Soybean Genotypes Resistant to *Phytophthora sojae* and Compensation for Yield Losses of Susceptible Isolines

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ABSTRACT

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Two isolines, with different alleles for resistance to *Phytophthora sojae*, of the soybean cultivars, Beeson, Century, and Williams were grown in replicated tests to assess yield losses attributable to this pathogen. Isolines susceptible to prevalent races of the pathogen had black seed coats as a marker trait; isolines resistant to prevalent races of the pathogen had yellow seed coats. Included in the tests were blends composed of equal numbers of seed of the two isolines for each cultivar. Tests were conducted at three locations in Indiana and one location in Ohio for three years. In six environments, where *Phytophthora* root and stem rot damaged soybean, isolines susceptible to prevalent races of the pathogen produced seed yields from 65 to 93% of the yields of isolines resistant to these races. In four of these environments, isoline blends produced yields equal to those of the resistant isoline. In two environments, where susceptible isolines averaged 65 and 69% of the yield of the resistant isoline; the blends averaged 89 and 83% of the yield of the resistant isoline. Where the pathogen reduced yields of susceptible isolines, yellow seeds of the isoline resistant to prevalent races of the pathogen contributed from 10 to 33% more seed than would be expected if resistant and susceptible isolines contributed equally to seed yield. The data demonstrate that plants of the resistant isoline were compensating for reduced productivity of the susceptible plants in the blend.

Phytophthora root and stem rot, caused by *Phytophthora sojae* (Kaufmann and Gerdeman), is a destructive disease of soybean (*Glycine max* (L.) Merr.) in the United States. Wrather et al. (19) estimated that the disease reduced soybean yields by 560,300 metric tons in the United States in 1994. In the North Central States, yield losses due to this pathogen have been estimated at 13% of total production for each of the years 1989 through 1991 (7).

Yield losses to *P. sojae* have been limited by incorporating into cultivars *Rps* alleles for resistance to prevalent races of the pathogen. As new races of the pathogen developed, additional *Rps* alleles were found that protect soybean against these races. Resistance alleles are incorporated into new cultivars, or backcrossed into productive cultivars, to provide soybean producers with adequate protection against the pathogen. During the past 25 years, more than 40 different races of the pathogen have been identified (1). During this

same time, 13 alleles that control resistance to multiple races of the pathogen have been identified at seven different loci (3). Several years are required to incorporate new *Rps* alleles into high-yielding cultivars, and yield losses due to new *P. sojae* races will continue to occur during resistant cultivar development. Planting blends of lower yielding resistant and higher yielding susceptible cultivars may provide a mechanism to optimize production until high-yielding resistant cultivars are available.

Blends of cultivars or isolines have been used to control losses due to pathogens in several agronomic crops. Yield losses of cereal grains, primarily due to rusts, have been reduced by growing blends of isolines or cultivars with different loci controlling resistance (6,8,18). These blends, or multi-lines, slow the rate of increase of prevalent races of the pathogen on host plants. Blends of soybean cultivars have been recommended as a strategy to delay shifts of soybean cyst nematode (*Heterodera glycines* Ichinohe) populations from one race to another in production fields (13). Anand et al. (2) reported that 50:50 blends of soybean cultivars resistant and susceptible to soybean cyst nematode were generally similar in yield to the resistant components and always higher in yield than susceptible components when grown in monoculture.

This study was conducted to evaluate the performance of isoline blends of soy-

bean cultivars having different alleles controlling resistance to different races of *P. sojae*. A marker trait for the different components of the blends permitted an accurate assessment of the contribution of each component of the blend to seed yield.

MATERIALS AND METHODS

Two isolines of the cultivars Beeson, Century, and Williams were included in the study. The isolines differed in alleles for resistance to prevalent races of *P. sojae*. Beeson (9) and Century (15) have the *Rps1-a* allele for resistance to races 1, 2, 10, 11, 13–18, 24, 26, 27, 31, 32, and 36 of *P. sojae* (1). Williams (5) has the *rps1* allele that results in susceptibility to all races of the pathogen. Beeson, Century, and Williams all had completely black or imperfect black seed coat color (*Sb*). The unique black or imperfect black seed coats were due to spontaneous mutations to the *i* allele at the *I* locus (17). Seeds with black seed coats had been selected from normal colored seed lots of each of these cultivars. The dark colored seeds of each cultivar were increased for use in this study. The black seed coat served as a neutral marker with respect to seed yield for these isolines (14).

A second isoline, Beeson 80, Century 84, and Williams 82, of each of the three cultivars was included in the study. Beeson 80 (16), with the *Rps1-c* allele, is resistant to races 1–3, 6–11, 13, 15, 17, 21, 23, 24, 26, 28–30, 32, 34, 36, 41, 42, and 44 of the pathogen (1). Century 84 (12) and Williams 82 (4) have the *Rps1-k* allele that confers resistance to races 1–11, 13–15, 17, 18, 21–24, 26, 36, 37, and 42–44 of *P. sojae* (1). These isolines all had the *i* alleles at the *I* locus and dark pigmentation is restricted to the hilum on seeds, the remainder of the seed coat is yellow (*Sy*). The yellow seed coat served as a convenient neutral marker for these isolines.

Plots of the six genotypes (Beeson [Sb], Beeson 80 [Sy], Century [Sb], Century 84 [Sy], Williams [Sb], and Williams 82 [Sy]) and three blends, composed of equal numbers of seed of the two isolines of each cultivar, were grown at Bluffton, and Davis, IN, and at Hoytville, OH. *P. sojae* commonly reduces seed yield of cultivars with the *Rps1-a* or *rps1* alleles at these locations. Cultivars with the *Rps1-c* or *Rps1-k* alleles typically do not show dis-

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ease symptoms or reduced seed yield due to *P. sojae* at these locations. Plots of these six genotypes and the blends also were grown at West Lafayette, IN, where yield losses due to this pathogen seldom occur. A split-plot randomized design was used at each location in which main plots were cultivars and three subplots consisted of 1)

the black seeded isoline indicating the *Rps1-a* or *rps1* alleles for *P. sojae* resistance, 2) the yellow seeded isoline indicating the *Rps1-c* or *Rps1-k* alleles for resistance, and 3) a blend of equal numbers of black and yellow seed of the two isolines. Each subplot consisted of four rows, 5 m in length and spaced 0.6 m apart, at the three Indiana

locations. Rows were end-trimmed to 3.7 m in length prior to maturity and the center two rows harvested for seed yield. At Hoytville, OH, subplots consisted of six rows 5 m in length with a 0.38 m spacing between rows. These plots were end-trimmed to 3.4 m prior to maturity and the center four rows harvested for seed yield. Each subplot at all locations was seeded with 450 seeds of each entry in the test. Six replications were grown at each location in each of 3 years of the test. Planting dates were between 11 and 23 May for the various locations in the 3 years of the tests.

During the growing seasons, observations were made of stunted and diseased plants with stem lesions symptomatic of *Phytophthora* root and stem rot. After harvest, data were recorded on seed yield as grams per plot and converted to kilograms per hectare before analyses. The number of black and yellow seeds in a 400-seed sample from each subplot in each replication was recorded. Analyses of variance were computed on data for each of the traits measured at each location for each year. After preliminary analyses of data, environments were placed in one of two fixed classes, disease present or disease absent. Within each of these classes, environments were considered random effects in the data analyses.

RESULTS

No data were recorded from the Bluffton location in 1992 because excessive rainfall resulted in ponding in the plot area and loss of many of the plots.

No plants were observed that exhibited symptoms of *Phytophthora* root and stem rot at any location in 1992 or at West Lafayette in any year of the tests. There were no significant differences in seed yields between isolines susceptible and resistant to *P. sojae* races at these locations (Table 1). Plots planted to blends of the isolines were similar in yield to the isoline components of the blends in these five environments. There were no significant differences in numbers of yellow and black seeds harvested from plots planted to blends of the isolines in each of these environments, except West Lafayette in 1993. In this environment, there were 10.5% more yellow seeds of the *Rps1-c* and *Rps1-k* isolines than the expected 200:200 ratio.

At six test location-year combinations (environments), yields of the *Rps1-a* and *rps1* isolines were significantly lower than yields of the *Rps1-c* and *Rps1-k* isolines (Table 2). Plants with typical *Phytophthora* root and stem rot symptoms were observed in these environments. Analyses of variance demonstrated that the interaction of variety $\times$ subplot component (black-seeded, yellow-seeded, blend) for seed yield was not significant in five of the six environments, which indicates that the differences in yields among the isolines and blends were consistent across environments.

Table 1. Average seed yields and incidence of yellow and black seeds of isolines with *Rps1-c* and *Rps1-k* alleles compared to isolines with *Rps1-a* and *rps1* alleles and isoline blends in environments with no significant yield reductions associated with *Phytophthora sojae*

Test site and isoline components	Yield (kg/ha)	Yellow seeds ^x (no.)	Black seeds ^y (no.)
Davis, 1992			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,252 a ^z	398	2
<i>Rps1-a</i> or <i>rps1</i>	3,282 a	1	399
Blend	3,072 a	217	183
Lafayette, 1992			
<i>Rps1-c</i> or <i>Rps1-k</i>	2,504 a	399	1
<i>Rps1-a</i> or <i>rps1</i>	2,467 a	2	398
Blend	2,440 a	210	190
Lafayette, 1993			
<i>Rps1-c</i> or <i>Rps1-k</i>	4,231 a	394	6
<i>Rps1-a</i> or <i>rps1</i>	4,070 a	5	395
Blend	4,199 a	221	179
Lafayette, 1994			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,142 a	397	3
<i>Rps1-a</i> or <i>rps1</i>	3,016 a	6	394
Blend	3,192 a	201	199
Hoytville, 1992			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,317 a	399	1
<i>Rps1-a</i> or <i>rps1</i>	3,314 a	0	400
Blend	3,309 a	203	197

^x Yellow seeds, from a sample of 400 seeds from each plot, indicate isolines with the *Rps1-c* and *Rps1-k* alleles.

^y Black seeds, from a sample of 400 seed from each plot, indicate isolines with the *Rps1-a* or *rps1* alleles.

^z Means followed by the same letter do not differ at the 0.05 probability level.

Table 2. Average seed yields and incidence of yellow and black seeds of isolines with *Rps1-c* and *Rps1-k* alleles compared to isolines with *Rps1-a* and *rps1* alleles and isoline blends in environments with significant yield reductions associated with *Phytophthora sojae*

Test site and isoline components	Yield (kg/ha)	Yellow seeds ^x (no.)	Black seeds ^y (no.)
Bluffton, 1993			
<i>Rps1-c</i> or <i>Rps1-k</i>	2,499 a ^z	398	2
<i>Rps1-a</i> or <i>rps1</i>	1,908 b	3	397
Blend	2,133 b	249	151
Bluffton, 1994			
<i>Rps1-c</i> or <i>Rps1-k</i>	2,684 a	398	2
<i>Rps1-a</i> or <i>rps1</i>	1,991 c	3	397
Blend	2,422 b	266	134
Davis, 1993			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,418 a	397	3
<i>Rps1-a</i> or <i>rps1</i>	2,603 b	4	396
Blend	3,356 a	259	141
Davis, 1994			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,541 a	399	1
<i>Rps1-a</i> or <i>rps1</i>	3,141 b	5	395
Blend	3,484 a	229	171
Hoytville, 1993			
<i>Rps1-c</i> or <i>Rps1-k</i>	1,997 a	399	1
<i>Rps1-a</i> or <i>rps1</i>	1,767 b	2	398
Blend	1,914 a	261	139
Hoytville, 1994			
<i>Rps1-c</i> or <i>Rps1-k</i>	3,605 a	399	1
<i>Rps1-a</i> or <i>rps1</i>	3,374 b	3	397
Blend	3,610 a	219	181

^x Yellow seeds, from a sample of 400 seeds from each plot, indicate isolines with the *Rps1-c* and *Rps1-k* alleles.

^y Black seeds, from a sample of 400 seed from each plot, indicate isolines with the *Rps1-a* or *rps1* alleles.

^z Means followed by the same letter do not differ at the 0.05 probability level.

At Davis and Hoytville, yields of the blends were similar to yields of the *Rps1-c*, *Rps1-k* isolines in 1993 and 1994. At Bluffton in 1993, the yield of the blend was not significantly different from the mean yield of the *Rps1-a*, *rps1* isolines. At this location in 1994, yield of the blend was intermediate to yields of the yellow- and black-seeded isolines. In each of these environments, except Hoytville in 1994, harvested seeds of the blends had significantly more yellow seeds (*Rps1-c* or *Rps1-k* isolines) than black seeds (*Rps1-a* or *rps1* isolines). This demonstrates that in the blends, plants of isolines with the *Rps1-c* or *Rps1-k* alleles were contributing considerably more to seed yield than were plants with the *Rps1-a* or *rps1* alleles.

Yield reductions due to *P. sojae* were different for isolines and blends of isolines for the three cultivars. The pathogen reduced yields of Century and Williams by 14% in environments where these isolines were significantly lower in yield than Century 84 and Williams 82 (Table 3). Isoline blends of these two cultivars were similar in yield to the cultivar containing the *Rps1-k* allele. Beeson, with the *Rps1-a* allele, produced only 65% of the yield of Beeson 80 with the *Rps1-c* allele. The blend of the two isolines of Beeson averaged 11% lower in seed yield than Beeson 80.

Compensation of the *Rps1-c*, *Rps1-k* components for seed yield of the *Rps1-a*, *rps1* components in the blends is also shown by the ratio of yellow to black seeds in blends of the three cultivars (Table 4). The Beeson blend had 35% more yellow seeds than the expected 200:200 ratio. In environments with no observable disease symptoms, the Beeson blend produced 12% more yellow seeds than the expected ratio. The difference of 23% in incidence of yellow seeds in environments with significant yield reductions compared to environments with no yield reductions due to the pathogen may be the most accurate estimate of the contribution of *Rps1-c* and *Rps1-k* plants in the blend. Similar calculations determine that the Century 84 isolate contributed 19% and the Williams 82 isolines 14% more seeds than would be expected with no *P. sojae* yield reductions. This compares with 22, 11, and 12% increases in seed yield of the respective blends compared to the isolines with the *Rps1-a* or *rps1* alleles.

DISCUSSION

Data from five environments, all locations in 1992 and from West Lafayette in each year of the study, suggest that *Phytophthora* root and stem rot was not severe enough to affect yields of the isolines with either the *Rps1-a* or *rps1* alleles. Another possibility is that prevalent races of the pathogen in these environments affected isolines with different alleles for resistance equally. However, the absence of any visi-

ble disease symptoms on plants suggests that the pathogen was not affecting plant growth or seed yield in these environments.

Averaged across all test environments where *P. sojae* reduced yields of isolines with the *Rps1-a* or *rps1* alleles, the isolines with the *Rps1-c* or *Rps1-k* alleles produced 499 kg ha⁻¹ or 20% greater seed yield than isolines with the *Rps1-a* or *rps1* alleles. The blend averaged 361 kg ha⁻¹ or 14% greater yield than the isolines with the *Rps1-a* or *rps1* alleles. We would have expected the yields of the blends to average 2,796 kg ha⁻¹, intermediate to yields of the component isolines, if *P. sojae* simply reduced yields of the *Rps1-a* and *rps1* components of the blend. However, plants with the *Rps1-c* or *Rps1-k* alleles compensated for the yield reduction of plants with the *Rps1-a* or *rps1* alleles, as shown by the significant increase in yield of the blend above the mean of the two components.

A 1993 survey reported that race 1 represented 31% of isolates and race 3 represented 26% of isolates of *P. sojae* found in Indiana (1). This survey also reported that races 4, 6–9, 13, 28, and 29 each constituted 2–6% of isolates found in the state. The *Rps1-a* allele in Beeson and Century would not have protected these cultivars against races 3, 4, 6–9, 28, and 29 of the pathogen. An Ohio survey reported that races 1, 3, 4, 7, and 9 were the most prevalent races of *P. sojae* in 1990 and 1991 (10). All but race 1 are virulent on both Beeson and Century. The susceptibility of Beeson and Century to prevalent races of *P. sojae* could account for the reduced yields of the two cultivars in these tests. Williams is susceptible to all races of the pathogen.

The *Rps1-k* allele in Century 84 and Williams 82 protects these cultivars against all prevalent races of *P. sojae* in Indiana except races 28 and 29. These two races represented a small percentage of races identified in the Indiana survey (1). The *Rps1-k* allele protects these cultivars against races 1, 3, 4, 7, and 9, the most prevalent races identified in the Ohio survey (10). However, the Ohio survey reported that 11.7 and 18.5% of the *P. sojae* races identified in 1990 and 1991, respectively, could defeat *Rps1-k*. Resistance to most of the prevalent races of *P. sojae* in both Indiana and Ohio undoubtedly was responsible for the high yields of the resistant isolines of these cultivars in this study.

Beeson 80, with the *Rps1-c* allele, is susceptible only to race 4 of prevalent races of the pathogen in both Indiana and Ohio. Resistance to prevalent races of the pathogen would account for the high yields of this cultivar compared to the susceptible isolate. *P. sojae* reduced yields of the susceptible isolate of Beeson more than yields of the susceptible isolate of the other two cultivars. Apparently, plants with the *Rps1-c* allele were not compensating for the reduced productivity of plants with the *Rps1-a* allele in the Beeson blend to the same extent as in the Century and Williams blends. Beeson has been reported to be less tolerant to *P. sojae* than either Century or Williams (11). Effects of the pathogen may have been severe enough in Beeson that resistant plants could not fully compensate for yield reductions of susceptible plants in the blend.

These data demonstrate that isolines resistant to prevalent races of *P. sojae* compensate, either partially or in full, for re-

Table 3. Yields of isolines with *Rps1-c* and *Rps1-k* alleles compared with isolines with *Rps1-a* and *rps1* alleles and blends of the isolines of three soybean cultivars

Isoline or blend	Beeson (kg/ha)	Century (kg/ha)	Williams (kg/ha)	Mean
Environments with no significant yield reductions due to <i>Phytophthora sojae</i>				
<i>Rps1-c</i> or <i>Rps1-k</i>	2,949 a ^z	3,222 a	3,696 a	3,289 a
<i>Rps1-a</i> or <i>rps1</i>	2,891 a	3,154 a	3,644 a	3,230 a
Blend	2,908 a	3,204 a	3,615 a	3,242 a
Environments with significant yield reductions due to <i>P. sojae</i>				
<i>Rps1-c</i> or <i>Rps1-k</i>	2,732 a	2,918 a	3,368 a	3,045 a
<i>Rps1-a</i> or <i>rps1</i>	2,023 c	2,554 b	2,942 b	2,546 b
Blend	2,471 b	2,844 a	3,284 a	2,907 a

^z Means followed by the same letter do not differ at the 0.05 probability level.

Table 4. Ratio of yellow (*Rps1-c* or *Rps1-k*) to black (*Rps1-a* or *rps1*) seeds in isolines and blends of three soybean cultivars

Isoline or blend	Beeson (no.) ^z	Century (no.)	Williams (no.)	Mean (no.)
Environments with no significant yield reductions due to <i>Phytophthora sojae</i>				
<i>Rps1-c</i> or <i>Rps1-k</i>	396:4	398:2	398:2	397:3
<i>Rps1-a</i> or <i>rps1</i>	3:397	3:397	2:398	3:397
Blend	224:176	210:190	200:200	211:189
Environments with significant yield reductions due to <i>P. sojae</i>				
<i>Rps1-c</i> or <i>Rps1-k</i>	399:1	398:2	398:2	398:2
<i>Rps1-a</i> or <i>rps1</i>	3:397	4:396	3:397	3:397
Blend	270:130	248:152	226:174	248:152

^z Average number of seeds based on a 400-seed sample from each plot at each location.

duced yields of susceptible isolines when grown in blends. Compensation is due to resistant plants effectively utilizing light, soil moisture, and nutrients underutilized by diseased plants in the blend. The information may be useful in minimizing disease losses associated with new races of the pathogen where alleles for resistance are not available in high-yielding cultivars. Blends of high-yielding, susceptible cultivars and lower-yielding, resistant cultivars may provide the best opportunity to optimize seed yield. In environments where disease pressure is nonexistent or minimal, the high-yielding, susceptible component could compensate for the lower-yielding, resistant component of the blend. Where prevalent races of the pathogen reduced yields of the susceptible component, the resistant component of the blend could partially compensate for these yield reductions.

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