glycines* in growth chamber experiment 2.

Factor A	Factor B	<i>G. max</i> dry weight (g/plant)		
		14 days	28 days	42 days
- <i>H. glycines</i> - interspecific/intraspecific competition		0.44	2.08	4.90
- <i>H. glycines</i> + competition with early emerged <i>C. album</i>		0.41	1.42	3.39
- <i>H. glycines</i> + competition with delay emerged <i>C. album</i>		0.44	1.48	3.73
- <i>H. glycines</i> + competition with <i>G. max</i>		0.38	1.43	3.59
+ <i>H. glycines</i> - interspecific and intraspecific competition		0.41	1.86	3.94
+ <i>H. glycines</i> + competition with early emerged <i>C. album</i>		0.41	1.23	2.80
+ <i>H. glycines</i> + competition with delay emerged <i>C. album</i>		0.44	1.51	3.53
+ <i>H. glycines</i> + competition with <i>G. max</i>		0.37	1.29	2.99
LSD value at $P = 0.05$		0.07	0.25	0.61
Main effect of <i>H. glycines</i> absence (A1)		+0.01	+0.07	+0.29
Main effect of <i>H. glycines</i> presence (A2)		-0.01	-0.07	-0.29
Main effect of plant competition absence (B1)		+0.02	+0.43	+0.81
Main effect of early emerged <i>C. album</i> competition (B2)		-0.01	-0.21	-0.51
Main effect of delay emerged <i>C. album</i> competition (B3)		+0.03	-0.04	+0.02
Main effect of <i>G. max</i> competition (B4)		-0.04	-0.18	-0.32

There were no A × B interactions ( $P = 0.05$ ) after 14, 28, and 42 days. Factor A and B were significant ( $P = 0.05$ ) after 28 and 42 days. The main effects of the presence or absence of *H. glycines* on *G. max* dry weights were calculated from the equation (1):  $A_i = \bar{x}_i - \bar{X}$  ( $i = 1, 2$ ) where  $\bar{x}_i$  = mean of factor A level  $i$  and  $\bar{X}$  = grand mean. The main effects of the presence or absence of intraspecific or interspecific competitions on *G. max* dry weights were calculated from the equation (2):  $B_j = \bar{x}_j - \bar{X}$  ( $j = 1, 2, 3, 4$ ) where  $\bar{x}_j$  = mean of factor B level  $j$  and  $\bar{X}$  = grand mean.

TABLE 3. Factorial analysis of *Glycine max* dry weights and *Chenopodium album* (0–42 days) competition in the presence or absence of *Heterodera glycines* in microplots.

Factor A	Factor B	G. max dry weight (g/plant)		
		14 days	28 days	42 days
-	<i>H. glycines</i> - interspecific/intraspecific competition	0.64	2.72	10.49
-	<i>H. glycines</i> + competition with early emerged <i>C. album</i>	0.64	2.11	7.13
-	<i>H. glycines</i> + competition with delay emerged <i>C. album</i>	0.63	2.70	10.28
-	<i>H. glycines</i> + competition with <i>G. max</i>	0.60	2.25	7.36
+	<i>H. glycines</i> - interspecific and intraspecific competition	0.54	2.27	8.21
+	<i>H. glycines</i> + competition with early emerged <i>C. album</i>	0.64	2.09	6.86
+	<i>H. glycines</i> + competition with delay emerged <i>C. album</i>	0.67	2.71	9.57
+	<i>H. glycines</i> + competition with <i>G. max</i>	0.58	2.29	6.87
LSD value at $P = 0.05$		0.11	0.38	1.46
Main effect of <i>H. glycines</i> absence (A1)		+0.01	+0.05	+0.47
Main effect of <i>H. glycines</i> presence (A2)		-0.01	-0.05	-0.47
Main effect of plant competition absence (B1)		-0.03	+0.10	+1.00
Main effect of early emerged <i>C. album</i> competition (B2)		+0.02	-0.29	-1.35
Main effect of delay emerged <i>C. album</i> competition (B3)		+0.03	+0.31	+1.58
Main effect of <i>G. max</i> competition (B4)		-0.03	-0.12	-1.23

There were no A × B interactions ( $P = 0.05$ ) after 14, 28, and 42 days. Factor A was significant ( $P = 0.05$ ) after 42 days. Factor B was significant ( $P = 0.05$ ) after 28 and 42 days. The main effects of the presence or absence of *H. glycines* on *G. max* dry weights were calculated from the equation (1):  $A_i = \bar{x}_i - \bar{X}$  ( $i = 1, 2$ ) where  $\bar{x}_i$  = mean of factor A level  $i$  and  $\bar{X}$  = grand mean. The main effects of the presence or absence of intraspecific or interspecific competitions on *G. max* dry weights were calculated from the equation (3):  $B_j = \bar{x}_j - \bar{X}$  ( $j = 1, 2, 3, 4$ ) where  $\bar{x}_j$  = mean of factor B level  $j$  and  $\bar{X}$  = grand mean.

lower and deviated significantly from 1.0 in the presence of *H. glycines*, compared with *C. album*, and the early emerged *C. album* in the absence of *H. glycines* (Table

4). *Glycine max*, therefore, became less competitive than *C. album*. RCC values of soybean with respect to delay emerged *C. album* exceeded 1.0 under both growth chamber and microplot conditions, and are not presented in Table 4.

The results of the aggressivity analysis were similar to that of the relative crowding coefficient in all experiments (Table 4). There was also a trend that the presence of *H. glycines* decreased the competitiveness of *G. max* as measured by the relative mixture response (Table 4). *Heterodera glycines* decreased the aggressivity of *G. max* from -0.06 to -0.21 in growth chamber experiment 1, and ca. 150–350% overall in all experiments, compared with plants grown in the absence of *H. glycines* (Table 4). *Heterodera glycines* increased the relative effects of intraspecific interference on *G. max* from 0.31 to 0.38 in growth chamber experiment 1, and ca. 10–50% overall in all experiments, compared with plants grown in the absence of *H. glycines* (Table 4). *Heterodera glycines* increased the relative effects of interspecific interference on *G. max* from 0.16 to 0.26 in growth chamber experiment 1, and ca. 60–350% overall in all experiments, compared with plants grown in the absence of *H. glycines* (Table 4).

## DISCUSSION

Both *H. glycines* and *C. album* had a detrimental impact on *G. max* by 42 days after planting. Although the statistical analysis indicated that there were no significant interactions between *H. glycines* and *C. album*, the relative crowding coefficient analysis showed that *H. glycines* decreased the competitiveness of *G. max* in relation to *C. album*. These results support the observation that nematode-infested fields frequently have more serious weed problems than noninfested sites.

The negative influence of competition by *C. album* appeared to affect *G. max* earlier in the growth period than the pathogenicity of *H. glycines*. This should be expected because *C. album* can compete for

TABLE 4. Effect of *Heterodera glycines* presence or absence on competitive relationships between *Glycine max* and *Chenopodium album*.

Relative emergence	<i>G. max</i> competition parameters with respect to <i>C. album</i>							
	a		Rx		Rm		RCC	
	-SCN	+SCN	-SCN	+SCN	-SCN	+SCN	-SCN ( $P > t$ )	+SCN ( $P > t$ )
Concomitant planting	-0.06	-0.21	0.16	0.26	0.31	0.38	0.93 (0.5125)	0.82 (0.0193)
<i>C. album</i> 7 days before	-0.41	-0.84	0.06	0.22	0.27	0.39	0.70 (0.0304)	0.48 (0.0002)
<i>C. album</i> 7 days after	0.80	0.70	-0.04	0.02	0.27	0.39		
<i>C. album</i> 7 days before	-0.27	-0.44	-0.03	0.04	0.32	0.36	0.80 (0.0079)	0.69 (0.0001)
<i>C. album</i> 7 days after	1.41	1.31	-0.44	-0.34	0.32	0.36		

Plants were harvested 42 days after planting in growth chamber experiments 1 and 2, and the microplot experiment.  $a = Ax/Am - Bx/Bm$ , where  $a$  is aggressivity,  $Ax$  and  $Bx$  are *G. max* and *C. album* dry weights in mixture, respectively, and  $Am$  and  $Bm$  are *G. max* and *C. album* dry weights in pure stand, respectively.  $Rm = (A - Am)/A$ , where  $Rm$  is relative monoculture response,  $A$  is *G. max* dry weight of only one plant per unit, and  $Am$  was previously defined.  $Rx = (Am - Ax)/Am$ , where  $Rx$  is relative mixture response, and others are as previously defined.  $RCC = (Ax/Am)/(Bx/Bm)$ , where  $RCC$  is relative crowding coefficient, and others are as previously defined. Student's  $t$ -test indicates if *G. max* RCC values are significantly different from 1.

resources beginning with seed germination, whereas *H. glycines* must locate, infect, and establish a pathogenic host-parasite relationship before a detrimental impact occurs.

It is interesting to note that the inoculum levels of 300 or fewer eggs and J2 of *H. glycines* per 100 cm<sup>3</sup> of soil did not affect the dry weight of *G. max* 28 days after planting under both growth chamber and microplot conditions. Both pest effects were generally significant, particularly 42 days after planting. The interactions were not significant, however, indicating that the nematode and weed acted independently with respect to soybean growth and development.

Watkinson and Gibson compared the influence of plant parasites on community structure with that of herbivores and predators (20). Gates et al. (5) confirmed that host-specific pathogen attack may alter the competitive relationships between different, co-occurring plant genotypes. Price et al. (11) stated that parasites affect ecosystem function as profoundly as any other elements in the system. The interactions they mediate are abundant, complex, subtle, and important as any others. The cumulative evidence suggests that parasites may modify the ecology and evolution of numerous types of interaction. The results in our studies, particularly the effects of *H.*

*glycines* on competitive relationships between early *G. max* development and *C. album*, support the need for further investigation on the joint impacts of nematodes and weeds on the growth and yield of agricultural crops.

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