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Grain Yield and Heterosis of Maize Hybrids under Nematode Infested and Nematicide Treated Conditions

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Abstract: Plant-parasitic nematodes are present on maize but resistant genotypes have not been identified in Uganda. This study was aimed at determining the level of nematode resistance among F_1 hybrids, and to estimate grain yield, heterosis and yield losses associated with maize hybrids under nematode infestation. The 30 F_1 hybrids and two local checks were evaluated in a split plot design with nematode treatment (nematode infested versus nematicide treated) as the whole plot factor, and the hybrids as subplot factors arranged in an 8 x 4 alpha-lattice design. The experiment was conducted simultaneously at three sites. The hybrids were also evaluated in a split plot design under greenhouse conditions at IITA-Namulonge. Results revealed 24 *P. zeae* susceptible hybrids compared to only six *P. zeae* resistant hybrids. Grain yield across sites was higher by about 400 kg ha^{-1} under nematicide treatment than under nematode infestation. The nematode tolerant/resistant hybrids exhibited yields ranging from 5.0 to 8.4 t ha^{-1} compared to 5.0 t ha^{-1} obtained from the best check. Grain yield loss was up to 28% among susceptible hybrids, indicating substantial economic yield losses due to nematodes. Under field conditions, desired heterosis was recorded on 18 hybrids for *P. zeae*, and on three hybrids for *Meloidogyne* spp. Under nematode infestation, only 16 hybrids had higher relative yield compared to the mean of both checks, the best check and the trial mean, whereas it was 20 hybrids under nematicide treated plots. Overall, most outstanding hybrids under nematode infestation were CML395/MP709, CML312/5057, CML312/CML206, CML312/CML444, CML395/CML312 and CML312/CML395. Therefore, grain yield loss due to nematodes is existent but can be significantly reduced by growing nematode resistant hybrids.

Key words: Grain yield, heterosis, Maize hybrid, *Meloidogyne* spp., *Pratylenchus zeae*, Yield loss.

Maize is the most important cereal crop and the second most important food crop after cassava in Africa (DeVries and Toenniessen, 2001; FAOSTAT, 2009) but mostly grown by small-scale farmers, who lack inputs such as fertilizer, chemicals, improved seed, irrigation and labor (Infonet-Biovision, 2009). Consequently, yields barely exceed 1.8 t ha^{-1} (FAOSTAT, 2009). Pests and diseases are indicated as the most important constraint to maize production among small-scale farmers in East and Southern Uganda (Kagoda *et al.*, 2010a). According to Imanywoha et al. (2005), maize yields have remained low in Uganda because some production constraints have not been addressed in the development of improved cultivars except the key biotic stresses such as turcicum leaf blight (TLB), maize streak virus (MSV), stem borers and weevils. Plant-parasitic nematodes are such constraints which have not been addressed for maize in Uganda and many other African countries.

Over 60 nematode species have been associated with maize (Jones and Perry, 2004; McDonald and Nicol, 2005) across the globe. In Uganda, the nematodes *Pratylenchus zeae* and *Meloidogyne* spp. are the most serious root pests of maize (Talwana et al., 2008; Kagoda et al., 2010a), and have potential to cause economic yield losses. Though nematode control options such as the use of nematicides, crop rotation, and bare fallow are effective, they are often inappropriate on a low value crop such as maize (Sikora, 1992). The use of host plant resistance as a nematode control option is cost-effective provided that resistance genes are readily available (Trudgill, 1991). Presence of resistance in maize to nematodes has been demonstrated, for example, to *P. zeae* (Kimenju et al., 1998; Oyekanmi et al., 2007) and *Meloidogyne* spp. (Windham and Williams, 1987; Windham and Williams, 1988; Windham and Williams, 1994a). However, the challenge is deploying the resistance trait into commonly acceptable and grown cultivars. The objectives of our study therefore, were to: i) determine the level of nematode resistance in maize hybrids ii) estimate heterosis for nematode resistance in maize, and iii) quantify the grain yield loss associated with nematode infestation in maize.

Materials and Methods

Germplasm: A total of 30 F_1 hybrids (including reciprocals) developed from a 6 x 6 full diallel mating design at the International Institute of Tropical Agriculture (IITA) – Namulonge, Uganda were used. The hybrids were developed from four CIMMYT inbred lines namely CML206, CML312, CML395 and CML444, known for their adaptability to maize growing conditions in Uganda (CIMMYT, 2001); one inbred line (MP709) from USDA-ARI Corn Host Plant Resistance Research Unit, Mississippi State known for being resistant to *Meloidogyne* spp. (Williams and Windham, 1998); and an inbred line (5057) from IITA-Nigeria known for its resistance to *P. zeae* (Oyekanmi et al., 2007). A nematode susceptible (H614D) and resistant check (DK8031) (Kimenju et al., 1998; Kagoda et al., 2010a), which are known for their adaptability to maize growing conditions in Uganda were included in the evaluation trials.

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Evaluation of the maize hybrids under field conditions: Field evaluations were conducted at three sites in Uganda, namely Namulonge (Central Uganda; 1200 masl; 0°32'N, 32°34'E), Bufulubi (Eastern Uganda; 1130 masl; 00° 49' N, 033° 42' E) and Kabanyolo (Central Uganda; 1,150 masl; 0° 28'N, 32° 37'E), which are characterized by greater than 40% sandy soils (Kagoda, 2010) and represent major maize growing areas in Uganda (MAAIF, 2011). Fields under natural infestation with nematodes were used for the evaluation trials. Where nematode initial populations (P_i) were low (< 500 *P. zeae* and < 100 *Meloidogyne* spp. per 100 g of soil), in the nematode unprotected plots, chopped nematode infested maize roots were applied per plant in the affected block but this only occurred in the Kabanyolo trial 2009B season. The genotypes for evaluation in the different sites constituted the 30 F_1 hybrids and the two local checks, DK8031 and H614D. The hybrids were evaluated in a split plot design with nematode treatments (nematode infested versus nematicide treated) as whole plots and the hybrids as subplots with two replications at Namulonge and three replications at Kabanyolo and Bufulubi. The hybrids were arranged in an 8 x 4 spatially adjusted alpha (0,1) lattice design for each of the nematode treatments. Field inter- and intra-row spacing was maintained at 75 cm x 30 cm. Two-row plots were planted per genotype consisting of 16 plants each. Two seeds were planted per hill and later thinned to one plant. Other standard cultural practices such as hand weeding were implemented at all the sites. Fertilizer to boost growth was applied as Di-ammonium phosphate (DAP) at planting at a rate of 7.5 kg N ha^{-1} and 19.2 kg P_2O_5 ha^{-1}. Fenamiphos (nemacur™), a non-volatile nematicide, was applied at a rate of 2.5 kg ha^{-1} (≈ 2.3 g per plant) and incorporated 5 – 8 cm soil depth with a hand hoe prior to planting in the nematode protected plots (Rhoades, 1979; Taylor et al., 1999).

Evaluation of the maize hybrids under greenhouse conditions: Additionally, the 30 F_1 maize hybrids and the two local checks were planted in plastic pots of 15 cm diameter containing 2500 ml of a potting mixture of heat-sterilized sandy loam soil and river sand (2:1) in a greenhouse. Two maize seeds were planted in each plastic pot, and for each maize hybrid, 12 pots were planted. The pots were arranged in a split plot design with two replications; the main plot factors were nematode treatments (nematode inoculated and non-inoculated) and the sub-plot factors were the 32 maize hybrids. The pots were placed on metallic mesh tables about 1 m from the ground to avoid contamination. Pots were watered twice a week with 0.5 litres each time. After 10 days, seedlings were thinned to one per pot and inoculated with 5000 *P. zeae* mixed stages or a mixture of 5000 *Meloidogyne* spp. juveniles and eggs (P_i).

Pratylenchus zeae and Meloidogyne spp. inoculum preparation: Pratylenchus zeae used for inoculation were initially extracted using the modified Baermann sieve method (Coyne et al., 2007) from infected maize roots, obtained from farmers' fields in Iganga District, Uganda. The *P. zeae* were multiplied on carrots (*Daucus carota* L.), cv. Nantes in the laboratory (Kagoda et al., 2010b) and maintained on susceptible maize hybrid H614D in pots under a shade house at IITA, Namulonge. *Meloidogyne* spp. juveniles and eggs were collected from galled tomato roots using a method described by Hussey and Barker (1973). The tomato plants were also maintained in pots under a shade house.

Quantification of nematode densities and assessment of root damage: For the field experiments, soil samples per plot were collected for nematode (vermiform) population (P_i) counting by species shortly before planting. The soil samples were collected in each plot using a trowel to a depth of 15 cm, discarding the upper 5 cm (Todd and Oakley, 1996; Coyne et al., 2006). Ten soil sub-samples per plot were combined to form one sample. From 50% flowering, root samples were taken from the root system of 10 randomly selected plants in each plot for final nematode (P_f) assessment in the field. In the greenhouse, all plants were uprooted at flowering stage (≈ 60 days after planting) for nematode assessment. At this stage, the nematodes were expected to have completed two generations (Dropkin, 1989).

In the laboratory, nematodes were extracted from a 100 ml soil sub-sample (P_i), and from a macerated 5 g fresh root mass (frm) sub-sample (P_f), using the modified Baermann sieve method. The samples were examined after a 48-hour extraction period, and nematodes counted using a stereomicroscope. Both P_i and P_f were estimated from three x 2-ml aliquots (taken from a 25-ml suspension). Therefore, $P_f - P_i$ refers to the nematode populations present in the roots after subtracting the initial populations in the soil in that plot at the time of planting. In the greenhouse, Oostenbrink's (1966) reproduction factor (RF), calculated as P_f/P_i, was used to assess resistance to nematodes with RF $\leq$ 1.5 indicating resistance to nematodes, 1.5 < RF $\leq$ 2.0 indicating moderately resistant, 10 $\geq$ RF > 2.0 indicating susceptibility and RF > 10 indicating very susceptible to nematodes (Ferris *et al.*, 1993).

Assessment of yield and other agronomic traits: In the field, plant height was recorded at 100% flowering as described by Magorokosho et al. (2007). Grain yield was recorded per plot at harvest and adjusted to 12.5% moisture (CIMMYT, 1985) using the formula:

$$\frac{\text{Grain weight (kg/plot)} \times 10 \times (100 - \text{Grain moisture content})}{87.5/\text{Plot area}}$$

A tolerance index (TI) for each genotype was calculated by comparing yield from nematode infested plots with yield from nematicide treated plots using the formula: (Yield of nematode infested plot/yield of nematicide treated plot) x 100. Specifically, TI < 100 represents least tolerant hybrids whereas TI ≥ 100 represents most nematode tolerant hybrids. Percentage yield loss was calculated as:

$$\frac{\text{Yield in nematicide treated plot} \\ -\text{Yield in nematode infested plot}}{\text{Yield in nematicide treated plot}} \times 100$$

Root damage was assessed from fresh root mass and the number of root lesions on root pieces in a 5 g root sample. Plant growth parameter assessment in the greenhouse was similar to that described for the field experiments.

Statistical analysis: Data from the field and greenhouse trials were tested for normality using the Proc Univariate normal plot procedure in SAS statistical package. Log and square root transformations were used where appropriate to transform the data prior to analysis. The nematode densities were $\log(x+10^3)$ transformed whereas grain yield was sqrt(x) transformed. The data were then subjected to analysis of variance as split plot experiments using the General Linear Model (Proc GLM) in SAS statistical package to enable separation of the variance components (Steel and Torrie, 1980). Differences between means were compared using Tukey's studentized range test at P = 0.05. Models used for analysing data followed procedures laid down for split plot designs (Steel and Torrie, 1980).

Pearson correlation and regression analyses were run using Proc corr and Proc reg procedures in SAS, respectively, to determine the type of relationships among traits. Heterosis (hybrid vigor) was computed for *P. zeae* under greenhouse and field conditions, and for *Meloidogyne* spp. under field conditions. Mid-parent heterosis (MPH) for nematode resistance were calculated as the performance of the F_1 hybrid compared with the average performance of its parents (Falconer, 1981; Srivastava, 1991). The formula used was: $[(F1 - MP)/MP] \times 100$, where F_1 = mean of the F_1 hybrid performance, MP = mean of the two parents of the cross, i.e., $(P_1 + P_2)/2$, where P_1 and P_2 are the means of the inbred parents. To ascertain any differences in vigour between pairs of reciprocal hybrids, a t-test of significance was carried out on mid-parent heterosis values obtained per replicate for *P. zeae* and *Meloidogyne* spp. The hypothesized mean difference between reciprocals was zero.

Relative yield (standard heterosis) was calculated using the formula:

$$\frac{\text{Yield of experimental hybrid}}{\text{Mean yield of the checks or Yield of the best check or Yield of trial mean}} \times 100$$

Ranking of hybrids based on grain yield was performed in Microsoft excel using the sort & filter procedure. Spearman rank correlation was then run using Proc corr procedure in SAS software to determine the differences between ranks of hybrids under nematode infestation and nematicide treatment.

Results

Analysis of variance of the various maize traits: Site effects had variations (P ≤ 0.05) for plant height, root mass and grain yield (Table 1). Nematode treatments (Nematode infested versus Nematicide treated conditions) were different (P ≤ 0.05) for only *P. zeae* and *Meloidogyne* spp. densities. The hybrids (including reciprocals) were different (P ≤ 0.05) for all traits measured except number of root lesions. Site x Hybrid interactions were different (P ≤ 0.05) for number of root lesions and grain yield.

Performance of maize hybrids across sites and treatments: Plant height among the hybrids was higher (P < 0.05) in five hybrids but lowest in four hybrids including the resistant check (Table 2). Four hybrids had the highest root mass, whereas five hybrids including both checks displayed the lowest root mass. The *P. zeae* densities were lower (P < 0.05) in five hybrids, including the resistant check, but highest in eight hybrids. Grain yield was higher (7.0 – 8.4 t ha^{-1}) in hybrids CML444/MP709, CML395/5057, CML312/CML206, CML444/CML395, CML444/CML312, CML312/CML444, CML395/CML312 and CML312/CML395 compared to only 4.7 to 5.0 t ha^{-1} obtained in MP709/5057, 5057/MP709, MP709/CML206, CML206/5057 and DK8031.

Yield losses and tolerance indices: At Bufulubi, significant differences in grain yield were recorded among hybrids under nematode infestation (Table 3). Yield loss ranged from 1 to 37% with highest loss observed in hybrids MP709/5057 and CML206/CML444. However, a total of 11 hybrids were tolerant (TI ≥100) to nematodes. At Kabanyolo, grain yield was higher (P < 0.05) than the mean of the trial in 14 hybrids, but lowest in only two hybrids (MP709/5057 and MP709/CML206) under nematode infestation. The yield losses at Kabanyolo ranged from 1 to 33% with the highest loss recorded in the hybrid MP709/5057. A total of six hybrids, including the resistant check, exhibited tolerance (TI ≥ 100) to nematodes. At Namulonge, no significant variation in grain yield was recorded under nematode infestation. Under nematicide treatment, the highest grain yield was recorded in CML312/CML444, CML206/CML444, CML395/5057, whereas the lowest grain yield was recorded in the hybrid check H614D and MP709/5057. Grain yield loss ranged from 1 to 66% with hybrid CML206/5057 having the highest loss. Tolerance was recorded in 14 hybrids.

Across sites, mean grain yield was higher (P < 0.05) under nematicide treated plots than nematode infested plots. Among hybrids, grain yield was higher (P < 0.05) in seven hybrids and lowest in only three hybrids under nematode infestation. The same hybrids with higher grain yield under nematode infestation maintained high yields under nematicide treatment. Hybrids with the highest TI recorded no grain yield loss under nematode infestation. The most nematode tolerant (TI > 110) hybrids were CML206/CML395, CML206/MP709 and CML395/CML312 compared to a TI of 85 obtained for the

TABLE 1. Mean squares for the various maize traits

Source of variation	DF	Plant height(cm)	Root mass (g)	No. of root lesions	*P. zeae* (per 100g frm)	*Meloidogyne* spp. (per 100g frm)	Grain yield (t ha^{-1})
Site	2	1433*	246*	191	44.71	1.60	8.76**
Rep	2	48.2	31.9	11.7	2.01	0.23	1.02
Trt	1	73.7	9.5	23.4	245.3*	10.2*	1.33
Rep*Trt	2	46.5	18.0	2.51	10.29	0.36	1.59
Hybrid	31	7.4***	2.5***	0.28	1.33***	0.12***	0.60***
Trt*Hybrid	31	3.0	0.6	0.16	0.39	0.05	0.14
Rep*Hybrid(Trt)	124	3.2	1.0	0.29	0.38	0.04	0.16
Site*Rep	3	35.4	3.7	39.1	21.01	2.16	0.21
Site*Trt	2	34.6	4.4	8.60	1.51	0.14	0.36
Site*Rep*Trt	3	26.0	6.6	2.52	11.22	2.88	1.54
Site*Hybrid	62	3.2	0.9	0.30*	0.47	0.05	0.31***
Site*Trt*Hybrid	62	3.3	0.5	0.24	0.38	0.04	0.12
Site*Rep*Hybrid(Trt)	186	3.9	0.8	0.21	0.37	0.05	0.12

Rep = Replicate; Trt = Treatment; frm = fresh root mass *, **, & *** mean significance at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

susceptible check. Overall, yield loss ranged from 1 to 28% with hybrids CML206/CML444 and MP709/CML395 exhibiting the highest yield loss.

Pearson correlations between grain yield and other traits: Under nematode infestation, grain yield was positive and correlated ($P < 0.001$) with plant height and root mass (Table 4). However, grain yield was negatively correlated ($P < 0.001$) with number of root lesions, and negative but non-significantly correlated with *P. zeae* and *Meloidogyne* spp. densities. Under nematicide treatment, grain yield displayed a positive correlation ($P < 0.001$) with plant height, root mass and number of

TABLE 2. Performance of individual F_1 hybrids across sites and treatments

	Entry	Plant height (cm)	Root mass (g)	No. of root lesions	*P. zeae* (per 100 g frm)	[m]Melo (per 100 g frm)	Grain yield (t ha^{-1})
1	MP709/5057	12.6(155)	6.2(30.0)	14.4	8.2(6329)	354	2.0(4.7)
	5057/MP709	12.7(156)	5.6(22.0)	13.7	8.1(5651)	251	2.2(5.0)
2	MP709/CML206	13.9(211)	6.8(37.3)	12.6	8.1(4478)	281	2.1(4.7)
	CML206/MP709	13.7(195)	6.6(36.8)	15.0	8.2(5148)	164	2.2(5.2)
3	MP709/CML444	13.1(167)	6.2(31.3)	15.2	8.5(8391)	418	2.3(5.8)
	CML444/MP709	14.3(203)	6.7(36.4)	14.4	8.2(6036)	573	2.6(7.0)
4	MP709/CML395	14.5(228)	6.6(35.7)	12.3	8.0(6450)	294	2.2(5.5)
	CML395/MP709	13.8(187)	6.1(29.4)	15.7	7.9(3821)	169	2.5(6.9)
5	MP709/CML312	14.7(239)	7.2(45.1)	13.5	8.3(5592)	372	2.4(6.3)
	CML312/MP709	14.9(245)	6.6(35.6)	14.4	8.5(9136)	605	2.3(6.0)
6	5057/CML206	12.3(145)	6.3(31.3)	11.8	8.3(5075)	547	2.4(6.0)
	CML206/5057	12.3(146)	6.5(34.4)	15.0	8.3(7599)	302	2.1(4.8)
7	5057/CML444	13.0(162)	6.7(36.5)	15.0	8.8(12548)	500	2.5(6.6)
	CML444/5057	12.8(159)	6.8(37.7)	14.9	8.7(8929)	557	2.4(6.2)
8	5057/CML395	12.7(155)	6.4(31.8)	15.1	8.6(9637)	328	2.4(6.1)
	CML395/5057	12.9(159)	6.4(32.7)	15.6	8.8(12619)	245	2.6(7.3)
9	5057/CML312	13.0(166)	7.1(42.8)	14.6	9.0(14222)	334	2.4(6.4)
	CML312/5057	13.3(171)	7.1(41.3)	15.5	8.6(9406)	411	2.5(6.6)
10	CML206/CML444	12.7(156)	7.3(45.7)	12.6	8.2(5341)	301	2.5(6.8)
	CML444/CML206	12.7(156)	7.4(47.1)	14.9	8.3(5207)	209	2.4(6.1)
11	CML206/CML395	12.1(141)	6.7(37.9)	16.2	8.0(4088)	334	2.2(5.9)
	CML395/CML206	12.7(161)	6.5(32.7)	17.9	8.2(4565)	110	2.4(6.1)
12	CML206/CML312	12.7(159)	7.4(46.7)	14.7	8.4(7016)	410	2.3(6.0)
	CML312/CML206	13.5(190)	7.1(41.7)	15.1	8.4(6676)	300	2.6(7.2)
13	CML444/CML395	13.0(165)	7.1(42.4)	15.7	8.3(5917)	1024	2.6(7.1)
	CML395/CML444	12.7(157)	6.9(40.2)	15.7	8.8(13049)	443	2.5(6.8)
14	CML444/CML312	13.7(185)	7.0(41.8)	16.4	8.7(12020)	495	2.7(7.6)
	CML312/CML444	14.5(219)	7.1(42.6)	18.5	8.7(11733)	263	2.7(7.8)
15	CML395/CML312	13.2(169)	6.9(39.8)	17.0	8.8(11830)	615	2.8(8.4)
	CML312/CML395	13.4(175)	6.4(33.0)	19.9	8.7(11579)	449	2.6(7.3)
16	DK8031	12.0(140)	6.1(28.9)	14.5	8.0(4840)	306	2.1(5.0)
17	H614D	14.1(195)	6.2(30.2)	16.3	8.5(8017)	647	2.1(5.4)
	$LSD_{0.05}$	**2.7**	**1.4**	**ns**	**1.0**	**ns**	**0.5**
	Mean	13.2(176)	6.7(36.8)	15.1	8.4(7905)	394	2.4(6.3)

[m] *Meloidogyne* spp.; ns = not significant; DK8031 = Resistant check; H614D = Susceptible check

TABLE 3. Grain yield, tolerance index (TI) and yield losses of individual hybrids and their reciprocals

		Bufulubi				Kabanyolo				Namulonge				Across sites			
		Yield (t ha^{-1})			%Yld	Yield (t ha^{-1})			%Yld	Yield (t ha^{-1})			%Yld	Yield (t ha^{-1})			%Yld
	Hybrids	Nema	No	†TI (%)	loss	Nema	No	TI (%)	loss	Nema	No	TI (%)	loss	Nema	No	TI (%)	loss
1	MP709/5057	4.4	7.0	63	37	3.6	5.4	67	33	4.3	2.7	159	0	4.1	5.3	77	23
	5057/MP709	4.1	5.0	82	18	5.2	6.4	81	19	4.2	5.0	84	16	4.5	5.6	80	20
2	MP709/CML206	4.8	5.3	91	9	4.4	5.6	79	21	3.0	4.1	73	27	4.1	5.1	80	20
	CML206/MP709	4.8	4.4	109	0	6.5	5.8	112	0	4.5	4.3	105	0	5.4	4.9	110	0
3	MP709/CML444	6.6	7.3	90	10	5.8	7.4	78	22	6.6	7.7	86	14	5.1	6.5	78	22
	CML444/MP709	7.7	6.1	126	0	7.3	7.8	94	6	4.8	5.1	94	6	7.2	6.8	106	0
4	MP709/CML395	6.1	7.0	87	13	4.8	5.5	87	13	1.8	3.9	46	54	4.7	6.4	73	27
	CML395/MP709	6.0	7.2	83	17	8.3	8.3	100	0	6.3	6.2	102	0	6.7	7.1	94	6
5	MP709/CML312	6.4	7.4	86	14	5.9	7.0	84	16	2.4	6.5	37	63	5.9	6.6	89	11
	CML312/MP709	6.4	6.3	102	0	6.0	7.3	82	18	5.3	4.9	108	0	5.2	6.7	78	22
6	5057/CML206	5.4	4.8	113	0	6.5	6.1	107	0	5.2	4.9	106	0	6.1	5.8	105	0
	CML206/5057	3.8	4.9	78	22	4.6	5.6	82	18	2.2	6.5	34	66	4.4	5.2	85	15
7	5057/CML444	5.2	5.6	93	7	7.6	8.4	90	10	7.4	5.6	132	0	6.6	6.6	100	0
	CML444/5057	4.9	6.0	82	18	7.6	7.4	103	0	5.1	4.8	106	0	6.1	6.2	98	2
8	5057/CML395	5.7	5.8	98	2	6.8	7.1	96	4	5.5	4.9	112	0	6.1	6.1	100	0
	CML395/5057	7.5	7.0	107	0	7.2	6.7	107	0	7.2	8.8	82	18	7.3	7.4	99	1
9	5057/CML312	5.7	6.0	95	5	5.1	7.2	71	29	6.2	8.2	76	24	5.6	7.0	80	20
	CML312/5057	4.4	6.2	71	29	7.7	7.8	99	1	4.5	6.7	67	33	6.1	6.9	88	12
10	CML206/CML444	5.0	7.9	63	37	6.7	7.7	87	13	5.4	8.1	67	33	5.7	7.9	72	28
	CML444/CML206	6.6	7.4	89	11	6.3	7.1	89	11	3.9	4.0	98	3	5.7	6.4	89	11
11	CML206/CML395	6.2	4.3	144	0	11.1	5.8	191	0	2.6	3.7	70	30	7.1	4.7	151	0
	CML395/CML206	5.9	6.7	88	12	6.9	7.6	91	9	3.9	4.4	89	11	5.8	6.5	89	11
12	CML206/CML312	5.2	7.0	74	26	6.9	7.2	96	4	4.6	4.0	115	0	5.7	6.2	92	8
	CML312/CML206	6.5	7.0	93	7	8.5	9.3	91	9	5.0	5.3	94	6	6.9	7.4	93	7
13	CML444/CML395	6.4	5.6	114	0	8.5	9.0	94	6	6.3	5.9	107	0	7.2	6.9	104	0
	CML395/CML444	6.6	6.7	99	1	7.8	8.8	89	11	6.4	3.5	183	0	7.0	6.7	104	0
14	CML444/CML312	7.2	5.3	136	0	10.2	9.7	105	0	3.3	7.1	46	54	7.9	7.4	107	0
	CML312/CML444	7.5	6.5	115	0	9.4	9.5	99	1	5.3	8.2	65	35	7.6	8.0	95	5
15	CML395/CML312	11.2	7.0	160	0	8.3	10.2	81	19	5.9	4.1	144	0	8.8	8.0	110	0
	CML312/CML395	7.5	7.8	96	4	8.2	8.5	96	4	6.0	4.5	133	0	7.4	7.1	104	0
16	DK8031	5.7	6.4	89	11	5.0	4.0	125	0	4.0	5.1	78	22	4.9	5.2	94	6
17	H614D	5.1	6.7	76	24	6.9	8.4	82	18	1.6	0.7	229	0	4.5	5.3	85	15
	$LSD_{(0.05)}$	1.4	ns			1.0	0.6			ns	2.2			0.8	ns		
	Mean	**6.0**	**6.3**			**6.9**	**7.4**			4.7	5.3			**6.0**	**6.4**		

† Tolerance index, Nema = Nematode infested, No = Nematicide treated; ns = not significant; DK8031 = Resistant check; H614D = Susceptible check

root lesions, but maintained negative and non-significant correlations with *P. zeae* and *Meloidogyne* spp. densities. *Pratylenchus zeae* densities were negative and correlated ($P < 0.05$) with plant height and root mass under nematode infestation but had a positive correlation ($P < 0.05$) with *Meloidogyne* spp. densities. Under nematicide treatment, *P. zeae* had a positive correlation ($P < 0.001$) with root mass, number of root lesions and *Meloidogyne* spp. densities but had a negative correlation with plant height. *Meloidogyne* spp. densities displayed a negative correlation ($P < 0.05$) with plant height and number of root lesions under nematode infestation.

Linear regression analysis: Plant height and root mass had a positive regression coefficient ($P < 0.001$) with grain yield under both nematode infested and nematicide treated plots (data not shown). The number of root lesions, *P. zeae* densities and *Meloidogyne* spp. densities had a negative and non-significant regression coefficient with grain yield.

Response of the hybrids to P. zeae infection in the greenhouse: Root mass was significantly higher (23 g) in the uninoculated pots than in the *P. zeae* inoculated pots (22 g) (data not shown). Mean *P. zeae* density was 44007 per 100 g frm in the inoculated pots whereas the uninoculated pots had no *P. zeae* (Table 5). Similarly, mean RF in the inoculated pots was 8.8. Based on RF, only five hybrids (including the resistant check) displayed resistance to *P. zeae*, whereas two hybrids were moderately resistant. The most resistant hybrids were 5057/MP709, 5057/CML444, CML206/CML312, CML395/CML312.

Hybrids 5057/MP709 and 5057/CML444 were among the most *P. zeae* resistant in the greenhouse. They also performed well in the field with grain yields of 5.0 and 6.6 t ha^{-1}, respectively, despite being mostly from exotic parents. Similarly, the hybrid CML395/CML312 exhibited *P. zeae* resistance in the greenhouse and yielded well in the field with 8.4 t ha^{-1}. Hybrids MP709/CML312 and CML312/CML206 were relatively resistant to *P. zeae* in the greenhouse and in the field resulting in higher grain yields (6.3 and 7.2 t ha^{-1}, respectively) compared to the resistant check (5.0 t ha^{-1}).

TABLE 4. Pearson correlation coefficients based on pooled data across the three sites

	Plant height	Root mass	No. of root lesions	*P. zeae*	*Meloidogyne* spp.	Grain yield
Plant height (cm)		0.382***	0.386***	-0.077ns	-0.084ns	0.327***
Root mass (g)	0.571***		0.569***	0.481***	0.100ns	0.277***
Number of root Lesions	-0.679***	-0.385***		0.292***	0.275***	0.294***
Pratylenchus zeae (per 100g frm)	-0.129*	-0.277***	0.039ns		0.329***	-0.028ns
Meloidogyne spp. (per 100g frm)	-0.120*	0.049ns	-0.223***	0.516***		-0.008ns
Grain yield (t ha^{-1})	0.464***	0.350***	-0.281***	-0.097ns	-0.029ns	

Lower diagonal = coefficients under nematode infestation; upper diagonal = coefficients under nematicide treatment. *, **, and *** represent significance at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$. ns = not significant.

Relative yield and heterosis of the maize hybrids: Negative heterosis for *P. zeae* and *Meloidogyne* spp. is an indication of an F_1 hybrid which is superior in resistance to nematodes compared to the mid-parent, susceptible parent or resistant parent. A total of 14 hybrids displayed negative heterosis for *P. zeae* resistance, whereas 16 hybrids had positive heterosis under greenhouse conditions (Table 6). Differences between reciprocals were significant ($P < 0.05$) for MP709/5057 and CML444/CML312. Under field conditions, negative heterosis for *P. zeae* was recorded on 18 hybrids, whereas 12 hybrids had positive heterosis (Table 7). For *Meloidogyne* spp., negative heterosis was recorded on three hybrids, whereas 27 hybrids displayed positive heterosis. No significant reciprocal differences were

TABLE 5. Hybrid performance in pots inoculated with *P. zeae* in the greenhouse

	Hybrids	Plant height	Root mass	+P.zeae (P_f)	+RF (P_f/P_i)	*P. zeae* status*
1	MP709/5057	41.1	19.5	56563	11.3	Very susceptible
	5057/MP709	44.1	26.6	4438	0.9	Resistant
2	MP709/CML206	44.1	16.3	20656	4.1	Susceptible
	CML206/MP709	42.5	21.5	31375	6.3	Susceptible
3	MP709/CML444	38.9	25.2	16063	3.2	Susceptible
	CML444/MP709	44.5	25.8	85219	17.0	Very susceptible
4	MP709/CML395	46.3	20.0	14469	2.9	Susceptible
	CML395/MP709	41.1	27.5	47781	9.6	Susceptible
5	MP709/CML312	47.7	22.4	9125	1.8	Moderately Resistant
	CML312/MP709	45.0	30.9	103375	20.7	Very susceptible
6	5057/CML206	40.4	20.0	188969	37.8	Very Susceptible
	CML206/5057	36.1	21.3	37625	7.5	Susceptible
7	5057/CML444	45.8	23.8	4531	0.9	Resistant
	CML444/5057	43.0	21.2	36156	7.2	Susceptible
8	5057/CML395	41.6	24.3	41125	8.2	Susceptible
	CML395/5057	42.8	22.4	67375	13.5	Very susceptible
9	5057/CML312	41.0	24.8	74906	15.0	Very susceptible
	CML312/5057	45.8	22.8	27969	5.6	Susceptible
10	CML206/CML444	42.0	20.6	27906	5.6	Susceptible
	CML444/CML206	34.6	19.2	34594	6.9	Susceptible
11	CML206/CML395	41.9	18.7	44563	8.9	Susceptible
	CML395/CML206	42.4	20.1	44219	8.8	Susceptible
12	CML206/CML312	45.6	23.3	2750	0.6	Resistant
	CML312/CML206	42.5	25.2	8563	1.7	Moderately Resistant
13	CML444/CML395	45.2	23.3	60719	12.1	Very susceptible
	CML395/CML444	50.2	20.3	21313	4.3	Susceptible
14	CML444/CML312	44.2	21.3	155750	31.2	Very susceptible
	CML312/CML444	43.8	22.2	54594	10.9	Very susceptible
15	CML395/CML312	49.1	21.2	3656	0.7	Resistant
	CML312/CML395	46.7	24.0	21094	4.2	Susceptible
16	DK8031	43.9	21.4	5781	1.2	Resistant
17	H614D	57.9	22.5	55000	11.0	Very susceptible
	Mean	43.8	22.5	44007	8.8	
	$LSD_{0.05}$	16.8	10.4			

+ The P_i used to calculate RF is 5000 *P. zeae* (juveniles and adults) per pot. **P. zeae* resistant hybrids have RF ≤ 1.5 based on actual RF means presented in parentheses. +Presented are values obtained only in the *P. zeae* inoculated pots. DK8031 = Resistant check; H614D = Susceptible check observed for both *P. zeae* and *Meloidogyne* spp. densities in all the hybrids.

Hybrids CML312/CML206, CML444/CML395, CML395/CML444, CML444/CML312, CML312/CML444, CML395/CML312, CML312/CML395, CML312/5057, CML395/5057, 5057/CML444, 5057/CML206, CML395/MP709, CML444/MP709 had higher relative yield (standard heterosis) compared to the mean of both checks, the best check and the trial mean, both under nematode infestation and nematicide treatment, indicating stability of performance under stressed and non-stressed environments (Table 8). Spearman rank correlation (Table 8) showed a change in rank order in grain yield in most of the hybrids under nematode infestation when compared to nematicide treated plots (r = 0.636; P = 0.0002).

Discussion

The study revealed variations in plant height, root mass and grain yield of hybrids between sites. The site x hybrid interaction observed for grain yield is an indicator of the differences in adaptability of the hybrids regardless of nematode infestation levels. The site x hybrid interaction effects recorded for number of root lesions could be explained by the different levels of *P. zeae* damage at the different sites. Traits such as plant height and root mass were generally higher under nematicide treatment than under nematode infested plots at all sites. These traits are known to improve once nematode populations are very low in most crops. Hybrids which were taller did not necessarily have significantly lower *P. zeae* populations except for MP709/CML206. Therefore, taller plants are not necessarily nematode free, which justifies the need to assess nematode densities. However, the high *P. zeae* densities recorded in stunted plants confirms reports that nematodes restrain plant growth. These results are consistent with previous observations (Kimenju et al., 1998; Patel et al., 2002; Luc et al., 2005). *Meloidogyne* spp. densities were quite low in most of these hybrids compared to *P. zeae* densities. This confirms earlier findings that *P. zeae* is more aggressive on maize than *Meloidogyne* spp. in Uganda (Talwana et al., 2008; Kagoda et al., 2010a). According to Olowe and Corbett (1976), *P. zeae* has a higher reproductive rate and tolerance to environmentally related stress compared to other nematode species, thus the high densities recorded in the current study. Hybrids with the highest root mass also had relatively lower *P. zeae* densities (< 6000 *P. zeae* per 100 g frm) and their yields exceeded 6.0 t ha^{-1}, indicating that these hybrids were resistant to nematodes. Patel et al. (2002) recorded considerable reduction in root mass and an almost ten-fold increase in *P. zeae* densities in maize inoculated with *P. zeae* indicating high damage potential especially on susceptible varieties. Kimenju et al. (1998) similarly observed nematodes to cause significant reductions in root mass of maize open pollinated varieties and hybrids. Similarly, *P. zeae* has been reported to limit root growth and eventual yield in rice (*Oryza sativa*) (Prot and Savary, 1993). Hybrids which had a relatively lower number of root lesions also exhibited lower *P. zeae* densities, which confirms the positive correlation obtained between root lesions and *P. zeae* densities. Presence of root lesions is characteristic of damage by root lesion nematodes. These results are consistent with previous observations (Olowe, 1977; Norton and Nyvall, 1999).

More nematodes were recorded at Bufulubi than at other sites. This is probably because sandy soils were more predominant in the experimental site at Bufulubi (61.1%) than the rest (41 - 49%) of the experimental sites (Kagoda, 2010). Both *P. zeae* and *Meloidogyne* spp. proliferate more in sandy soils than other soil types (Norton, 1978; Dropkin, 1989). However, yield losses due to nematodes manifested more at Namulonge (9.6%) than at Bufulubi (4.8%) probably because of maize being more adapted in Eastern Uganda (Bufulubi inclusive) than in the central region (Namulonge) (NARO, 2002).

Hybrids such as CML206/CML395 and its reciprocal; MP709/CML206 and CML395/MP709 had lower *P. zeae* populations compared to the resistant check (DK8031). Such hybrids are characterized by penetration of fewer *P. zeae*, delayed egg laying and nematode reproduction, less root necrosis and cell wall thickening around the parasitic zone (Kathiresan and Mehta, 2002). Relatively lower *Meloidogyne* spp. densities were observed in some hybrids with CML206 or MP709 constituting the parental combination, when compared to the resistant check. This is because genotypes CML206 and MP709 possess genes for resistance to nematodes (Williams and Windham, 1998; Kagoda, 2010). Root-knot resistance is characterized by slow nematode development or no development when compared with susceptible hosts (Lawrence and Clark, 1986; Windham and Williams, 1994b).

Grain yield across sites was higher by about 400 kg ha^{-1} under nematicide treated plots when compared to the nematode infested plots, a clear indication that nematodes are associated with yield loss in maize. Similarly, yield losses due to nematode damage among hybrids rose to 28% compared to a yield loss of 15% in the susceptible cultivar (H614D) across sites. The tolerance index was below 100% in hybrids which registered yield losses, which indicates that nematodes played a significant role in reducing grain yield in such hybrids. The nematode resistant/tolerant CIMMYT lines such as CML444, CML395 and CML206 are adapted to the subtropical conditions in Uganda, and greatly influenced high grain yields compared to inbreds MP709 and 5057 which are exotic despite being nematode resistant. However, the hybrid CML395/MP709 had low nematode densities and a grain yield of 7.0 t ha^{-1} under nematode infestation signifying its adaptability to the environment.

The negative correlations and regression coefficients observed between grain yield and number of root

TABLE 6. Heterosis for resistance to *Pratylenchus zeae* under greenhouse conditions

	Hybrid	F_1	P_1	P_2	MPH (%)
1	MP709/5057	56563	5563	91500	16.5
	5057/MP709	4438	91500	5563	-90.9
	t-value				11.0**
2	MP709/CML206	20656	5563	11521	141.8
	CML206/MP709	31375	11521	5563	267.3
	t-value				-0.18ns
3	MP709/CML444	16063	5563	39604	-28.9
	CML444/MP709	85219	39604	5563	277.4
	t-value				-0.95ns
4	MP709/CML395	14469	5563	31083	-21.0
	CML395xMP709	47781	31083	5563	160.8
	t-value				-0.752ns
5	MP709/CML312	9125	5563	35875	-56.0
	CML312/MP709	103375	35875	5563	398.9
	t-value				-0.957ns
6	5057xCML206	188969	91500	11521	266.9
	CML206x5057	37625	11521	91500	-27.0
	t-value				0.9ns
7	5057xCML444	4531	91500	39604	-93.1
	CML444x5057	36156	39604	91500	-44.8
	t-value				-1.07ns
8	5057/CML395	41125	91500	31083	-32.9
	CML395/5057	67375	31083	91500	9.9
	t-value				-0.468ns
9	5057xCML312	74906	91500	35875	17.6
	CML312x5057	27969	35875	91500	-56.1
	t-value				1.02ns
10	CML206/CML444	27906	11521	39604	9.2
	CML444/CML206	34594	39604	11521	35.3
	t-value				-0.1ns
11	CML206xCML395	44563	11521	31083	109.2
	CML395xCML206	44219	31083	11521	107.6
	t-value				-0.602ns
12	CML206xCML312	2750	11521	35875	-88.4
	CML312xCML206	8563	35875	11521	-63.9
	t-value				-1.388ns
13	CML444/CML395	60719	39604	31083	71.8
	CML395/CML444	21313	31083	39604	-39.7
	t-value				1.08ns
14	CML444/CML312	155750	39604	35875	312.7
	CML312/CML444	54594	35875	39604	44.7
	t-value				5.57*
15	CML395/CML312	3656	31083	35875	-89.1
	CML312/CML395	21094	35875	31083	-37.0
	t-value				-1.131ns

F_1 =First filial generation, P_1 = Female parent, P_2 = Male parent, MPH = Mid-parent heterosis, ns = not significant

TABLE 7. Heterosis for resistance to *P. zeae* and *Meloidogyne* spp. under field conditions across the three sites

		P. zeae (per 100 g frm)		*Meloidogyne* spp. (per 100 g frm)	
	Hybrid	F_1	MPH (%)	F_1	MPH (%)
1	MP709/5057	11516	46	551	159
	5057/MP709	10820	37	427	100
	t-value		-0.025ns		-0.307ns
2	MP709/CML206	7460	-4	532	115
	CML206/MP709	9047	17	248	0
	t-value		0.016ns		1.69ns
3	MP709/CML444	14005	22	629	160
	CML444/MP709	10493	-8	944	290
	t-value		0.438ns		-1.74ns
4	MP709/CML395	12452	2	526	66
	CML395/MP709	7011	-43	255	-20
	t-value		0.88ns		0.57ns
5	MP709/CML312	9458	-44	583	39
	CML312/MP709	16886	-1	1138	171
	t-value		-0.436ns		-0.245ns
6	5057/CML206	8701	-5	605	168
	CML206/5057	12143	32	512	127
	t-value		-0.642ns		-0.02ns
7	5057/CML444	19676	52	807	265
	CML444/5057	14524	12	879	298
	t-value		0.728ns		0.173ns
8	5057/CML395	17319	27	485	64
	CML395/5057	21304	56	376	27
	t-value		0.049ns		0.33ns
9	5057/CML312	20791	13	581	45
	CML312/5057	16119	-13	737	84
	t-value		-0.029ns		-0.82ns
10	CML206/CML444	9041	-29	488	91
	CML444/CML206	8363	-35	306	20
	t-value		-0.161ns		0.596ns
11	CML206/CML395	7409	-45	518	57
	CML395/CML206	7631	-44	200	-39
	t-value		0.236ns		2.56ns
12	CML206/CML312	10987	-40	718	66
	CML312/CML206	10486	-43	475	10
	t-value		0.218ns		0.88ns
13	CML444/CML395	10126	-41	1866	473
	CML395/CML444	21075	22	667	105
	t-value		-0.977ns		-0.211ns
14	CML444/CML312	18162	-18	803	87
	CML312/CML444	20039	-9	347	-19
	t-value		0.486ns		1.76ns
15	CML395/CML312	20190	-11	1023	103
	CML312/CML395	20016	-12	773	53
	t-value		-0.103ns		0.78ns

F_1 =First filial generation, P_1 = Female parent, P_2 = Male parent, MPH = Mid-parent heterosis

lesions, grain yield and *P. zeae* densities, and grain yield and *Meloidogyne* spp. densities are evidence that nematodes are associated with reduced grain yield in susceptible maize cultivars. Similarly, Tarte (1971) found a highly significant negative correlation between *P. zeae* densities and yield of maize. However, even under nematicide treatment, negative correlations were observed between grain yield and the low nematode densities. This calls for use of management practices which completely give the maize plant a comparative advantage over the nematodes such as breeding for resistant varieties.

Hybrids MP709/CML312 and CML395/CML312 maintained the highest plant heights in the greenhouse and in the field. These hybrids were, therefore, tolerant to nematodes. According to Begna et al. (2000), taller hybrids produce a higher dry matter yield but the translocation rate of assimilates to the kernels of taller hybrids is lower than for shorter hybrids. This implies that breeding for maize varieties with short stature but with resistance to nematodes and other stresses offers higher grain yields than the tall varieties. The difference in root mass in the uninoculated pots compared to the *P. zeae* inoculated pots can be attributed to feeding of *P. zeae* on the root system of the *P. zeae* inoculated plants. However, the difference in root mass between the *P. zeae* inoculated and uninoculated pots was by a small margin. This is because

Table 8. Relative yield of hybrids and their rank under nematode infestation and nematicide treated plots across the three sites

		Nematodes infested plots					Nematicide treated plots				
				[R]Relative yield over					Relative yield over		
Fldno.	Hybrid	Grain yield	Rank	Mean of checks	Best check	Trial mean	Grain yield	Rank	Mean of checks	Best check	Trial mean
1	MP709/5057	4.1	30	87	84	68	5.3	26	101	100	83
	5057/MP709	4.5	27	96	92	75	5.6	25	107	106	88
2	MP709/CML206	4.1	29	87	84	68	5.1	28	97	96	80
	CML206/MP709	5.4	23	115	110	90	4.9	29	93	92	77
3	MP709/CML444	5.1	25	109	104	85	6.5	17	124	123	102
	CML444/MP709	7.2	6	153	147	120	6.8	12	130	128	106
4	MP709/CML395	4.7	26	100	96	78	6.4	20	122	121	100
	CML395/MP709	6.7	11	143	137	112	7.1	8	135	134	111
5	MP709/CML312	5.9	17	126	120	98	6.6	16	126	125	103
	CML312/MP709	5.2	24	111	106	87	6.7	13	128	126	105
6	5057/CML206	6.1	13	130	124	102	5.8	24	110	109	91
	CML206/5057	4.4	28	94	90	73	5.2	27	99	98	81
7	5057/CML444	6.6	12	140	135	110	6.6	15	126	125	103
	CML444/5057	6.1	14	130	124	102	6.2	22	118	117	97
8	5057/CML395	6.1	16	130	124	102	6.1	23	116	115	95
	CML395/5057	7.3	5	155	149	122	7.4	5	141	140	116
9	5057/CML312	5.6	22	119	114	93	7.0	9	133	132	109
	CML312/5057	6.1	15	130	124	102	6.9	11	131	130	108
10	CML206/CML444	5.7	20	121	116	95	7.9	3	150	149	123
	CML444/CML206	5.7	21	121	116	95	6.4	19	122	121	100
11	CML206/CML395	7.1	8	151	145	118	4.7	30	90	89	73
	CML395/CML206	5.8	18	123	118	97	6.5	18	124	123	102
12	CML206/CML312	5.7	19	121	116	95	6.2	21	118	117	97
	CML312/CML206	6.9	10	147	141	115	7.4	4	141	140	116
13	CML444/CML395	7.2	7	153	147	120	6.9	10	131	130	108
	CML395/CML444	7.0	9	149	143	117	6.7	14	128	126	105
14	CML444/CML312	7.9	2	168	161	132	7.4	6	141	140	116
	CML312/CML444	7.6	3	162	155	127	8.0	1	152	151	125
15	CML395/CML312	8.8	1	187	180	147	8.0	2	152	151	125
	CML312/CML395	7.4	4	157	151	123	7.1	7	135	134	111
16	DK8031	4.9				82	5.2				81
17	H614D	4.5				75	5.3				83
	Trial mean	6.0					6.4				
	Check Mean	4.7					5.25				

[R] Relative yield calculated based either on the mean of the checks, the best check or the trial mean

roots sometimes proliferate at a higher rate to absorb nitrogen in the subsoil depleted by nematodes in the top soils leading to high root mass in nematode infested plots than the non-infested (Evans, 1982; Haverkort et al., 1994). Mean *P. zeae* density was 44007 per 100 g frm in the inoculated pots, which indicates that the nematodes increased by 8.8-fold in the two months the experiment was conducted. However, the five most resistant hybrids had *P. zeae* densities far below the mean (< 6000 *P. zeae* per 100 g frm) and RF < 1.5. This demonstrates that a nematode resistant hybrid should have the capacity to reduce entry and rapid multiplication of nematodes in its root system. According to Kathiresan and Mehta (2002), nematode penetration in resistant crops is reduced by mechanical and biochemical barriers present in the plant. A number of *P. zeae* resistant hybrids in the greenhouse trial recorded high grain yields compared to the resistant check when planted in the field. This indicates that greenhouse data was quite reliable in explaining performance in the field. Similar observations were reported by Speijer and De Waele (1997).

Inbred lines MP709, 5057, CML206, and CML444 evidently had genes for *P. zeae* resistance and tolerance (Kagoda, 2010), which explains the negative heterosis observed in their hybrid combinations. Likewise, field and greenhouse evaluation provided evidence that inbred lines MP709, 5057 and CML444 have genes for resistance to *Meloidogyne* spp. (Kagoda, 2010). Notably, these are dominant or epistatic genes for *P. zeae* and *Meloidogyne* spp. resistance since dominance and epistasis are the underlying genetic basis for heterosis (Falconer, 1981). According to Cromley et al. (2002), single cross hybrids would have adequate level of resistance if at least one parent has resistance.

The wide range in relative yield among hybrids under nematode infestation than under nematicide treatment suggests that the yield benefit of hybrid vigour declines sharply among nematode susceptible maize hybrids compared to nematode resistant hybrids. The change in rank order for grain yield observed in most of the hybrids, based on spearman correlation, under nematode infestation when compared to nematicide treated plots confirms that hybrid performance can be affected by the presence of nematodes.

To sum up, 1) there is a considerable improvement in grain yield (≈ 400 kg ha^{-1}) when nematicides are used against nematodes in maize; (2) a grain yield loss of up to 28% can be obtained due to nematode infestation in maize, which seriously compromises yield when susceptible varieties are grown; 3) desired heterosis for *P. zeae* was recorded on 60% of the maize hybrids, which suggests that such hybrids are good sources of resistance to *P. zeae*; 4) hybrids such as CML395/MP709, CML312/5057, CML312/CML206, CML312/CML444, CML395/CML312 and CML312/CML395 would be recommended for advancement in breeding programs since they exhibited high levels of either nematode tolerance or resistance by displaying high grain yields, high mid-parent heterosis to *P. zeae* and high relative yields compared to the checks and the trial mean under nematode pressure. These hybrids would be advanced by evaluating them for adaptability across more environments before release.

Literature Cited

Begna, S. H., Hamilton, R. I., Dwyer, L. M., Stewart, D. W., and Smith, D. L. 2000. Variability among maize hybrids differing in canopy architecture for above-ground dry matter and grain yield. Maydica 45:135–141.

CIMMYT. 1985. Managing trials and reporting data for CIMMYT International Maize Testing Program. Mexico, D.F. CIMMYT.

CIMMYT. 2001. Maize inbred lines released by CIMMYT. A Compilation of 454 CIMMYT Maize Lines (CMLs), CML1 – CML454. August 2001. Second Draft. CIMMYT, Mexico.

Coyne, D. L., Nicol, J. M., and Claudius-Cole, B. 2007. Practical Plant Nematology: A Field and Laboratoty Guide. SP-IPM Secretariat, International Institute of Tropical Agriculture (IITA), Cotonou, Benin.

Coyne, D. L., Kagoda, F., Wambugu, E., and Ragama, P. 2006. Response of cassava to nematicide application and plant-parasitic nematode infection in East Africa, with emphasis on root knot nematodes. International Journal of Pest Management 52:215–223.

Cromley, J. M. D., Hallauer, A. R., and Martinson, C. A. 2002. Inheritance of gray leaf spot resistance in corn. Journal of Iowa Academy of Science 109:25–29.

DeVries, J., and Toenniessen, G. 2001. Securing the Harvest, Biotechnology, Breeding and Seed Systems for African Crops. CAB International, New York.

Dropkin, V. H. 1989. Introduction to Plant Nematology. John Wiley and Sons, New York.

Evans, K. 1982. Effects of infestation with *Globodera rostochiensis* (Wollenweber) Behrends R01 on the growth of four potato cultivars. Crop Protection 1:169–179.

FAOSTAT. 2009. Food and Agriculture Organisation Statistics. [Online]. Available by http://www.fao.org (verified 18 October 2010).

Falconer, D. S. 1981. Introduction to Quantitative Genetics. 2 ed. Longman, New York.

Ferris, H., Carlson, H., Viglierchio, D., Westerdahl, B. W. F., Anderson, C., Jurma, A., and Kirby, D. 1993. Host status of selected crops to *Meloidogyne chitwoodi*. Annals of Applied Nematology 25:849–857.

Haverkort, A. J., Groenwold, J., and Van De Waart, M. 1994. The influence of cyst nematodes and drought on potato growth. European Journal of Plant Pathology 100:381–394.

Hussey, R. S., and Barker, K. R. 1973. A comparison of methods of collecting inocula of *Meloidogyne* spp. including a new technique. Plant Disease Reporter 11:1025–1028.

Imanywoha, J., Bigirwa, G., Kalule, T., and Walusimbi, M. 2005. Development of maize varieties resistant to ear rot and weevils in Uganda. *in* Biotechnology, Breeding and Seed Systems for African Crops. Second General Meeting of the Rockefeller Foundation-Supported Program, Nairobi, Kenya.

Infonet-Biovision. 2009. Maize - General information and agronomical aspects. [Online]. Available by http://www.infonet-biovision.org/default/ct/123/crops (verified 29 October).

Jones, T. J., and Perry, N. R. 2004. Plant-parasitic nematodes-small animals, big impact. Pp. 4 Biologist, Vol. 51.

Kagoda, F. 2010. Genetic studies and recurrent selection for nematode resistance in maize. PhD Thesis, University of KwaZulu Natal, Pietermaritzburg, South Africa.

Kagoda, F., Derera, J., Tongoona, P., and Coyne, D. L. 2010a. Awareness of plant-parasitic nematodes and maize varietal preferences by smallholder farmers in East and Southern Uganda: implications for assessing maize nematode resistance breeding needs in Africa. International Journal of Pest Management 56(3): 217–222.

Kagoda, F., Coyne, D. L., Mbiru, E., Derera, J., and Tongoona, P. 2010b. Monoxenic culture of *Pratylenchus zeae* on carrot discs. Nematologia Mediterranea 38:107–108.

Kathiresan, T., and Mehta, U. K. 2002. Penetration, multiplication and histopathological response of *Pratylenchus zeae* in resistant and susceptible sugarcane clones. International Journal of Nematology 12:189–196.

Kimenju, J. W., Waudo, S. W., Mwang'ombe, A. W., Sikora, R. A., and Schuster, R. P. 1998. Distribution of lesion nematodes associated with maize in Kenya and susceptibility of maize cultivars to *Pratylenchus zeae*. African Crop Science Journal 6:367–375.

Lawrence, G. W., and Clark, C. A. 1986. Infection and morphological development of *Meloidogyne incognita* in roots of susceptible and resistant sweetpotato cultivars. Plant disease 70:545–547.

Luc, M., Sikora, R. A., and Bridge, J. 2005. Plant-Parasitic Nematodes in Subtropical and Tropical Agriculture. 2 ed. CABI Publishing, Egham, UK.

MAAIF. 2011. Statistical Abstract 2011. Ministry of Agriculture, Animal Industry and Fisheries. Agricultural Planning Department.

Magorokosho, C., Vivek, B., Bänziger, M., and MacRobert, J. 2007. Characterization of maize germplasm grown in eastern and southern Africa: Results of the 2006 regional trials coordinated by CIMMYT. CIMMYT, Harare, Zimbabwe.

McDonald, A. H., and Nicol, J. M. 2005. Nematode parasites of cereals. Pp. 131–191 *in* M. Luc, R. A. Sikora and J. Bridge, eds. Plant-Parasitic Nematodes in Subtropical and Tropical Agriculture, 2 ed. CABI Publishing, Egham, UK.

NARO. 2002. Addressing the challenges of poverty eradication and modernisation of agriculture. pp. 66, In: G. W. Otim-Nape, (ed.) Improved Technologies by NARO, 1192-2002. National Agricultural Research Organisation.

Norton, D. C. 1978. Ecology of plant-parasitic nematodes. John Wiley and Sons, Inc., Canada.

Norton, D. C., and Nyvall, R. F. 1999. Nematodes that attack maize in Iowa. Pest Management 2–1. Iowa State University, University Extension, Iowa.

Olowe, T. 1977. Histological changes in maize root induced by *Pratylenchus brachyurus* and *P. zeae* in the absence of other microorganisms. Nigeria Journal of Plant Protection 3:41–51.

Olowe, T., and Corbett, D. C. M. 1976. Aspects of the biology of *Pratylenchus brachyurus* and *P. zeae*. Nematologica 22:202–211.

Oostenbrink, M. 1966. Major characteristics of the relation between nematodes and plants Mededlingen voor landbouwhogeschool Wageningen 66:3–46.

Oyekanmi, E. O., Coyne, D. L., and Fawole, B. 2007. Screening of selected microorganisms and maize genotypes for *Pratylenchus zeae* management and improved yield of *Zea mays* L. University of Ibadan, Nigeria.

Patel, N. B., Patel, D. J., and Patel, A. D. 2002. Effect of *Pratylenchus zeae* on maize. Indian Phytopathology 55:333–334.

Prot, J., and Savary, S. 1993. Interpreting upland rice yield and *Pratylenchus zeae* relationships: Correspondence Analyses. Journal of Nematology 25:277–285.

Rhoades, H. L. 1979. Evaluation of nematicides and methods of their application for control of nematodes on field corn Nematropica 9:43–47.

Sikora, R. A. 1992. Management of the antagonistic potential in agricultural ecosystems for the biological control of plant parasitic nematodes. Annual Review of Phytopathology 30:245–270.

Speijer, P. R., and De Waele, D. 1997. Screening of Musa germplasm for resistance and tolerance to nematodes.

Srivastava, H. K. 1991. Theories of heterosis. Classical and modern. Pp. 305 *in* A. K. Mandal, P. K. Ganguli and S. P. Banerjee, eds. Advances in plant breeding 1. CBS, Delhi.

Steel, R. G. D., and Torrie, J. H. 1980. Principles and procedures for statistics. 2nd ed. McGraw-Hill Book Co., New York.

Talwana, H. L., Butseya, M. M., and Tusime, G. 2008. Occurrence of plant parasitic nematodes and factors that enhance population build-up in cereal-based cropping systems in uganda. African Crop Science Journal 16:119–131.

Tarte, R. 1971. The relationship between pre-plant populations of *Pratylenchus zeae* and growth and yield of corn. Journal of Nematology 3:330–331.

Taylor, S. P., Vanstone, V. A., Ware, A. H., McKay, A. C., Szot, D., and Russ, M. H. 1999. Measuring yield loss in cereals caused by root lesion nematodes (*Pratylenchus neglectus* and *P. thornei*) with and without nematicide. Australian Journal of Agricultural Research 50:617–622.

Todd, T. C., and Oakley, T. R. 1996. Seasonal dynamics and yield relationships of *Pratylenchus* spp. in corn roots. Supplement to the Journal of Nematology 28:676–681.

Trudgill, D. L. 1991. Resistance to and tolerance of plant-parasitic nematodes in plants. Annual Review of Phytopathology 29:167–192.

Williams, W. P., and Windham, G. L. 1998. Registration of root-knot nematode resistant maize germplasm lines Mp709, Mp710. Mp711, and Mp712 Crop Science 38:563.

Windham, G. L., and Williams, W. P. 1987. Host suitability of commercial corn hybrids to *Meloidogyne arenaria* and *M. incognita*. Annals of Applied Nematology 1:13–16.

Windham, G. L., and Williams, W. P. 1988. Resistance of maize inbreds to *Meloidogyne incognita* and *M. arenaria*. Plant Disease Report 72:67–69.

Windham, G. L., and Williams, W. P. 1994a. Reproduction of *Meloidogyne incognita* and *M. arenaria* on tropical corn hybrids. Supplement to the Journal of Nematology 26:753–755.

Windham, G. L., and Williams, L. F. 1994b. Penetration and development of Meloidogyne incognita in roots of resistant and susceptible corn genotypes. Journal of Nematology 26:80–85.