

## Disease Resistance in Five Cycles of 'BS9' Corn Synthetic Selected for Resistance to Two Generations of European Corn Borer

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### ABSTRACT

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A corn (*Zea mays*) synthetic, BS9, was evaluated to determine if  $S_1$  recurrent selection for resistance to European corn borer, *Ostrinia nubilalis*, resulted in correlated changes in resistance to *Exserohilum turcicum*, causal organism of northern corn leaf blight, or resistance to *Diplodia maydis*, causal organism of Diplodia stalk rot. On a 1-to-9 scale (1 = highly resistant and 9 = highly susceptible), first-generation borer damage ratings decreased from 3.6 to 2.4, and second-generation damage ratings decreased from 6.5 to 4.3 in the populations BS9C0 and BS9(CB)C4, respectively. Percentage of leaf area infected with leaf blight was rated six times after inoculation with *E. turcicum*; ratings were transformed to the natural logarithm (lnNLB), and dates of ratings were transformed to the natural logarithm of days after first inoculation

(lnDAY). Linear and quadratic components of the regression of lnNLB on cycles of selection were significant, resulting in a significant increase in leaf blight infection from the C0 to C4 population of BS9. Ratings expressed as percentage of leaf area blighted, in terms of the linear regression, increased from 4.6 and 5.8% at day 16 to 38.9 and 41.7% at day 71 for BS9C0 and BS9(CB)C4, respectively. Selection for borer resistance did not affect Diplodia stalk-rot ratings. Selection for resistance to one pest, therefore, cannot be expected to increase the resistance to other pests, although DIMBOA (2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) content in a corn plant has been correlated with resistance to a wide range of pests.

*Additional key words:* corn disease, corn stalk rot, *Exserohilum turcicum*, *Helminthosporium turcicum*, maize, *Ostrinia nubilalis*.

The primary objective of recurrent selection is to increase the frequency of favorable alleles while maintaining genetic variability for quantitatively inherited traits such as yield or European corn borer, *Ostrinia nubilalis* (Hubner), resistance. Usually, it is preferred that other agronomic traits not be changed. To assess progress from recurrent selection, the traits under selection and the effects imposed on other traits, such as disease resistance, must be evaluated.

The corn (*Zea mays* L.) synthetic, BS9(CB)C4, was released in 1982 after four cycles of  $S_1$  recurrent selection (9) for borer resistance because of its potential value in breeding programs for resistance to the two generations of European corn borer normally found in Iowa (28). The two generations correspond to two growth stages of the plant. Resistance to the first generation is expressed as antibiosis to the first and second instars, which feed in the whorl of the plant before tassel emergence. First-generation resistance, therefore, is leaf-feeding resistance (5). Second-generation larvae emerge during or soon after anthesis and feed on pollen accumulations in the leaf axils and on collar, sheath, and husk tissue. Resistance to second generation is expressed as antibiosis to the first and second instars and, therefore, is sheath-collar-feeding resistance. Klenke et al (13) evaluated the changes in borer resistance in BS9 and reported that recurrent selection significantly increased resistance to both first and second generation.

Recurrent selection has been successful in the synthetic, BS1, in separate programs for resistance to leaf-feeding and DIMBOA (2,4-dihydroxy-7-methoxy-(2H)-1,4-benzoxazin-3(4H)-one) content with equal and significant increases in DIMBOA content in the corn leaf whorl tissue and leaf-feeding resistance regardless of the trait under selection (33). DIMBOA is a cyclic hydroxamic acid that has been isolated in corn plants (34) and is the active chemical agent highly correlated with leaf-feeding resistance (14,16,25,26).

DIMBOA content in the corn plant has been related to resistance to a wide range of pests. Stalk-rot-resistant, high-density tissue has been reported to contain more of the DIMBOA-containing glycoside fraction than stalk-rot-susceptible, low-density tissue (1). Significant correlations have also been reported between DIMBOA concentration and northern corn leaf blight (*Exserohilum turcicum* (Pass.) Leonard & Suggs (= *Helminthosporium turcicum* Pass.)) reactions (19,20,23). DIMBOA concentration has also been correlated with *Erwinia* (*Erwinia chrysanthemi* Burkholder, McFadden & Dimock) soft rot (2,10) and corn leaf aphid (*Rhopalosiphum maidis* Fitch) infestations (18). One study (17), however, could not relate DIMBOA concentrations and *Erwinia* soft rot reaction.

Sheath-collar-feeding resistance and DIMBOA content are not related (15). Two studies (30,32) have reported first-generation resistance in several exotic corn germ plasm sources that have a low DIMBOA content. Silica content in sheath and collar tissue has been found highly correlated with sheath-collar-feeding resistance suggesting that DIMBOA concentration is a primary factor for leaf-feeding resistance and silica content is a primary factor for sheath-collar-feeding resistance (27). DIMBOA we found to be a secondary factor in sheath-collar-feeding resistance if the effect of silica content was removed (27).

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Selection for resistance to one pest, which would increase DIMBOA content if it is the primary factor that causes resistance, has not increased the resistance level to other pests in some instances. Selection for Diplodia stalk-rot resistance (*Diplodia maydis* (Berk.) Sacc.) did not increase leaf-feeding resistance or northern corn leaf blight resistance (21). Guthrie et al (4) evaluated 7,537 genotypes during a 12-yr period for resistance to both leaf-feeding and northern corn leaf blight and found a near-zero correlation.

BS9 contains mostly U.S. Corn Belt germ plasm, and all studies in which data have been obtained for DIMBOA and leaf-feeding resistance in this type of germ plasm show a high correlation for DIMBOA concentration with leaf-feeding resistance. Also, B49 and CI31A were two lines used in the synthesis of BS9, and both lines have high concentrations of DIMBOA and are highly resistant to leaf-feeding. Reports of the association of DIMBOA with resistance to other corn pests would suggest that BS9 is a good population in which to evaluate the relationship of increases in borer resistance with changes in disease resistance. The objective of this study was to determine if four cycles of  $S_1$  recurrent selection for European corn borer resistance had resulted in changes in resistance to *D. maydis*, causing Diplodia stalk rot, or resistance to *E. turcicum*.

## MATERIALS AND METHODS

The development of BS9 has been described previously by Russell and Guthrie (28). The original population, BS9C0 (Cycle 0), was developed by mating 10 corn inbred lines, i.e., B49, B50, B52, B54, B55, B57, B68, CI31A, Mo17, and SD10. These lines, with the exception of SD10, were selected on the basis of their combining abilities and resistance to both borer generations (24). Resistance reactions of the first nine lines vary from low- to high-intermediate, except the high resistance of B49 and CI31A to first-generation borers and the high resistance of B52 to second-generation. SD10 is susceptible to both generations but was included for its earliness, good root system, and good plant type.

**European corn borer ratings.** The five populations of BS9 (C0 through C4) were evaluated for resistance to first and second generations of borer in two locations, Ames and Ankeny, IA, for 2 yr, 1983 and 1984. Entries were hand-planted in single-row plots, 0.76 m  $\times$  4.32 m, and plants were thinned to a final density of 51,666 plants per hectare. The experimental design was a split-plot in which treatments (borer infestations) were the whole plots, replicated three times in each environment, and cultivars were the subplots. The borer rearing and infestation techniques used in this experiment have been described by Guthrie et al (7). The first-generation borer infestation treatment was evaluated on a 1-to-9-rating scale (1 = resistant and 9 = susceptible) described by Guthrie et al (5) for leaf-feeding resistance. The second-generation borer infestation treatment was evaluated on a similar 1-to-9-rating scale described by Guthrie et al (8) for sheath-collar-feeding resistance. Combined analysis of variance, according to the split-plot model (31), was made for the four experiments, equating years and locations to four random environments.

**Stalk quality evaluations.** Evaluations for Diplodia stalk-rot resistance were conducted at the Agronomy and Agricultural Engineering Research Center near Ames in 1983 and 1984. The experimental design was a randomized complete block with 10 replications of the five BS9 populations (C0 through C4). Evaluations of pressure required for stalk-rind puncture were conducted only in 1984.

Agronomic practices, including planting date, fertilization, and weed control, were followed to promote high productivity. Entries were hand-planted in single-row plots, 0.76  $\times$  4.40 m. Seed were planted two per hill in 13 hills, spaced 33.9 cm, and plants were later thinned to one plant per hill for a final density of 38,750 plants per hectare.

Inoculations with *D. maydis* were made 11 August 1983 and 3 August 1984, approximately 1–2 wk after pollination was completed. All plants were inoculated in the second elongated internode with a conidial suspension of *D. maydis* (11). Stalk-rind

puncture data were taken on 10 competitive plants in 1984 at approximately the same date as stalk-rot inoculations. Stalks inoculated with *D. maydis* were also punched with a rind penetrometer equipped with a Dillon force gauge in the first internode above the primary ear where mature European corn borer larvae normally enter the stalk. The pressure required to puncture the stalk was recorded in pounds and later converted to kilograms.

Ratings for Diplodia stalk-rot resistance were taken in September, approximately 40 days after inoculation. Stalks were split longitudinally and rated 1 to 6 for stalk-rot development as follows: 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% of the inoculated internode infected, respectively; 5 = infection extending into one or both of the adjacent internodes; and 6 = prematurely dead plant. Combined analyses of variance for the randomized complete block were made for the two experiments, equating years to two random environments.

**Northern corn leaf blight ratings.** For evaluations of *E. turcicum* resistance, field plots were planted at the Atomic Energy Research Farm near Ames and the Agronomy South Farm near Champaign, IL, in 1983 and 1984. In 1983, the experiment at Champaign was abandoned because of extreme weather conditions, thus, evaluations were made in three environments. The experimental design was a randomized complete block with 10 replications of the five BS9 populations (C0 through C4).

Entries were hand-planted in single-row plots, 0.76  $\times$  2.29 m. Each plot consisted of five hills spaced at 76.2 m. Six seeds were planted in each hill, and plants were later thinned to four per hill for a final density of 68,889 plants per hectare. The three center hills were planted to one of the five entries, and the two end hills were planted to an early-maturity, susceptible hybrid that served as spreader plants.

Plants in each plot were sprayed twice (1 wk apart) at the end of June with 10 ml per plant of a conidial suspension of *E. turcicum* of about 1,500 conidia per milliliter. Six ratings were taken at 10-day intervals in Ames, and four ratings were taken at 13-day intervals in Champaign, beginning approximately 16 days after first inoculation and ending when natural senescence began to interfere with the ratings. Leaf blight reaction was recorded on a percentage of leaf-area-infected scale (A. L. Hooker, *personal communication*) for each of the middle hills as follows: 0 = no symptoms, 1 = almost no sign of blight, 3 = 1–3 small lesions, 5 = 1–5 large lesions (up to 2–3 cm), 10 = a few lesions but visible from a short distance (10% blighted), 20 = a few lesions on leaves above ear (20% blighted), 30 = leaves below ear over half blighted and/or showing signs of ripping or tearing in necrotic spots (30% blighted), 40 = 40% of plant blighted, 50 = leaves below ear almost totally blighted (50% blighted), 60 = 60% blighted, 70 = 70% blighted, 80 = leaves above ear over half blighted (80% blighted), 90 = 90% blighted, 100 = all leaves totally blighted and/or death of plant from the pathogen.

The data were transformed to the natural logarithm of the leaf blight ratings (lnNLB), and the natural logarithm of days after first inoculation (lnDAY). This transformation is similar to that used by Gregory (3) for dispersal gradients to give the greatest fit to a straight line, which is necessary to combine the data over the three environments and to do statistical analysis. The fit of the transformation for exponential growth (lnNLB only) was tried, but results were not as good as with the Gregory transformation ( $R^2 = 0.789$  and  $R^2 = 0.828$ , respectively); therefore, the Gregory transformation was used to improve statistical validity. The data were analyzed on a per-plot basis as a split-plot in time (31). The combined analysis of variance was made for the three experiments, equating years and locations to three random environments. Although the residual mean square was significant ( $P < 0.05$ ), the linear sum of squares accounted for 97.1% of the total sum of squares for leaf blight ratings within environments and, therefore, the transformation was assumed adequate to permit a combined analysis of the three environments.

## RESULTS AND DISCUSSION

The combined analyses of variance (data not shown) indicated

highly significant differences ( $P < 0.01$ ) among the five cycles of BS9 for stalk-rind puncture and northern corn leaf blight ratings, but no significant differences were indicated for *Diplodia* stalk-rot ratings. The genotype environment interaction was significant for *Diplodia* stalk-rot ratings but not leaf blight ratings; therefore, only the combined analyses of variance and mean values across environments will be discussed.

Differences in  $\ln\text{NLB}$  for days after first inoculation ( $\ln\text{DAY}$ ) were also highly significant, with the linear increase of  $\ln\text{NLB}$  accounting for most of the variation. The significant linear increases in  $\ln\text{NLB}$  in relation to  $\ln\text{DAY}$  for BS9C0, BS9(CB)C2, and BS9(CB)C4 are shown in Figure 1. These linear increases in terms of ratings expressed as percentage of leaf area blighted at 16 days ( $\ln\text{DAY} = 2.77$ ) and at 71 days ( $\ln\text{DAY} = 4.26$ ) after first inoculation with *E. turcicum* were, respectively: 4.6–38.9% for BS9C0, 4.6–35.9% for BS9(CB)C2, and 5.8–41.7% for BS9(CB)C4.

Molot and Anglade (23) reported a highly significant correlation ( $r = 0.76^{**}$ ) between mean resistance ratings for northern corn leaf blight and first-generation feeding. They also reported a linear relationship between the concentrations of MBOA, which is stoichiometrically related to the precursor DIMBOA, and the ratings for leaf blight with first-generation feeding ( $r = -0.77$  and  $r = -0.95$ , respectively) and concluded that the resistance to these two organisms was dependent on the MBOA concentrations in the leaf tissues.

The significant decreases in leaf-feeding and sheath-collar-feeding damage ratings are shown in Figure 2. The fourth cycle of selection (C4) was significantly less than the C0 for leaf-feeding ratings (2.4 and 3.6, respectively) and for sheath-collar-feeding ratings (4.3 and 6.5, respectively). The linear and quadratic effects of cycles in the analysis of variance of  $\ln\text{NLB}$  were highly significant, and BS9(CB)C4 was significantly greater for  $\ln\text{NLB}$  than BS9C0 (LSD [0.05] = 0.10) at 16 days and 58 days after first inoculation (Fig. 2). The lack of, or possibly negative, association of resistance to leaf feeding and *E. turcicum*, therefore, does not agree with the data presented by Molot and Anglade (23). Our data do, however, support findings of no association between the

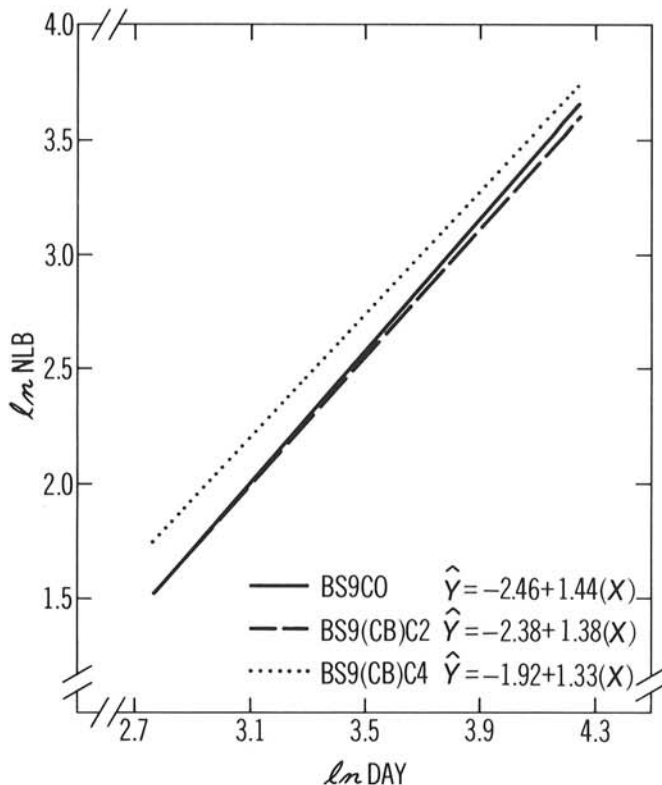


Fig. 1. Linear increases in the natural logarithm of the proportion of northern corn leaf blighted tissue ( $\ln\text{NLB}$ ) in relation to the natural logarithm of days after first inoculation ( $\ln\text{DAY}$ ) of three BS9 populations.

resistances of maize to leaf feeding and *E. turcicum* reported by Guthrie et al (4).

The data presented by Long et al (19,20) and Molot and Anglade (23) may conflict with the findings in this report because the nature of the lines selected could bias the analysis. Long et al (19,20) used a fixed set of inbred lines in which a significant correlation between DIMBOA concentration and *E. turcicum* reaction was possible. The inclusion of the DIMBOA-deficient mutant (bx) genotype and the Bx genotype in the Long et al (19,20) correlations would, also, tend to inflate the figures because of the extreme values displayed by these genotypes. Molot and Anglade (23) studied corn borer, *E. turcicum*, and DIMBOA reactions in inbred lines selected for their similar reactions to corn borer and *E. turcicum*. Lines selected for either resistance to both corn borer and leaf blight or susceptibility to both, therefore, would be expected to give a positive correlation between corn borer and leaf blight and negative correlations between DIMBOA concentration and corn borer or reactions of *E. turcicum* if DIMBOA concentration is truly related to corn borer leaf-feeding reaction.

The DIMBOA concentration decreases with plant age (15), and, therefore, if a DIMBOA effect is present, the effect will decrease with the age of the plant. The DIMBOA effect, as a primary factor for both leaf blight and leaf-feeding ratings, should result in lower disease and feeding damage early in the season and a lower rate of disease increase in populations with higher leaf-feeding resistance. In Figure 1, however, BS9(CB)C4 had a higher intercept, and, although the rate of disease increase was smaller, it was not significantly different from BS9C0 or BS9(CB)C2. If the DIMBOA concentration in BS9 is the primary factor for resistance

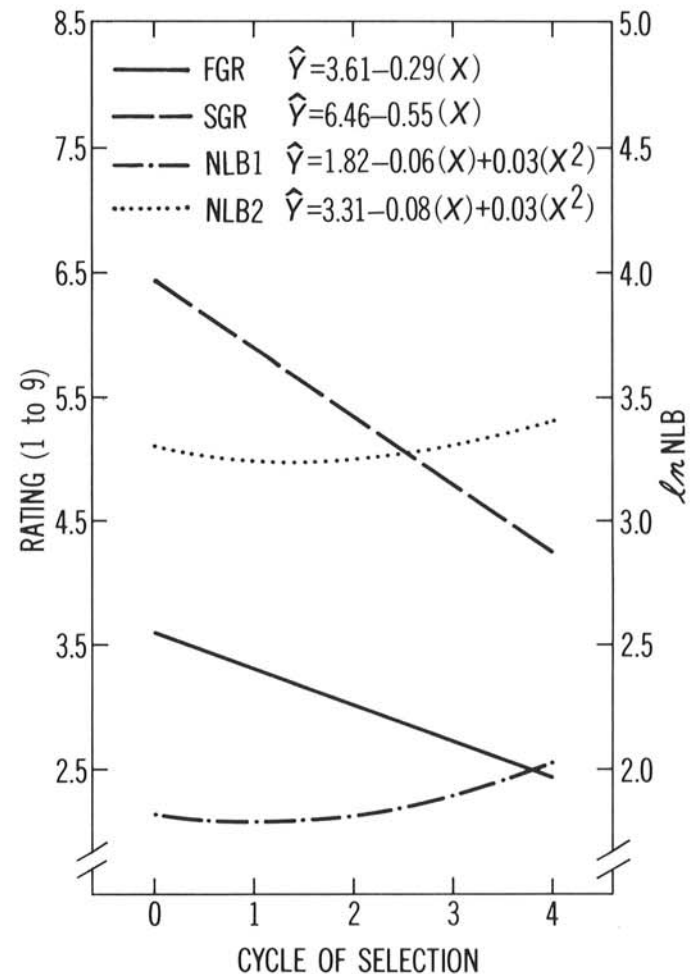


Fig. 2. Change in European corn borer damage ratings of first-generation (FGR) and second-generation (SGR) and the natural logarithm of the proportion of northern corn leaf blighted tissues ( $\ln\text{NLB}$ ) about 16 days (NLB1) and about 58 days (NLB2) after the first inoculation of five BS9 populations with *E. turcicum*.

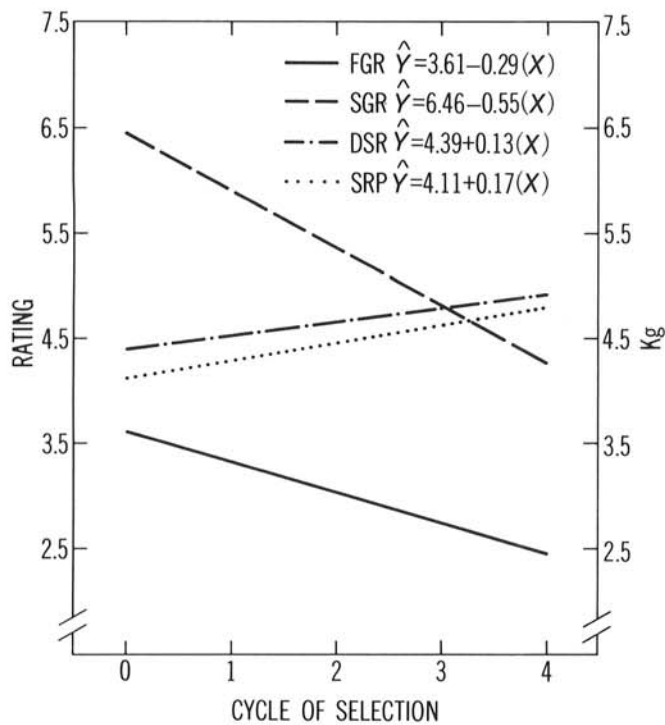


Fig. 3. Change in ratings of European corn borer damage of first-generation (FGR) and second-generation (SGR), on a 1-to-9 scale; Diplodia stalk rot severity (DSR), on a 1-to-6 scale; and resistance to stalk rind puncture (SRP), measured in kilograms, of five BS9 populations.

to first-generation borer, then DIMBOA probably is not a primary factor for resistance to *E. turcicum* in BS9. The absence of any correlation between sheath-collar-feeding ratings and leaf blight ratings was also noted in our experiments.

Similarly, Figure 3 shows no association between Diplodia stalk rot ratings and leaf-feeding ratings, both of which have been correlated with DIMBOA concentration (1 and 14, respectively). Although not significant, the stalk rot ratings were increased from a mean rating of 4.39 for BS9C0 to 4.91 for BS9(CB)C4 as a correlated response to recurrent selection for first- and second-generation borer resistance.

Leaf-feeding and sheath-collar-feeding ratings both decreased in subsequent cycles of BS9, but this decrease was caused by independent selection for the two types of resistance rather than a relationship of resistance to the two generations. Klenke (12) found no significant correlations between leaf-feeding and sheath-collar feeding ratings in  $S_1$  lines from the BS9C0 or BS9(CB)C4 population, which agrees with other studies for the lack of relationship (6,15,24,29).

Resistance to stalk rind puncture was increased significantly from 4.11 kg in BS9C0 to 4.79 kg in BS9(CB)C4. Klenke (12), however, found no significant correlation for stalk rind puncture with leaf-feeding or sheath-collar-feeding ratings. The increase in stalk rind puncture in BS9 may be associated with hardness of stalk that may increase resistance to stalk tunneling by the borer, which was the main criterion for selection in BS9. Second-generation resistance, however, is a visual rating for sheath-collar-feeding resistance, which may be associated with some type of antibiosis. Stalk rind puncture and stalk rot ratings both increased, but a discussion of a relationship between them may not be valid because the stalk rot ratings did not show a significant change. Martin and Russell (22) reported a highly significant correlation between stalk rind puncture and Diplodia stalk rot ratings ( $r = -0.93^{**}$ ).

Our study has shown that increased resistance to corn borer does not impart improved disease resistance and confirms the observations by Guthrie et al (4) that researchers working with large numbers of corn genotypes cannot select for resistance to one pest and expect an increase in resistance to other pests. Because DIMBOA content did not seem to be the primary factor for disease

resistance, selection for high DIMBOA content (also predicted by Tseng et al [33]) cannot be expected to cause resistance to several species of pests.

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