Pennisetum glaucum subsp. monodii accessions with Striga resistance in West Africa

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Abstract

Wild pearl millets (Pennisetum glaucum subsp. monodii) were evaluated as potential sources of resistance to the hemi-parasitic weed Striga hermonthica. Resistance of 274 P. glaucum subsp. monodii accessions was evaluated in four trials in Mali and Niger from 1997 to 1998. Seventy five accessions were selected from that collection for evaluation in three additional trials in Niger and Nigeria in 2000. Data were collected for maximum number of emerged striga per host plant, days to striga emergence, downy mildew incidence (caused by Sclerospora graminicola), and days to host flowering. Across the seven trials, maximum striga scores ranged from 0.2 (Sadoré Niger field trial in 2000) to 14.9 (Sadoré pot trial in 2000) striga per plant. Maximum striga scores for the 75 selected accessions averaged overall locations ranged from 0.8 to 8.8 striga per plant. Regression analyses of accession mean within a trial vs. trial mean identified 11 accessions with consistently low striga emergence (intercepts and slopes were not different from zero, \( P > 0.05 \)) overall trials. Covariance analysis indicated that days to striga emergence, downy mildew incidence, and days to host flowering were significant (\( P < 0.01 \)) covariates with maximum striga. When significant relationships existed, striga emergence was negatively correlated with days to striga emergence and downy mildew incidence. Nine accessions were classified as resistant (mean striga \( =0, P > 0.05 \)) by least-squares means calculated from covariance analysis. Four accessions (PS 202, PS 637, PS 639, and PS 727) were classified as resistant by both regression and covariance analyses, and are likely to be useful sources of striga resistance for cultivated pearl millet in West Africa. In addition to its striga resistance, PS 202 also expressed downy mildew resistance at all locations (mean incidence \( =0.8\% \)), whereas the other three accessions were susceptible, with incidence \( >83\% \).

Keywords: Downy mildew; Host resistance; Pearl millet; Pennisetum glaucum; Striga; Striga hermonthica; Sclerospora graminicola

1. Introduction

Striga hermonthica is a persistent, hemi-parasitic weed that attacks several grasses in many countries throughout sub-Saharan Africa, and particularly the staple grains maize, sorghum, and pearl millet. Significant reductions in pearl millet grain yield, stem and shoot weight, and transpiration ratios occur with striga infestation (Boukar et al., 1996, Graves et al., 1990). In contrast to the efforts to identify and select for resistance in maize (Kim et al., 1998) and sorghum (Ejeta et al., 1997), comparatively few efforts have been directed to identifying resistance in pearl millet. Striga damage ratings tend to be lower for pearl millet than for maize or sorghum (Kim et al., 1994), however, knowledge of the extent of the damage sustained and progress in breeding for resistance is minimal, reflecting international research priorities directed to a subsistence crop grown by some of the world’s poorest populations. In the absence of known resistance, cultural management approaches that serve to stabilize crop yield in marginal environments have been emphasized for minimizing the effects of striga on pearl millet (Hess et al., 1996).
Rubiales (2003) states that resistance in crops to parasitic weeds tends to be scarce, complex in nature, and of low heritability, but concludes that wild relatives of crops are likely to be valuable as sources of resistance. When *Sorghum arundinaceum* and *Sorghum bicolor* were evaluated for resistance to *S. asiatica* and *S. hermonthica*, germination of parasite seeds was lower for *S. arundinaceum*. In addition, *S. asiatica* had less impact on growth and grain production of *S. arundinaceum* than of *S. bicolor* (Gurney et al., 2002).

The data from the sorghum/striga pathosystem suggest that wild relatives of pearl millet may be useful sources of resistance to striga. Parker and Wilson (1983) identified apparent striga resistance in semi-wild shibras, which are naturally occurring hybrids between pearl millet and its wild subspecies *monodii*. Progeny derived from the original shibras were determined to segregate for striga emergence in pot trials. Ramaiah (1984) later considered selections from Parker and Wilson’s study to be generally susceptible in pot trials, and no further information on these selections are available.

A collection of 274 wild pearl millet (*Pennisetum glaucum* subsp. *monodii*) accessions was previously screened for resistance to striga (Wilson et al., 2000). The results of field studies showed that heritable differences for host-plant resistance exist (broad sense heritability = 0.55). Agar-gel tests indicated that this resistance was attributable to mechanism(s) other than production of low levels of exudates that stimulate striga seed germination. It has been suggested that much of the site-to-site variation in apparent resistance in sorghum results from the influence of environmental factors on the expression of resistance (Parker and Riches, 1993). Eco-geographic differences in striga populations in West Africa are not well understood. Resistance would be most useful if it were found to be effective after multiple evaluations in diverse regions in West Africa. Additional trials were therefore conducted with the objective of more precisely identifying resistant accessions to be used as sources of striga resistance for cultivated pearl millet in West Africa.

2. Materials and methods

The *P. glaucum* subsp. *monodii* accessions evaluated in this study are held at the USDA-ARS *Pennisetum* collection at Tifton, GA, USA. They were acquired between 1975 and 1988. The accessions have been regenerated at least twice by selfing since original acquisition. A collection of 274 *P. glaucum* subsp. *monodii* accessions had been previously screened in field trials in 1997 and 1998 at Samanko, Mali, and in 1998 at Cinzana, Mali and Sadoré, Niger (Wilson et al., 2000). From the collection of 274 accessions, 75 accessions (27% of the population) with low numbers of emerged striga were selected to be evaluated in three additional trials in Niger and Nigeria in 2000. Two trials were conducted in Sadoré, Niger since prior attempts at assessing resistance at that location had only limited success. Maiduguri, Nigeria was added as a new site to evaluate this germplasm.

Both field and pot trials were established at Sadoré, Niger. The field trial was sown on 23 June 2000 in a randomized complete block design with four replications. Plots consisted of 10 hills spaced 1 m apart within 10 m-long rows, and plots were spaced 1 m apart. The trial was sown in a naturally infested field, but to increase homogeneity of infestation, rows were infested with 3 g seed collected from local striga plants and mixed into the upper 5 cm of soil over each row at sowing. Date of first striga emergence in the plot was recorded, and counts of striga associated with plants in each plot were made on 14 and 27 August, and 8 and 20 September 2000. Total number of surviving hills, and date of 50% *Pennisetum* flowering were recorded. For each plot, assessment values were expressed as the mean maximum number of emerged striga per hill, determined here and elsewhere as (maximum striga emergence per plot) * (number of hills per plot)⁻¹.

The pot trial was sown on 28 July 2000 in a randomized complete block design with four replications. Soil was prepared by thoroughly mixing sand, clay, and cow manure (5:1:2 v/v/v) that had been obtained from striga-free areas and air dried. The soil mix was used to fill 1-l pots that were subsequently infested by mixing 8000 viable *S. hermonthica* seeds into the upper 5 cm of soil. Following infestation, 1 cm of non-infested soil mix was used to top off each pot to avoid accidental dissemination of striga seed by wind, rain, or watering. Stands were thinned to a single plant in each pot on 10 August 2000. Date of striga emergence, days to 50% *Pennisetum* flowering and incidence of downy mildew (caused by *Sclerospora graminicola*) were recorded. Emerged striga plants in each plot were counted on 4, 18 September, 4, 17, and 31 October 2000. Striga values were expressed as the maximum number of emerged striga plants per pot.

The trial grown at Maiduguri, Nigeria was planted on 15 June 2000 in a randomized complete block with three replications. Natural striga infestation was supplemented with striga seed as described above. Single-row plots were 6 m long with 0.5 m spacing between hills (13 hills per row) and between rows. Hills were thinned to one plant. In each plot, date of first striga emergence was recorded, and total emerged striga per plot was assessed on 15 August and 13 September 2000. Data for date of 50% *Pennisetum* flowering, total *Pennisetum* plants per plot, and downy mildew incidence were recorded. Striga values for the plots were expressed as the mean maximum number of striga per hill.
Data for the set of 75 accessions were analyzed over the seven trials conducted from 1997 to 2000. Maximum striga values were transformed to log(striga + 0.05) to normalize treatment variances. Correlations among transformed striga means for accessions across locations were calculated to determine the consistency of the striga emergence response, and to determine if eco-geographic relationships could be discerned.

Regression analyses were conducted on maximum striga emergence to compare the stability of the response of the accessions across the different environments (Finlay and Wilkinson, 1963). The mean striga emergence of the individual accessions in each trial was regressed on the mean striga emergence for all accessions in each trial. Deviations of the calculated intercepts and slopes from 0 were determined by Student’s t-tests. Regression equations with intercepts and slopes not different from 0 indicate low striga and stable performance across trials.

Data for maximum striga number across trials were also analyzed by analysis of covariance. Sums of squares were partitioned into trial, replication within trial, and accession, with days to *Pennisetum* flowering, downy mildew incidence (assessed in all trials except in Sadoré field trial in 2000), and days to striga emergence as covariates. Least-squares means of maximum striga emergence for the accessions were calculated.

Downy mildew incidence was analyzed across and within trials. Fisher’s lsd was used to identify resistant accessions with low levels of downy mildew incidence. Correlations of incidence means for accessions across trials were evaluated to determine variation among sites.

### 3. Results

Results from the first four trials for the entire collection of 274 accessions were previously presented (Wilson et al., 2000). From within those trials, data for the subset of the 75 selected accessions were extracted for further analysis of log-transformed data. For these 75 accessions, mean maximum striga emergence across accessions within locations ranged from 0.0 to 15.2 striga per hill (mean = 3.3 striga) at Samanko, Mali in 1997. Differences among accessions were significant at $P = 0.033$. At Samanko in 1998, striga values ranged from 1.1 to 16.3 (mean = 4.9), and differences among accessions were not significant at $P = 0.12$. At Cinzana, Mali in 1998, striga values ranged from 0.0 to 4.1 (mean = 1.2) and differences among accessions were significant at $P = 0.01$. At Sadoré, Niger in 1998, striga values ranged from 0.0 to 1.6 (mean = 0.3) and differences among accessions were significant at $P = 0.08$.

Infection levels varied in the three experiments conducted in 2000. As in 1998, drought conditions in the Sadoré 2000 field trial led to few emerged striga. Mean striga emergence for the accessions ranged from 0.0 to 1.1 striga per hill (mean = 0.2 striga). Differences among accessions were not significant at $P = 0.52$. In contrast to the field trial, conditions were highly favorable for infection in the Sadoré 2000 pot trial. Mean striga emergence for the accessions ranged from 0.0 to 34.8 striga per pot (mean = 14.9 striga), and differences among accessions were significant at $P = 0.0001$. Conditions resulted in moderately severe striga infection at Maiduguri, Nigeria in 2000. Mean striga emergence for the accessions ranged from 0.0 to 7.5 striga per hill (mean = 1.3 striga), however, differences among accessions were not significant at $P = 0.33$. The generally low heritabilities frequently observed in striga trials were evident in these assays of accessions selected for their higher levels of resistance from a larger population with greater phenotypic variation.

Correlations of log-transformed means of emerged striga for the accessions were determined within trials to examine if trends in eco-geographical differences in striga populations could be discerned. Data from Samanko in 1997 and 1998 were not correlated ($P > 0.10$) (Table 1). Data from Samanko 1997 were positively correlated with data from all unrelated trials in 2000. Data from Cinzana 1998 was negatively correlated with data from the Samanko 1997 and 1998 trials, and also with data from the Sadoré 2000 pot trial.

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Samanko 1997</td>
<td>0.052</td>
<td>-0.272**</td>
<td>0.155</td>
<td>0.393***</td>
<td>0.312***</td>
</tr>
<tr>
<td>Samanko 1998</td>
<td>-0.212*</td>
<td>-0.227*</td>
<td>0.046</td>
<td>-0.095</td>
<td>-0.017</td>
</tr>
<tr>
<td>Cinzana 1998</td>
<td>-0.026</td>
<td>0.136</td>
<td>-0.238</td>
<td>-0.208*</td>
<td>-0.177</td>
</tr>
<tr>
<td>Sadoré 1998</td>
<td>-0.301</td>
<td>-0.312</td>
<td>0.391***</td>
<td>0.325***</td>
<td>0.128</td>
</tr>
<tr>
<td>Sadoré (F) 2000</td>
<td>-0.292</td>
<td>-0.324</td>
<td>-0.309</td>
<td>0.345***</td>
<td>0.090</td>
</tr>
<tr>
<td>Sadoré (P) 2000</td>
<td>-0.295</td>
<td>-0.245</td>
<td>-0.306</td>
<td>-0.274**</td>
<td>-0.177</td>
</tr>
</tbody>
</table>

*, **, and *** indicate significance at $P = 0.10$, 0.05, and 0.01, respectively.

aData were transformed to log (striga + 0.05) prior to calculation of correlations.

b*(F) = field trial (P) = pot trial.
The Cinzana trial may have had a unique striga population or environmental conditions. Data from all three trials conducted at Sadoré were positively correlated, indicating the consistency of these trials. The Maiduguri 2000 data was correlated only with Samanko 1997 and with the Sadoré 2000 pot trial. Patterns of relationships over other trials were inconsistent and gave inconclusive results.

Regressions of striga emergence means for accessions against the striga means of all accessions across trials allowed the relative stability of accessions across trials to be characterized. When assessed at \( P = 0.05 \), regression equations for 61 accessions had intercept = 0 and slope > 0, and equations for three accessions had intercept < 0 and slope > 0. A slope greater than 0 suggests striga emergence on an accession increased with increased striga pressure in the trial due to either greater striga infestation or more favorable environmental conditions for infection. Eleven accessions, PS numbers 202, 203, 637, 639, 641, 642, 656, 663, 727, 728, and 729, had regression equations with intercept and slope = 0. As slope greater than 0 suggests striga emergence, these accessions had least-squares means that did not differ from zero (\( P < 0.05 \) (Table 2). This group would be characterized as having consistently low and stable levels of striga emergence across the seven different evaluations, regardless of the level of striga pressure or environmental conditions.

When log-transformed values of maximum striga emergence were correlated with days to striga emergence or downy mildew incidence, the relationships were always negative (Table 3). The relationships of log-transformed values of maximum striga emergence with days to *Pennisetum* flowering were inconsistent across trials (Table 3). Correlations were positive in two trials, negative in two trials, and not significant in three. Within each trial, correlations were significant with at least two of these variables, except the Sadoré field trials in 1998 and 2000, which had very low striga pressure.

Days to striga emergence, downy mildew incidence, and days to *Pennisetum* flowering were all significant covariates affecting log-transformed values for maximum striga emergence (\( P < 0.01 \)). Nine of the accessions, PS numbers 161, 198, 202, 540, 633, 634, 637, 639, and 727, had least-squares means that did not differ from zero (\( P < 0.05 \) (Table 2). When results of the regression analyses for stability and least-squares means derived from analysis of covariance were compared, four accessions, PS 202, 637, 639 and 727, were classified as resistant by both methods (Table 2).

Identifying downy mildew resistance in these evaluations was secondary in priority to identifying striga resistance. Data were recorded because previous experiments indicated it was a significant covariate with striga emergence. Downy mildew incidence varied by trial, accession, and trial × accession interaction (\( P < 0.05 \)). Mean downy mildew incidence over all accessions within a location ranged from 16.7% at Sadoré 1998 to 46.4% at Samanko 1997. Mean downy mildew incidence for specific accessions across all trials ranged from 0.0 to 89.3%.

Despite the variation in mean downy mildew incidence over locations and significant trial × accession interactions, incidence was positively correlated in all

<table>
<thead>
<tr>
<th>Accession</th>
<th>Origin</th>
<th>Striga emergence regression equation&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Null hypothesis</th>
<th>Striga least-squares mean</th>
<th>Downy mildew incidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>PS 161</td>
<td>Unknown</td>
<td>( y = 0.067 + 0.799x )</td>
<td>Intercept = 0</td>
<td>0.8293</td>
<td>2.8</td>
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<tr>
<td>PS 198</td>
<td>Senegal</td>
<td>( y = 0.590 + 0.468x )</td>
<td>Slope = 0</td>
<td>&lt;0.0001</td>
<td>1.4</td>
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<tr>
<td>PS 202</td>
<td>Senegal</td>
<td>( y = 1.424 + 0.154x )</td>
<td></td>
<td>0.4959</td>
<td>2.7</td>
</tr>
<tr>
<td>PS 203</td>
<td>Senegal</td>
<td>( y = 2.926 + 0.196x )</td>
<td></td>
<td>0.3126</td>
<td>4.1*</td>
</tr>
<tr>
<td>PS 540</td>
<td>Niger</td>
<td>( y = 0.850 + 0.365x )</td>
<td></td>
<td>0.3438</td>
<td>2.4</td>
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<tr>
<td>PS 633</td>
<td>Niger</td>
<td>( y = 0.203 + 0.221x )</td>
<td></td>
<td>0.1042</td>
<td>4.1</td>
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<td>PS 634</td>
<td>Niger</td>
<td>( y = 0.118 + 0.333x )</td>
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<td>0.4706</td>
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<td>PS 637</td>
<td>Niger</td>
<td>( y = 0.730 + 0.053x )</td>
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<td>0.6887</td>
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<tr>
<td>PS 639</td>
<td>Niger</td>
<td>( y = 0.728 + 0.161x )</td>
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<td>0.4293</td>
<td>2.1</td>
</tr>
<tr>
<td>PS 641</td>
<td>Niger</td>
<td>( y = 1.059 + 0.011x )</td>
<td></td>
<td>0.1317</td>
<td>2.8</td>
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<tr>
<td>PS 642</td>
<td>Niger</td>
<td>( y = 0.787 + 0.359x )</td>
<td></td>
<td>0.3126</td>
<td>5.5**</td>
</tr>
<tr>
<td>PS 656</td>
<td>Niger</td>
<td>( y = 1.290 + 0.472x )</td>
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<td>0.5309</td>
<td>5.0**</td>
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<td>PS 663</td>
<td>Niger</td>
<td>( y = 1.398 + 0.321x )</td>
<td></td>
<td>0.3454</td>
<td>3.9*</td>
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<td>PS 727</td>
<td>Niger</td>
<td>( y = 0.891 + 0.235x )</td>
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<td>0.3954</td>
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<tr>
<td>PS 728</td>
<td>Niger</td>
<td>( y = 1.548 + 0.033x )</td>
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<td>0.2071</td>
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<tr>
<td>PS 729</td>
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<td>( y = 1.915 + 0.034x )</td>
<td></td>
<td>0.3585</td>
<td>7.8**</td>
</tr>
</tbody>
</table>

<sup>a</sup> and ** indicate that the least-squares mean, derived from analysis of covariance, was significantly different from zero at \( P = 0.05 \) and 0.01, respectively.

<sup>1</sup>Indicates that downy mildew incidence differed from the most resistant accession by Fisher’s LSD (LSD<sub>P=0.05</sub> = 16.9).

<sup>2</sup>Regression of accession mean on trial mean for seven trials conducted in west Africa.
pairwise comparisons between trials \((r > 0.38, P < 0.0031)\). Inconsistency among the trials could be the result of differential pathogenicity of pathogen populations among locations, and the occurrence of environmental conditions conducive for infection coinciding with availability of susceptible tissue due to growth stage. Although trial and trial \(\times\) accession sums of squares were significant, identification of accessions with low overall incidence were of particular interest. Accessions with <10% downy mildew incidence were PS 194 (0.0%), PS 200 (5.1%), PS 202 (0.8%), PS 203 (9.9%), PS 206 (4.6%), PS 214 (1.0%), and PS 215 (9.8%) from Senegal; PS 143 (5.3%), PS 459 (4.2%), PS 567 (9.7%) from Niger; PS 512 (4.8%) from Mali; and PS 78 (9.2%), and PS 161 (7.8%) of unknown origin. Accession PS 202 expressed resistance to both striga and downy mildew.

4. Discussion

This study has successfully identified wild pearl millet accessions with resistance to \(S. hermonthica\). The possibility that resistance to a different species, \(S. lutea\), exists in pearl millet was implied in previous studies (Mathur and Bhargava, 1971), although additional evaluations are required to confirm the results. Multi-location and multi-year trials are essential in identifying stable resistance (Haussmann et al., 2001b). The differences that existed among the present trials were due to either genetic differences among the striga populations, or variation in local environmental conditions that affected the success of striga infection.

Genetic differences in striga populations must be considered. Differences in pathogenicity to sorghum and pearl millet exist among sub-populations of \(S. hermonthica\) collected from different hosts and regions in Niger (Freitag et al., 1996). Sub-populations infesting maize, sorghum, and pearl millet in Nigeria also exhibit differential pathogenicity (Kim et al., 1994). Laboratory and field trials assessing resistance in sorghum provided strong evidence of differences in \(S. hermonthica\) populations between the Mali and Niger region vs. Kenya (Haussmann et al., 2001a, b).

The differences observed among the present trials are not solely attributable to environmental conditions favoring or inhibiting infection. Striga emergence on accessions in trials with moderate to high levels of infestation (Samanko 1997 and 1998, Cinzana 1998, Maiduguri 2000, and the Sadoré 2000 pot trial) were rarely positively correlated. In contrast, all trials conducted at Sadoré were correlated, indicating a high consistency of those evaluations in spite of the erratic success of trial establishment. Cinzana may have a unique striga population, since data from this site tended to be negatively correlated to data from other sites. The role of environmental conditions for striga attachment and subsequent development cannot be discounted, however, since data from Samanko in 1997 and 1998 were not correlated. Differences in environmental conditions between the years are a likely source of this variation since location and striga populations were common across years. Residual genetic heterogeneity within the \(P. glaucum\) subsp. \(monodii\) accessions is another potential source of variation in these evaluations. Based on the available information, it is not possible to estimate the relative importance of variation in environment, striga populations, or heterogeneity in the host in these trials.

Because eco-geographic differences in striga populations adapted to pearl millet potentially exist, stable resistance is desired. Within the constraints of the present experiments, some accessions have been identified with apparent resistance expressed over seven trials in three countries. Further experiments will be required to determine if this resistance is effective in other sites in West Africa, as well as in the Horn or eastern regions of Africa.

Host factors that affect striga emergence are the cumulative manifestation of low production of exudates.
required to stimulate striga seed germination, escape and mechanical barriers, and active host resistance response mechanisms. Prior studies indicated that differences in stimulation of striga seed germination did not exist among the tested wild Pennisetum accessions (Wilson et al., 2000). As an obligate parasite, striga infection affects partitioning responses in the host (Graves et al., 1990). Likewise, host factors that affect photosynthetic partitioning and plant development, such as maturity or responses to downy mildew infection, are likely to affect striga development. These studies confirm previous observations that variables in addition to resistance responses can affect striga emergence (Wilson et al., 2000). These factors will need to be considered during the transfer of this resistance to cultivated pearl millet. In the present study, 16 accessions with potential resistance were identified from the initial collection of 274 accessions, and four of those accessions should be of particular interest. Controlled studies to determine mechanisms of resistance will be more feasible with this number of accessions.

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References


