Relationship between grain development stage and sorghum cultivar susceptibility to grain mould

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Five sorghum (Sorghum bicolor) cultivars were evaluated in field trials in Ethiopia to determine the grain development stage(s) most susceptible to mould pathogens. Four growth stages (anthesis, milk, dough and physiological maturity) were compared. Damage to grains and the incidence of fungi were significantly affected by cultivar × growth stage interactions. These effects were due to the change in susceptibility between milk and dough stages in some cultivars or an absence of growth stage effect in others. In general, a higher incidence of fungi and damage to grains occurred when moisture was applied to panicles during dough or milk stages. This was particularly the case with the major mould fungi (Fusarium proliferatum, F. thapsinum, F. graminearum and Bipolaris sorghicola). Frequencies of Alternaria spp. and Epicoccum spp. increased significantly from dough stage onwards. The incidence of Fusarium spp. and B. sorghicola was negatively correlated with percentage seed germination and positively with grain discoloration. A negative correlation was found between the incidence of B. sorghicola and 1000-grain mass. In the greenhouse, artificial inoculation of plants at soft dough stage with Curvularia lunata, F. thapsinum and Phoma sorghina reduced seed germination by 52, 46 and 48 %, respectively, compared with inoculation at anthesis. Results suggested that susceptible sorghum cultivars could respond better to control practices during late milk to soft dough growth stages than at other stages of development.

Key words: Bipolaris, Fusarium, grain mould, sorghum, susceptible stage.

Grain mould is a major disease of sorghum (Sorghum bicolor (L.) Moench) that limits production worldwide (Singh & Agarwal 1993; Menkir et al. 1996). Commonly reported grain mould fungi include Fusarium verticillioides (Sacc.) Nirenberg, Curvularia lunata (Wakker) Boedijn, Fusarium incarnatum (Desm.) Sacc. and Phoma sorghina (Sacc.) Boerema, Dorenb. & Kesteren (Forbes et al. 1992; Singh & Agarwal 1993; Singh & Bandyopadhyay 2000). Fungi in the genera Alternaria, Helminthosporium, Drechslera, Bipolaris, Colletotrichum and Cladosporium are also frequently isolated from sorghum grain (Williams & Rao 1981; Menkir et al. 1996), although their importance as grain mould pathogens has not been ascertained (Forbes et al. 1992).

Symptoms of grain mould include pink, white, orange, grey or black discolorations on the surface of grains (Singh & Agarwal 1993). Infected panicles usually produce smaller and/or discoloured kernels with reduced viability. Grain may also be contaminated with mycotoxins that are harmful to animals and humans (Williams & Rao 1981; Singh & Agarwal 1993; Bhat et al. 2000). Moulded grain is also not suitable for malting as pathogens can survive the malting process and contaminate beer with metabolic products that are toxic to consumers (Ilori et al. 1991).

Identification of the susceptible host stage is considered one of the main prerequisites in the development of plant disease forecasting systems (Maloy 1993). By understanding the relationship between the plant and disease development, the time at which control measures need to be implemented can be predicted more precisely. Consequently, unnecessary use of crop protection chemicals such as fungicides could be avoided, thereby reducing management costs and pollution of the environment. Infection of panicles can occur at any stage from young inflorescence to maturity, provided that free moisture is present (Tarr 1962). However, whether or not the degree of infection at different development stages varies, has yet to be ascertained.

Reports suggest that the grain mould susceptible stage may vary for different sorghum varieties. Some studies have indicated that the incidence of grain mould pathogens increases significantly during dough stages and decreases at maturity (Singh & Agarwal 1993; Melake-Berhan et al. 1996; Menkir et al. 1996). By contrast, grains have been reported to be susceptible even after physiological maturity (Bandyopadhyay et al. 1991). Singh & Agarwal (1993) noted that infections at
later seed development stages are generally limited to the outer surface of seed coats and, hence, may not significantly affect grain yield. Somani & Indira (1999) found that the extent of grain mass loss due to mould pathogens under greenhouse conditions was less as grains developed from anthesis to maturity. However, such findings have not been confirmed under field conditions. Since grain damage associated with moulds is complex and diverse (Williams & Rao 1981; Singh & Agarwal 1993), it is essential to consider other grain mould damage parameters like grain discoloration and seed germination (in addition to grain mass) in the study of relationships between mould severity and grain development stage.

There is a dearth of information on Ethiopian sorghum cultivars, not only on mould development in relation to grain development stages, but also with regard to their overall susceptibility to grain moulds. This study was conducted to assess the susceptibility of five sorghum cultivars to grain mould pathogens. The major objective was to determine the role of grain development stages on the incidence of mould pathogens and damage to grain under field conditions. One hybrid sorghum from South Africa was also evaluated for its reaction to mould pathogens following artificial inoculation at different growth stages in the greenhouse.

Materials and methods

Field experiment

Ethiopian sorghum cultivars Awash1050, Seredo, ETS2111, ETS2752 and IS9302 were used. Seredo has light brown grain and is of intermediate maturity (<80 days to flowering) while the remainder are late-maturing cultivars (>80 days to flowering). Grains of ETS2752 and ETS2111 are straw-coloured while those of IS9302 and Awash1050 are yellow and red, respectively. Except for ETS2111 (compact and oval), the cultivars have a compact and elliptical panicle shape.

Cultivars were planted during the 2000/2001 season at the Alema University Campus Research Station, Raaree, Ethiopia. Each plot consisted of four rows, 5 m in length with a 75 cm inter-row spacing. Diammonium phosphate (150 kg ha\(^{-1}\)) was applied at planting by broadcasting. Plots were over-seeded and two weeks after emergence, seedlings were thinned to a 20 cm intra-row spacing (25 plants per row). When c. 50 cm high, plants were fertilised with urea (100 kg ha\(^{-1}\)) as side-dressing (Temam 1992). Cultivation and weeding were carried out manually as required.

Four grain development stages, based on descriptions by Shapiro & Peterson (1997) and Zadoks et al. (1974), were selected for comparison, viz.:

1. Head emergence to complete anthesis (Zadoks code 59–69).
2. Blist er (partially formed grains with clear liquid) to milk (grains have thick milky liquid throughout) (Zadoks code 71–75).
3. Late milk (kernels contain semi-solid white liquid) to dough (almost white solid substances fill the grain) (Zadoks code 77–85).
4. Hard dough (firm grain, difficult to crush between fingers) to physiological maturity (formation of black spot at the kernel tip) (Zadoks code 87–91).

In the text below, the above growth stages are referred to as anthesis, milk, dough and physiological maturity, respectively.

Moisture was applied to panicles at the above growth stages with some modification of the method described by Bandyopadhyay & Mughogho (1988). When the respective growth stages were reached, four random panicles per replicate were sprayed with tap water until run-off each morning and afternoon. After wetting, each panicle was covered with a plastic bag for two three hour periods, viz. 9:00 to 12:00 and 15:00 to 18:00. This procedure was continued during each of the four grain development stages until the onset of the subsequent growth stage. Control panicles were not sprayed or covered with plastic bags.

Plots were arranged according to a split-plot design with three blocks, sorghum cultivar and growth stage being main and subplot treatments, respectively. Data from a weather station approximately 100 m from the experiment site indicated that mean total rainfall (RF) and relative humidity (RH) during the experiment period (flowering to physiological maturity) were 132.4 mm and 44.5–88.5 %, respectively, for Seredo. Awash1050, ETS2111 and IS9302 were subjected to 30.3 mm RF and 31–70.5 % RH and ETS2752 to 30 mm RF and 20.3–66.7 % RH. The different values for rainfall, temperature and relative humidity are due to differences in maturity periods of the cultivars.
Grain was harvested at physiological maturity (c. 13 % moisture content). Panicles from all treatments were threshed manually and grain from the four treated panicles was pooled to represent a single replicate. One hundred grains were randomly selected from each of the three replicates of a particular growth stage, surface-disinfested in 1 % sodium hypochlorite for three minutes and rinsed three times in sterile distilled water. After drying on sterile blotting paper, five seeds were plated on each of 20 plastic Petri dishes (9 cm diam.) containing 2 % malt extract agar (MEA) (Difco®) supplemented with 100 µl l⁻¹ streptomycin sulphate (Bandyopadhyay et al. 1991). Plates were incubated at 25 °C and each grain was examined for grain mould pathogens within 7–14 days of incubation. Where possible, fungi were identified in situ under a light microscope. Alternatively, pure cultures were obtained for identification by transferring isolates to MEA. Some isolates, particularly Fusarium spp., were identified at the South African Medical Research Council, Tygerberg. Percentage incidence of each grain mould pathogen was calculated.

Threshed grains (30 g) from each replicate were spread in a glass Petri dish to determine the extent of discoloration (Audilakshmi et al. 1999). Using a stereo microscope (x30 magnification), grain mould severity was assessed as a visual estimate of the percentage of grain surface discoloured. The mass of 1000 grains was determined using a Sartorius (Type B6100) balance. A further 100 grains from each replicate were used to evaluate seed germination on moistened, sterile filter paper in glass Petri dishes. Five grains per plate were incubated at room temperature for nine days during which time they were monitored for germination. Grains were recorded as having germinated normally when they had well-developed roots and shoots with limited lesion development (ISTA 1999).

Data were subjected to analysis of variance (ANOVA) using the statistical package Minitab (Minitab 1998) and comparisons of means were performed according to Duncan’s multiple-range test.

Greenhouse experiment

Anthesis (Zadoks code 69) and soft dough (Zadoks code 85) stages were compared using the grain mould susceptible sorghum hybrid NK283. Five seeds were sown in each of 18 5-kg-capacity plastic pots filled with steam-sterilised soil. Two weeks after emergence the seedlings were culled to one per pot. Spore suspensions (10⁵ spores ml⁻¹ sterile distilled water) was prepared from cultures of C. lunata, Fusarium thapsinum Klittich, J F Leslie, P E Nelson & Marasas and P. sorghina, grown for 10 days on MEA at 25 °C. At the respective growth stages, inoculum of each isolate was sprayed until run-off onto three panicles in separate pots using a hypodermic syringe. Inoculated panicles as well as three uninoculated control panicles were covered with plastic bags for five days. Grain damage parameters and seed germination were determined as above. When growth of roots and/or shoots was retarded relative to the control or when systemic lesions developed on these structures, grains were considered to have germinated abnormally.

Results

Field experiment

Effect of cultivar × growth stage interaction on the incidence of grain mould pathogens: analysis of variance indicated that, with the exception of C. lunata, whose incidence was significantly (P ≤ 0.01) affected by cultivar only, cultivar × growth stage interaction significantly affected the incidence of fungi from sorghum grains. Significantly more Fusarium proliferatum (Matsush.) Nirenberg was isolated from moisture-treated grains at dough growth stage in cultivars Seredo and ETS2111 (Table 1). Isolation frequencies at milk and maturity growth stages were not significantly different from isolations at dough stage in Awash1050. In IS9302 and ETS2752, growth stage did not significantly affect the isolation frequency of F. proliferatum from grains. The same trend was evident for F. thapsinum except that in Awash-1050, the milk stage had a significantly lower incidence than the dough stage, but both these stages had a higher incidence than the other growth stages. The frequency of F. graminearum at dough stage was significantly higher than at all other growth stages in Seredo. There was no significant difference in incidence of F. graminearum in grains treated with moisture during anthesis, milk or maturity growth stages in Seredo. P. sorghina occurred at a low incidence in all cultivars. However, a significantly higher isolation frequency was associated with anthesis, followed by dough and milk stages in Seredo.
<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Incidence (%)&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Fusarium proliferatum</th>
<th>Fusarium thapsinum</th>
<th>Curvularia lunata</th>
<th>Bipolaris sorghicola</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seredo</td>
<td>ETS2111</td>
<td>IS9302</td>
<td>ETS2752</td>
<td>Awash 1050</td>
</tr>
<tr>
<td>Anthesis</td>
<td>4.00 b</td>
<td>6.33 c</td>
<td>0 a</td>
<td>0 a</td>
<td>7.33 c</td>
</tr>
<tr>
<td>Milk</td>
<td>3.00 b</td>
<td>12.00 b</td>
<td>0.67 a</td>
<td>0 a</td>
<td>10.33 ab</td>
</tr>
<tr>
<td>Dough</td>
<td>14.33 a</td>
<td>26.33 a</td>
<td>2.33 a</td>
<td>0.33 a</td>
<td>11.33 a</td>
</tr>
<tr>
<td>Maturity</td>
<td>3.67 b</td>
<td>6.67 c</td>
<td>0.67 a</td>
<td>0 a</td>
<td>10.00 ab</td>
</tr>
<tr>
<td>Control</td>
<td>2.33 b</td>
<td>6.33 c</td>
<td>0 a</td>
<td>0.33 a</td>
<td>8.67 bc</td>
</tr>
<tr>
<td>Mean&lt;sup&gt;b&lt;/sup&gt;</td>
<td>5.47 c</td>
<td>11.53 a</td>
<td>0.73 d</td>
<td>0.13d</td>
<td>9.53 b</td>
</tr>
</tbody>
</table>

<sup>a</sup>Mean of 300 grains from three replicates; values in columns within fungal species followed by the same letter do not differ significantly according to Duncan’s multiple-range test (P ≤ 0.05).

<sup>b</sup>Means of cultivars in rows within fungal species followed by the same letter do not differ significantly according to Duncan’s multiple-range test (P ≤ 0.05).
Similarly, most cultivars exhibited a low incidence of *Bipolaris sorghicola* (Lefebvre & Sherwin) Alcorn, except Seredo, in which all growth stages had a significantly higher incidence than the control. There was no significant differences in the incidence of *C. lunata* among growth stages for all cultivars, but in ETS2111 a relatively lower incidence occurred at milk stage.

Alternaria spp. were frequently isolated at all growth stages from all cultivars (Table 2). Isolation frequencies in Seredo, IS9302 and Awash1050 did not differ significantly between growth stages or from the control. In ETS2111, isolation frequencies significantly higher than the control were associated with milk, dough and maturity growth stages, while in ETS2752 a significant increase in frequency of *Alternaria* spp. occurred at dough and maturity stages. The incidence of *Cladosporium* spp. was not consistently associated with growth stage. No significant difference in *Cladosporium* spp. incidence was recorded in Seredo, while in ETS2111 the incidence prior to maturity was relatively less than the control. In Awash1050, the incidence of *Cladosporium* spp. was significantly less at anthesis than at other growth stages except milk. Conversely, in IS9302 the incidence at anthesis and milk stages was significantly higher than the control. Generally, the frequency of *Epicoccum* spp. was lower in ETS2111, IS9302 and ETS2752 than in the other cultivars, although in the latter there was an increased incidence at dough stage relative to the control. In Seredo and Awash1050, an increased incidence of *Epicoccum* spp. was recorded at post-anthesis stages.

**Cultivar and growth stage main effects on pathogen incidence:** In Tables 1 and 2, mean incidence values in columns for each pathogen indicate the main effects of growth stages while mean values in rows show main effects of cultivars. Cultivars Seredo, ETS2111 and Awash1050 were more susceptible to most of the grain mould pathogens. A significantly higher incidence of *Fusarium* spp.
was recorded in these cultivars (Table 1). Isolation frequencies of *P. sorghina* and *B. sorghicola* were significantly higher in Seredo than in other cultivars. The incidence of *C. lunata* in all cultivars was very low. All cultivars had a high incidence of *Alternaria* spp. with a significantly higher frequency of this genus in Awash1050 (Table 2). Similarly, *Cladosporium* spp. were common in all cultivars although the highest incidence was recorded in IS9302 and the lowest in Seredo. Awash1050 and Seredo were colonised more by *Epicoccum* spp. while the incidence of this genus was significantly lower in ETS2752 than in most other cultivars.

Within growth stage main effects, the dough followed by the milk stage, was more susceptible to *F. proliferatum* and *F. thapsinum* (Table 1). Although a significantly higher incidence of *F. graminearum* occurred at the dough stage, there was no significant difference in the incidence of this species among the remaining growth stages. Similarly, other growth stages were less susceptible to *B. sorghicola* than the dough stage. Although the incidence of *Cladosporium* spp. was not significantly affected by growth stage, *Alternaria* spp. and *Epicoccum* spp. increased significantly after the milk stage (Table 2).

**Cultivar and growth stage main effects on grain damage:** damage to grains was significantly affected by growth stage (Table 2). There was significantly more grain discoloration associated with moisture application to panicles during the dough stage in cultivars ETS2111 and Awash1050, and during the milk stage in IS9302 (Table 3). No significant differences in grain discoloration across growth stages were evident in ETS2752.

Significantly lower seed germination in ETS2111 was associated with panicles treated with moisture at dough and milk stages. There was no significant difference in percentage germination among treatments at anthesis, milk and dough stages in Seredo and Awash1050, but the dough stage treatment in both cultivars resulted in significantly

### Table 3. Grain damage on sorghum cultivars after moisture application to panicles during different growth stages in the field.

<table>
<thead>
<tr>
<th>Growth stage</th>
<th>Extent of damage*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seredo</td>
</tr>
<tr>
<td>Grain discoloration (%)</td>
<td></td>
</tr>
<tr>
<td>Anthesis</td>
<td>16.67 c</td>
</tr>
<tr>
<td>Milk</td>
<td>20.67 b</td>
</tr>
<tr>
<td>Dough</td>
<td>25.67 a</td>
</tr>
<tr>
<td>Maturity</td>
<td>16.67 c</td>
</tr>
<tr>
<td>Control</td>
<td>13.33 c</td>
</tr>
<tr>
<td>Mean†</td>
<td>18.60 a</td>
</tr>
<tr>
<td>Seed germination (%)†</td>
<td></td>
</tr>
<tr>
<td>Anthesis</td>
<td>75.67 abc</td>
</tr>
<tr>
<td>Milk</td>
<td>73.33 bc</td>
</tr>
<tr>
<td>Dough</td>
<td>69.67 c</td>
</tr>
<tr>
<td>Maturity</td>
<td>81.67 a</td>
</tr>
<tr>
<td>Control</td>
<td>80.67 ab</td>
</tr>
<tr>
<td>Mean</td>
<td>76.20 c</td>
</tr>
<tr>
<td>1000-grain mass (g)*</td>
<td></td>
</tr>
<tr>
<td>Anthesis</td>
<td>26.67 ab</td>
</tr>
<tr>
<td>Milk</td>
<td>25.33 bc</td>
</tr>
<tr>
<td>Dough</td>
<td>23.00 c</td>
</tr>
<tr>
<td>Maturity</td>
<td>27.67 ab</td>
</tr>
<tr>
<td>Control</td>
<td>28.67 a</td>
</tr>
<tr>
<td>Mean</td>
<td>26.27 bc</td>
</tr>
</tbody>
</table>

*Mean of 100 grains from each of three replicates; values in columns within damage parameters followed by the same letter do not differ significantly according to Duncan's multiple-range test ($P \leq 0.05$).

†Means of cultivars in rows within damage parameters followed by the same letter do not differ significantly according to Duncan's multiple-range test ($P \leq 0.05$).
lower germination than the control. Growth stage had no significant effect on seed germination and 1000-grain mass in IS9302, but 1000-grain mass at anthesis and dough stages was significantly lower than the control. In ETS2752, there was a significantly lower percentage germination at anthesis compared with the control and significantly lower 1000-grain mass was recorded at anthesis, milk and dough stages than at maturity. A lower 1000-grain mass was recorded at milk than at other growth stages in cultivar ETS2111. No significant difference in 1000-grain mass was found between milk and dough stages in Seredo.

Significantly more discoloration of grains was evident in cultivars Seredo and Awash1050 and the least in ETS2752. Percentage germination was significantly lower in Seredo and ETS2111 compared with the other cultivars. A significantly higher 1000-grain mass was recorded for Awash1050 than for the other cultivars. Averaged over cultivars, moisture application during dough stage, followed by milk stage, resulted in the highest seed damage. Seed germination was significantly lower at dough than at other growth stages. Although grain discoloration at milk stage was significantly higher, 1000-grain mass at this stage was not significantly different from those observed at other stages.

Correlation analysis revealed significant relationships between the incidence of some mould fungi and grain damage parameters (Table 4). In cultivars Awash1050, Seredo and ETS2111, incidences of Fusarium spp. and Bipolaris sorghicola correlated negatively with percentage germination and positively with grain discoloration (refer to Tables 1 and 2). A negative correlation ($P \leq 0.05$) was found between isolation frequency of Bipolaris sorghicola and 1000-grain mass. Correlations between the incidence of the remaining fungi and grain damage parameters were not significant.

Greenhouse experiment

Inoculation of plants in the greenhouse with the three pathogens at soft dough growth stage resulted in consistently greater abnormal germination than inoculation during anthesis (Fig. 1). Compared to anthesis, inoculation at the soft dough stage with C. lunata, F. thapsinum and P. sorghina increased abnormal germination by 57, 51 and 60 %, respectively.

Discussion

Results of the present study indicate that in the field, incidence of grain mould pathogens on sorghum grains generally was higher when moisture was applied to panicles during the milk to dough development stages compared with physiological maturity and/or anthesis stages. The greater susceptibility of the dough stage was also confirmed by artificial inoculation with different grain mould pathogens under greenhouse conditions. Moreover, incidences at the milk and dough development stages were shown to be associated with loss in grain mass and germination. Elsewhere, field experiments involving observations at different growth stages indicated the highest incidences of grain mould on sorghum between 25 and 35 days after anthesis with an increase in incidence starting at soft dough stage (Melake-Berhan et al. 1996). Forbes et al. (1988) also observed that the incidence of sorghum seeds infected with F. verticillioides increased towards the dough stage. Similarly, Narendrappa et al. (1988) found the highest incidence on seeds (95.6 %) when sorghum heads were inoculated at soft dough stage with the grain mould fungus,
Gonatobrytis ramosa Rieis. Incidence on grain was 81.6, 89.9 and 42.0 % with inoculations at anthesis, grain-fill and fully formed grains, respectively. Similar trends have been observed in susceptibility of hosts other than sorghum with regard to seed infection in the field. Altermeria alternata (Fr.:Fr.) Kiessl., C. lunata, F. incarnatum, F. verticillioides and Phoma spp. were isolated from seeds of pearl millet (Pennisetum glaucum (L.) R. Br.) at all seed development stages, although increased incidence was more evident during grain-fill to physiological maturity stages (Ingle & Raut 1993).

Susceptibility of growth stages observed in different cultivars in the present study could be due to reduced expression of resistance mechanisms during the respective stages. Studies on temporal expression of sorghum resistance to grain moulds have shown significant reductions in concentrations of flavan-4-ols in susceptible cultivars beginning at the soft dough stage, while in resistant varieties concentrations remained high throughout seed development stages (Melake-Berhan et al. 1996). Similarly, Jambunathan et al. (1991) reported a difference in the concentrations of flavan-4-ols in susceptible and resistant varieties at, or after, 30 days post-flowering.

Somani & Indira (1999) found that sorghum inoculated with C. lunata and F. verticillioides at anthesis did not set seed and the mass of seeds increased linearly with inoculation at later growth stages. This is consistent with the present study where the 1000-grain mass generally increased with increasing growth stage. Contrary to findings of Somani & Indira (1999), moist conditions at anthesis did not have a significant effect on seed mass in the present study. This could have been partially due to differences in the susceptibility of the sorghum varieties used. The present results partly agree with those of Narendrappa et al. (1988), indicating that artificial inoculation of freshly emerging sorghum panicles with G. ramosa failed to result in infection, and with those of Mills (1983) showing that most biotic interactions related to seed deterioration occur during seed enlargement, but that nutrients and moisture are limiting factors at anthesis and ripening, respectively.

In the present study, despite the relatively high incidence of Altermeria, Cladosporium and E. pocicum at most growth stages, their presence was not significantly associated with grain discoloration, seed mass or percentage germination. Such fungi have been considered seed surface colonizers at later development stages, with little capacity to penetrate deep into grains (Forbes et al. 1992; Singh & Agarwal 1993). Accordingly, they are often regarded as not being true pathogens and do not significantly influence grain damage parameters (Gaudet & Kokko 1986; Menkir et al. 1996). The lack of significant associations between grain damage parameters and C. lunata and P. sorghina
could probably be ascribed to their infections levels not having reached the damage threshold. Differences in the incidence of sorghum grain mould pathogens have been reported without significant difference in grain loss parameters such as 1000-grain mass (Lukade, 1986). Nevertheless, significant correlations between grain damage parameters and Fusarium spp. and B. sorghicola in this study, indicated the importance of control of sorghum grain mould has not often been encouraged mainly from an economical point of view (Williams & Rao 1981; Singh & Bandyopadhyay 2000). However, where resistant varieties are not available, fungicides could profitably be used on susceptible but high-yielding cultivars through well-timed application at the most susceptible growth stages.

Acknowledgements
We wish to thank J P Rheeder (PROMEC, Medical Research Council, Tygerberg, South Africa) for identification of Fusarium cultures. We are also grateful to W M Kriel, Department of Plant Sciences (Plant Pathology), University of the Free State, for assistance in identification of other fungi. This project was financed by a World Bank Supported Agricultural Research and Training Project (Alemaya University component, Ethiopia).

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Accepted 12 February 2004

Associate Editor was T A S Aveling