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Indirect selection for resistance to *Stenocarpella maydis* and *Fusarium graminearum* and the prospects of selecting for high-yielding and resistant maize hybrids

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With 2 figures and 5 tables

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Abstract

Stenocarpella maydis and *Fusarium graminearum* affect grain yield and quality as a result of mycotoxins produced. A negative association of yield with resistance to cob rots has been reported. The objectives of this study were therefore to investigate the influence of cob characteristics on the response to *F. graminearum* and *S. maydis* disease reaction and evaluate the prospects of direct selection for high-yielding and resistant maize hybrids. In this study, the pathogens were directly introduced to the cob through toothpick inoculation. Correlation of husk cover to disease severity of each pathogen, separately toothpick inoculated, was significant ($P < 0.01$). However, the low *r* values (<0.45) of traits associated with the response to inoculation by *S. maydis* and *F. graminearum* imply that indirect selection would not be beneficial for obtaining the type of resistance shown under inoculation. Several hybrids combined good yields with at least moderate resistance to both pathogens.

Key words: cob rot — correlation — husk cover — yield — hybrid

Diseases are an important biotic factor leading to low maize production. Among the diseases that compound productivity, cob rots caused by *Stenocarpella maydis* and *Fusarium graminearum* are the predominant pathogens world-over contaminating maize grains with mycotoxins and reducing yield and profits (Rossouw et al. 2002, Munkvold 2003, Masango et al. 2014). Cultural control approaches have been used to control cob rots but with limited success, leaving breeding for resistance as the most viable and economical approach (Munkvold 2003). Resistance to cob rots in maize may, however, be associated with undesirable traits such as small seeds and low yields (Duvick 2001, Tembo et al. 2016). Yield has being cited by farmers as a critically important trait to maintain when breeding for resistance (Mukanga et al. 2011). During the evaluation of test genotypes for resistance, appropriate test environments are essential to enhance their suitability across environments. This is needed to select for resistance to cob rots as indirect selection, based on related agronomic traits such as husk cover, drooping and kernel texture, is not effective (Rossouw et al. 2002, Czembor and Ochodzki 2009). Thus, breeding for multiple resistance to endemic cob rot pathogens such as *S. maydis* and *F. graminearum* is compounded by efficient selection systems. To achieve an efficient selection system, understanding the factors influencing selection is the key.

Rain has been suggested as the most influential weather factor leading to infection and development of cobs by pathogens. In small cereals, prolonged periods of wetness and high relative humidity increase growth and infection, due to higher rates of sporulation and faster transport (Agrios 2005). The relationship between disease severity to husk cover and cob drooping may help differentiate between the role of water in pathogen entry and its role in promoting disease development after pathogen entry. The more the husk is open at the cob tip, the more rain water seeps inside the husks and onto kernels, while fully drooped cobs drain most of the rain water from the cob creating a drier micro-environment which may not favour infection by fungal pathogens (Rossouw et al. 2002). Indeed, good husk cover and cob drooping are correlated with cob rot resistance (Rossouw et al. 2002). The previous practice to screening genotypes for reaction to cob rots and correlated responses to husk and drooping was by whorl placement inoculation (Rossouw et al. 2002). This inoculation technique primarily allows both the pathogen and rain water to enter through the same way (silk or open cob tips). In order to improve selection for resistance to cob rots, there is a need to further investigate the role of cob husk cover on cob rot infection and development, when the pathogen is directly introduced to the cob as this enhances cob rot infection and development (Clements et al. 2003). A strong correlation between cob rot disease development and poor husk cover will offer a suitable tool for indirect selection to this complex. The role of kernel texture (whether dent or flint) in infection and consequent severity of cob rot has also not been well studied (Czembor and Ochodzki 2009). The objective of this study were therefore to evaluate the influence of cob and kernel characteristics on reaction to *F. graminearum* and *S. maydis* disease reaction and to evaluate the prospects of direct selection for high-yielding hybrids resistant to *F. graminearum* and *S. maydis.*

Materials and Methods

Experimental conduct, pathogen culture and inoculation: The experiments were conducted at Namulonge (0°32′N, 32°35′E; altitude 1150 m), Masaka (0°20′S, 31°44′E, altitude 1315 m) and Bulindi (1°25′N, 31°21′E; altitude 1140 m) districts of Uganda in 2011 first (A) season (from March to August). Twelve tropical inbred lines with varying resistance to *S. maydis* and *F. graminearum*, used by Tembo et al. (2013), were utilized (Table 1). These materials were mated in a 12×12 half-diallel during the second (B) cropping season (September to December/January) of 2010 at National Crop Resource Research Institute (NaCRRI) at Namulonge. The resulting 66 hybrids were evaluated at Namulonge, Masaka and Bulindi. Each experiment was planted following a randomized complete block design (RCBD) with two replications. Plants were established at a spacing of 75 cm × 30 cm in 5 m long rows with 17 plants per row. Two seeds where initially planted per hill but were subsequently thinned to one plant per hill, 4 weeks

Table 1: Inbred lines used in the half-diallel including their reaction responses to *Stenocarpella maydis* and *Fusarium graminearum* when evaluated previously at NaCRRI in Namulonge

Parent	Inbred line[1]	Grain type	Reaction to *Stenocarpella maydis*	Reaction to *Fusarium graminearum*
1	WL 429-35	Flint	R	R
2	CKL 05017	Flint	R	R
3	CML 506	Semi-flint	M	R
4	WL 118-10	Flint	R	R
5	WL 118-22	Flint	S	M
6	CKL 05018	Flint	M	M
7	CKL 05004	Flint	M	R
8	NML 166	Dent	M	R
9	CML 384	Flint	S	M
10	NML 89	Dent	S	S
11	NML 56	Dent	S	M
12	CZL 8	Flint	S	S

[1] Line designations are as follows: WL and NML lines are weevil resistant and elite lines from NaCCRI. CML, CMK and CZL are elite CIMMYT maize lines from Mexico, Kenya and Zimbabwe, respectively.
S, susceptible; R, resistant; M, moderate; NaCRRI, National Crop Resource Research Institute.

after germination. Each plot had three rows. The first two rows were not inoculated and used to evaluate yield, husk cover, drooping and kernel type. The non-inoculated cobs were also used to assess natural development of cob rots. At least five plants in the third row were inoculated with either *F. graminearum* or *S. maydis*. The inoculum was prepared as by Tembo et al. (2013). Standard cultural practices such as weeding and appropriate fertilizer applications were followed in all the experiments.

Measurement and characterization of associated traits: Cob drooping and husk cover were scored. At harvest, cob drooping was rated using a scale of 1 – fully erect cob to 5 – for fully drooped against the stalk. A score of three was given to cobs which were along the horizontal plane. For husk cover, at least six cobs were selected randomly from the non-inoculated plots. The husk cover rating was performed by placing the palm around the husk leaves as they extend beyond the cob tip such that the base of the palm rests on the tip of the cob (Demissie et al. 2008). The ratings were performed as follows: (i) the husk leaves longer than the index finger; (ii) longer than the middle finger; (iii) longer than ring fingers; (iv) longer than pinky finger and (v) when the husk leaves are not longer than the pinky finger (exposed cob tip). The mean husk rating was determined and recorded for each genotype.

Measurements for yield, kernel texture and disease reaction: The first two non-inoculated rows were harvested, bulked and checked for cob rots infection prior to weighing after carrying out measurements on husk cover and drooping. The maize cobs in the first two row plots were weighed and then converted to t/ha. Kernel texture for the 66 hybrids was also characterized from non-inoculated rows, with one classified as dent, two semi-dent, three semi-flint and four flint. In the third row of each plot, five separate plants were inoculated with each pathogen, and a visual estimate of disease severity was made for each cob, assessed as percentage of the colonized cob from the point of infection, and the mean severity rating computed. Severity rating were performed using a scale of 1–5 for *S. maydis* as 1 = 0–25%; 2 = 26–50%, 3 = 51–75%, 4 = 76–99% and 5 = 100% (completely rotten) (Kapindu et al. 1999): for *F. graminearum,* it was 1 = 1–3%, 2 = 3–10%, 3 = 11–25%, 4 = 26–50%, 5 = 51–75% and 6 = 76–100% (Reid et al. 1992).

Data analysis: Diallel analysis was performed using Griffing's (1956) Method four, fixed model for responses to *S. maydis*, *F. graminearum*, husk cover, drooping and yield using generalized linear models. A mixed model was used, with replications and locations being random and genotypes being fixed. The correlated responses of *S. maydis*, *F. graminearum*, cob drooping, husk cover, kernel texture and yield disease severity were computed. A stepwise multiple regression was performed on cob drooping, husk cover and kernel texture on their responses to *S. maydis* and *F. graminearum.* The correlation of determination (r^2) values for the stepwise multiple regression was computed. All the above data analysis were performed using GenStat (Payne et al. 2011). The performance of each hybrid, averaged across locations, for yield and disease severity scores for *S. maydis* and *F. graminearum* was graphically analysed on a scatter plot in EXCEL.

Results

Genotypic responses to *F. graminearum, S. maydis*, in cobs with varying husk cover and cob drooping attributes

There were significant differences among genotypic responses to *F. graminearum*, *S. maydis,* husk cover, cob drooping and yield (non-inoculated) across locations ($P < 0.001$) (Table 2). The difference on each particular genotype per location for kernel texture was negligible and was therefore not included in the analysis of variance (Table 2). No meaningful disease development to *F. graminearum* and *S. maydis* was observed in non-inoculated cobs. The genotype × locational (G×L) interactions were significant ($P \leq 0.05$) for *F. graminearum* yield, husk cover and drooping. They were, however, of lesser effect than the genotypic effects themselves. The GCA effects showed that inbred lines 4 and 12 (identified in Table 1) had significant effects across all variables except the effect on drooping for inbred 12, which was not significant (Table 3). Inbred four had significant desirable effects to disease severity (*S. maydis* and *F. graminearum*), husk cover, and drooping while inbred 12 only had desirable significant effect for yield.

Relationship responses for *S. maydis*, *F. graminearum*, husk cover, drooping kernel texture and yield

Only husk cover and seed type were highly significantly correlated with both diseases across locations ($P < 0.01$) (Table 4). The strongest correlation to disease severity occurred across locations between husk cover and *F. graminearum* ($P < 0.001$; $r = 0.45$).

The stepwise regression of husk cover, cob drooping and kernel texture to *S. maydis* severity showed that much of the contribution to the phenotypic variance was attributed to kernel texture apart from Bulindi where there was almost equal contribution with husk cover (data not shown). With regard to *F. graminearum,* husk cover and kernel texture contributed significantly ($P < 0.01$) in Namulonge and Masaka, respectively (data not shown). Data from pooled means in all locations showed that husk cover was the major contributor to phenotypic variance ($P < 0.001$; $r^2 = 0.16$) for *F. graminearum* (data not shown).

Hybrid response for yield and disease infection

The scatter plot revealed that 16 and 13 hybrids exceeded the mean yield (7.1 t/ha) while having lower than average disease scores, 3.87 for *S. maydis* and 2.58 for *F. graminearum,* respectively (Figs 1 and 2). Further analysis of these superior genotypes (appearing within the box in Figs 1 and 2) revealed that Parent 3×Parent 12 (3×12) had the highest mean yield of 9.2 t/ha with an *S. maydis* score of 3.7 (Table 5). Ranking of the four most resistant hybrids showed that 3×4 had the lowest

Table 2: Mean squares for reaction to *S. maydis*, *F. graminearum* infection in material with varying husk cover and cob drooping attributes evaluated in Namulonge, Bulindi and Masaka and across all locations in the first rain season of 2011

		Mean squares				
Source	Df	*S. maydis*	*F. graminearum*	Husk cover	Drooping	Yield
Location	2	2.16	4.05	15.5**	63.7**	166***
Rep/location	3	0.39	0.53	0.18	0.57	0.40
Genotype	65	0.85***	1.33***	1.73***	1.40***	2.84***
GCA	11	4.15***	4.48***	6.76***	5.71***	6.62***
SCA	54	0.18*	0.69*	0.71	0.52	2.07*
Genotype × Location	130	0.13	0.47**	0.68***	0.55***	1.33**
GCA × Location	22	0.21	0.67**	1.28***	0.98***	1.33***
SCA × Location	108	0.12	0.43*	0.58***	0.46***	1.32**
Error	195	0.14	0.31	0.23	0.22	0.48

Data significant at *P = 0.05, **P = 0.01 and ***P = 0.001.
MS, mean square.

Table 3: General combining ability effects for parental lines evaluated across three locations (Namulonge, Bulindi and Masaka) in the first rain season of 2011

Parent[1]	*S. maydis*	*F. graminearum*	Husk cover	Drooping	Yield
P1	−0.01	0.04	−0.22	0.12	0.22
P2	−0.16	−0.53**	−0.28	−0.29*	0.20
P3	−0.33**	−0.28	0.56***	0.12	−0.16
P4	−0.91***	−0.53**	−0.42**	0.62***	−0.56**
P5	−0.08	0.19	−0.28	0.48***	0.15
P6	0.11	0.26	0.47**	0.2	−0.32
P7	0.01	0.16	0.10	−0.28	−0.53*
P8	0.09	0.06	−0.45**	−0.21	−0.55**
P9	0.21	−0.13	−0.24	0.07	0.59**
P10	0.22*	0.19	−0.11	−1.06***	−0.04
P11	0.19	−0.31	−0.22	−0.06	0.02
P12	0.64***	0.89***	1.10***	0.26	0.97***
SE	0.17	0.17	0.15	0.15	0.21
LSD	0.47	0.47	0.41	0.41	0.58

GCA significantly different from 0 at *P = 0.05, **P = 0.01 and ***P = 0.001, respectively.
[1]Letter P denotes parents, corresponding to the inbred lines numbered 1–12 in Table 1.

Table 4: Responses of *S. maydis*, *F. graminearum*, husk cover, drooping and yield of mean values evaluated in Namulonge, Bulindi, Masaka and across all locations in the first rain season of 2011

Location	Variable	*S. maydis*	*F. graminearum*	Husk cover	Drooping	Texture
Namulonge	*F. graminearum*	0.36**				
	Husk cover	0.22	0.31**			
	Drooping	−0.19	0.03	−0.08		
	Texture	−0.27*	−0.19	−0.32**	0.23	
	Yield	0.16	0.13	0.12	0.2	−0.12
Bulindi	*F. graminearum*	0.34**				
	Husk cover	0.31**	0.21			
	Drooping	−0.31**	−0.13	−0.02		
	Texture	−0.36**	−0.16	−0.08	0.31**	
	Yield	0.26*	0.16	0.45***	−0.01	−0.03
Masaka	*F. graminearum*	0.43***				
	Husk cover	0.21	0.17			
	Drooping	−0.08	−0.04	0.28*		
	Texture	−0.41***	−0.33**	−0.22	0.22	
	Yield	0.16	0.03	0.03	−0.19	−0.05
Across	*F. graminearum*	0.51***				
	Husk cover	0.36**	0.45***			
	Drooping	−0.30*	−0.02	0.09		
	Texture	−0.40**	−0.29*	−0.27*	0.32**	
	Yield	0.30*	0.17	0.22	0.07	−0.1

Correlation significant at *P = 0.05, **P = 0.01 and ***P = 0.001.

mean *S. maydis* severity score (2.5) with a yield of 7.2 t/ha. With *F. graminearum,* hybrid 2×9 was ranked among the top two high-yielding hybrids (8.2 t/ha) and among the two most resistant hybrids (1.7). The highest mean yield and lowest disease score for *F. graminearum* were 8.7 t/ha and 1.3, associated with hybrids 1×2 and 4×11, respectively. There were significant differences for yield between hybrids 2×9 and 4×11, but not between 2×9 and 1×2.

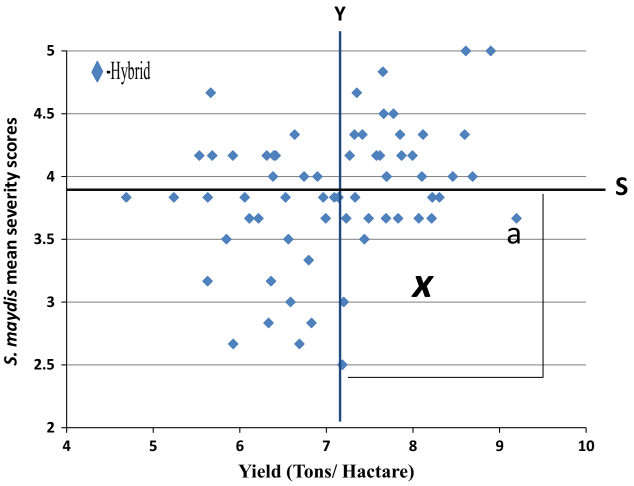

Fig. 1: Mean responses of genotypes across locations to *S. maydis* and yield. Lines Y and S depict the mean yield in t/ha and *S. maydis* mean severity scores across genotypes locations respectively. X – region with high-yielding and resistant genotypes. a – 3×12, *S. maydis*-resistant genotype with highest yield

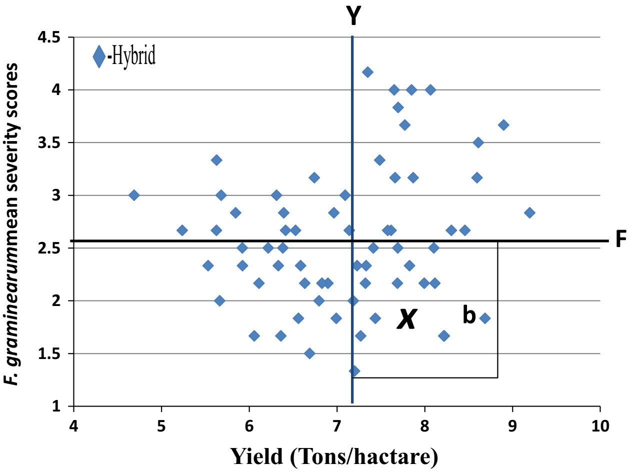

Fig. 2: Mean responses of genotypes across locations to *F. graminearum* and yield. Lines Y and F depicts the mean yield in t/ha and *F. graminearum* mean severity scores across genotypes and across locations, respectively. X – region with high-yielding and resistant genotypes. b – 1×2, *F. graminearum*-resistant genotype with highest yield

Discussion

The aim of the disease-resistant breeding is to effectively select and produce disease-resistant varieties. Proper selection of varieties coupled with appropriate test environments to optimize selection and to enhance the suitability of varieties across agroecologies is essential. Correlation of husk cover and cob drooping (on non-inoculated cobs) across locations was significantly related to the disease severity of *S. maydis* [$r = 0.36$ and 0.3, respectively (inoculated cobs)] (Table 4). Husk cover was significantly correlated to *F. graminearum* ($r = 0.45$), but cob drooping was not. Since toothpick inoculation was used to effectively place the pathogen directly onto the developing cob and no significant disease development on non-inoculated cobs was observed, the most likely explanation of the relationship of these traits is that rain water penetration was encouraged by upright cobs with poor husk cover, thus providing a more conducive environment for the development of the disease. Similar studies under natural infection and whorl placement inoculation showed similar results (Rossouw et al. 2002, Alakonya et al. 2008). These results also vindicate suggestions (Alakonya et al. 2008) that rain water has a direct influence on cob rot severity. In this regard, environments prone to rain during the critical period should be used for screening genotypes against cob rots.

The weak correlation of cob drooping with *S. maydis* ($r = -0.30$) and the lack of correlation with *F. graminearum* may have been due to the genotypes which were involved. Fifty-nine per cent of the genotypes across locations were in an upright position. No genotypes had a mean of completely drooped or near complete drooping (mean value of 5 or 4.5). The lack of fully expressed drooping trait with the evaluated genotypes coupled with some interaction with husk cover led to low correlations and non for *S. maydis* and *F. graminearum,* respectively. Previous studies had indicated that higher correlation ($P = 0.01$) exists between drooping and disease severity (Rossouw et al. 2002). The reason being that fully drooped cobs drain off most rain water and thereby posses relatively less influence on disease development as compared to those which are erect (Rossouw et al. 2002). The variations with correlation of agronomic traits (such as husk cover and cob drooping) to mean disease severity in specific locations was due to interaction of the traits with locations (Table 2). Seed texture correlated negatively with both *S. maydis* ($P < 0.01$) and *F. graminearum* exhibiting significant correlation (r) values of −0.40 and 0.29, respectively, across locations, implying that the flint types were relatively more resistant than the dent. However, earlier studies contradict these results, with dent kernels being more resistant than flint material (Czembor and Ochodzki 2009, Matiello et al. 2015). The contradictory results may suggest that there could be other interacting genetic factors that influence resistance to cob rots. Increase in phenol content, amylose content and chitinase activity in kernels was found to have a negative correlation to disease severity, implying that higher concentrations of these reduce disease severity (Wit et al. 2011, Hefny et al. 2012). Overall, across locations, the stepwise regression showed that agronomic traits, husk cover and kernel texture explained more of the phenotypic variation when regressed against resistance to *F. graminearum* and *S. maydis,* respectively (Data not shown). However, the low r values of agronomic traits with disease severity (Table 4) and lack of consistency in specific locations of the agronomic traits, r^2 values as computed by stepwise regression, indicates that agronomic traits can only supplement direct selection for resistance, but not substitute for it. Similar observations indicated that indirect selection by using agronomic traits is not appropriate with cob rots (Rossouw et al. 2002, Hefny et al. 2012).

The fact that resistance to cob rots may be linked to undesirable traits makes selection a challenge (Duvick 2001). However, as yield is the highest ranked priority trait for the farmer (Mukanga et al. 2011), it is necessary to maintain it when breeding for cob rot resistance varieties. The low correlation values for yield to *S. maydis* ($r = 0.30$) and *F. graminearum* ($r = 0.17$) disease response across locations (Table 4) indicate that there is potential to select for a high-yielding and resistant hybrid. Previous studies reported that high-yielding and resistant genotypes to *S. maydis* exists (Moremoholo et al. 2010). Of the

Table 5: Top performing four hybrids for yield and for disease response for hybrids simultaneous above the mean for yield (disease free) and below the mean for either *S. maydis* or *F. graminearum* severity (inoculated, averaged across three locations) evaluated in the first season of 2011

	S. maydis				*F. graminearum*			
Trait	Genotype[1]	Yield	Score	Score[2]	Genotype[1]	Yield	Score	Score[3]
Yield	3×12	**9.2**	3.7	*2.8*	1×2	**8.7**	1.8	*3.7*
	7×9	**8.3**	3.8	*2.6*	2×9	**8.2**	1.7	*3.8*
	2×9	**8.2**	3.83	*1.7*	2×5	**8.2**	1.7	*3.7*
	2×5	**8.2**	3.6	*1.7*	1×12	**8.1**	2.2	*4.3*
Disease	3×4	7.2	**2.5**	*2*	4×11	7.2	**1.3**	*3*
	4×11	7.2	**3**	*1.3*	2×9	8.2	**1.7**	*3.8*
	3×5	7.4	**3.5**	*1.8*	2×5	8.2	**1.7**	*3.7*
	3×12	9.2	**3.7**	*2.8*	9×11	7.3	**1.7**	*4.2*

LSD – Fisher's protected least significant different test performed at P = 0.05; *S. maydis* score LSD = 0.6; *F. graminearum score* LSD = 0.9; yield LSD = 1.1 t/ha.

[1] Hybrid cross where, for example 3×12 means inbred line three female parent and 12 pollen donor.

[2] Corresponding *F. graminearum* score.

[3] Corresponding *S. maydis* score.

66 hybrids, 16 (24%) and 13 (20%) of the hybrids were classified as high yielding and resistant to *S. maydis* of *F. graminearum,* respectively (Figs 1 and 2). The performance of specific single crosses suggests that three-way cross-hybrids will allow combining of higher resistance and yield. With *F. graminearum,* single crosses with 1×2 and 2×9 appear good enough to be produced and marketed (Table 5). However, to reduce seed costs, a three-way cross of (1×2 or 2×9)×12 may benefit from the high general combining ability of inbred 12 for yield. The cross of 3×12 gave 9.2 t/ha (well above the mean of 7.1 t/ha) with reasonable resistance to *S. maydis* (3.7, below the mean value of 3.8) (Table 5). The cross of 3×4 had higher resistance to *S. maydis* (2.5) and a yield of 7.2 t/ha. With *F. graminearum* 3×12 had a mean *F. graminearum* score of 2.8 and 3 × 4 had a score of 2.0. This may imply that a three-way cross between a resistant single cross (3×4) and inbred 12 could produce good resistance to both pathogens combined with high yield. However, underlying issues of gene interactions and epistasis in maize may interfere with expected outcome (El-Badawy 2012). Therefore, there is a need to evaluate hybrid (CML 506×WL 118–10) × CZL 8 across locations to assess its performance.

Overall, these results show that closed husk cover reduced severity of the two cob rot pathogens, *S. maydis* and *F. graminearum*, when toothpick inoculated. The likely reason is an exclusion of rain water by morphological features of the cob such as cob husk cover and drooping attributes. In this regard, environments which have a high rainfall probability in mid- to late-season rains should be used for screening genotypes against *S. maydis* and *F. graminearum* cob rot. In addition, indirect selection for resistance, using agronomic traits such as husk cover, cob drooping and kernel texture should be used as a supplement to direct selection and not a substitute of it. The results also reveal that it is possible to produce cob rot-resistant and high-yielding farmer-preferred hybrid varieties. A three- way cross of (CML 506×WL 118–10) × CZL 8 has been predicted as the best hybrid to posses high yield and multiple resistance attributes to both pathogens.

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