

Generation Means Analysis for Estimation of Genetic Parameters for *Striga hermonthica* Resistance in Maize (*Zea mays* L.)

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Abstract

Striga hermonthica is a parasitic weed species that causes considerable yield loss in susceptible maize cultivars in western Kenya. A generation means analysis was conducted to estimate gene effects influencing resistance/tolerance to *Striga hermonthica* in maize cultivars adapted to western Kenya. A resistant inbred line developed by Maseno University, MSMP1/P2 was crossed to *Striga* susceptible inbred line 5057. Experimental units comprised of resistant parent P₁, susceptible parent P₂, their F₁ and F₂ generations, and BC₁P₁ and BC₁P₂ generations. The six generations were evaluated under *Striga* sick plots at Nyahera during the short rains of 2012 and long rains of 2013. Field evaluation for entries were grown in a randomized complete block design with three replicates. The results showed significant differences among generations for emerged *Striga*, *Striga* damage rating and maize growth including Plant and Ear height. Most of the additive, dominance, additive x additive, additive x dominance and dominance x dominance effects were significant indicating the importance of the additive, dominance and epistatic modes of gene actions in controlling emerged *Striga*, *Striga* damage rating, plant and ear height. Most components conferring *Striga* tolerance behaved in a qualitative manner. Dominance effects had higher mean values over additive effects. Significant dominant genetic effects (d) for *Striga* emergence and *Striga* damage rating suggested preponderance of non-additive genetic effects in the inheritance of *Striga* tolerance. The results also reveal the involvement of duplicate epistasis where the dominance estimate and dominance x dominance interaction had opposite signs. The presence of duplicate type of gene interaction confirms the importance of dominance gene effects.

Keywords: maize, *Zea mays*, *Striga hermonthica*, gene action, dominance, additive, generation mean analysis

1. Introduction.

Striga hermonthica (Del.) Benth., is a menacing parasitic weed that belongs to the family Scrophulariaceae and constitutes one of the greatest biotic constraints to food crop production, undermining the struggle to attain food security and economic growth in Sub-Saharan Africa (Sauerborn, 1991). Continuous mono-cropping with no fallow in turn has led to a gradual increase in populations of *Striga* species, which have become a serious threat to cereal production (Ariga, 1996). It is noteworthy that areas that have *Striga* problems are generally also characterized by low productivity, a shortened or non-existent fallow period, low fertilizer inputs as well as non-pesticide use and lack of improved seeds (Abayo et al., 1997).

The most effective way to minimize the yield loss due to *Striga* infestation is to use resistant crop varieties (Verkleij & Kuijper, 2000; Haussmann & Hess, 2000; Rich & Ejeta, 2008) because these do not require additional inputs such as labor and chemicals. Resistance to *Striga* refers to the ability of the host plant to stimulate the germination of *Striga* seeds but prevents the attachment of the parasite to its roots or to decimate the attached parasite (Badu-Apraku & Akinwale, 2011). A tolerant genotype on the other hand germinates and supports as many *Striga* plants as the sensitive genotype but produces more grain yield and shows fewer *Striga* damage symptoms (Kim, 1994). When infested, the resistant genotype is able to support a significantly fewer *Striga* plants and produces a higher yield than a susceptible genotype (Dogget, 1988; Ejeta et al., 1992; Haussmann et al., 2000; Rodenburg et al., 2006). Resistance or tolerance to *Striga* is quantitatively inherited (Ejeta et al., 1997; Lane et al., 1997; Kim, 1994). Reports of genetic resistance to *Striga* have been documented in rice (*Oryza sativa*; Bennetzen et al., 2000; Gurney et al., 2006), sorghum (*Sorghum bicolor*; Maiti et al., 1984;

Hess et al., 1992; Vogler et al., 1996; Haussmann et al., 2004) and maize (Adetimirin et al., 2000; Gethi & Smith, 2004; Menkir, 2006). Identifying source germplasm with different resistance mechanisms can facilitate combining several resistance genes to obtain more durable and stable polygenic resistance to *Striga* in cereals (Ejeta et al., 2000; Menkir, 2006). Several studies have been conducted to characterize mechanisms of resistance to *Striga* in other crops, including cowpea (*Vigna unguiculata*; Riopel & Timko, 1995), sorghum [*Sorghum bicolor* (L.) Moench] (Hess et al., 1992; Arnaud et al., 1999; Mohamed et al., 2003; Rich et al., 2004; Noubissie et al., 2012), rice (Harahap et al., 1993; Gurney et al., 2006; Jamil et al., 2011), pearl millet [*Pennisetum glaucum* (L.) R. Br.] (Kountche et al., 2013) and maize [*Zea mays* L.] (Amusan et al., 2008; Karaya et al., 2012). However, this information on the nature of resistance to *Striga* is not readily available to farmers since they are only in journals and books (Atera et al., 2014). Maize resistance can be expressed through low stimulation of *Striga* seed germination (Gurney et al., 2003; Pierce et al., 2003; Kiruki et al., 2006), low haustorial induction (Gurney et al., 2003), avoidance through root architecture (fewer thin branches) (Amusan et al., 2008), escape by early maturity (Oswald & Ransom, 2004), resistance to attachment (Amusan et al., 2008) and failure to support attached parasites (Lane et al., 1997; Gurney et al., 2003; Amusan et al., 2008). In maize, attempts have been made to introduce tolerance/resistance from both land races and wild relatives *Zea diploperennis* (teosinte) and *Tripsacum dactyloides* (Kling et al., 2000). ZD05, a progeny of backcrosses between International Institute of Tropical Agriculture (IITA) developed tropical maize germplasm and teosinte has been registered as *Striga* resistant line, TZSTR1108 (Menkir et al., 2006). These resistant and tolerant materials have fewer attached *Striga hermonthica* than susceptible lines and in addition show delayed parasitic post attachment development and higher mortality of attached parasites (Amusan et al., 2008). Another wild relative of maize, *Tripsacum dactyloides* (L.) has been shown to display post attachment resistance to *Striga hermonthica* and high level of tolerance (Hearne, 2009). However, breeding for resistance to *Striga* in maize, with scarcity of donor source and known mechanism of resistance, has been challenging (Amusan et al., 2008). Results of a few studies have shown that recurrent selection was effective in improving maize for *Striga* resistance (Menkir & Kling, 2007; Badu-Apraku et al., 2006, 2008). Recurrent selection is a cyclical scheme designed to increase the frequency of favorable alleles in a population and has been widely used effectively to improve quantitative traits in maize breeding populations (Sprague & Eberhart, 1977; Hallauer & Miranda, 1988; Kling et al., 2000; Menkir & Kling, 1999, 2007; Badu-Apraku et al., 2006, 2008). When inherited through additive gene action, the favorable genes are expected to make equal contribution to the improvement of the trait (Badu-Apraku et al., 2009). Better knowledge of the mode of gene action controlling the inheritance of resistance would enhance the identification and development of resistant varieties (Akanvou & Doku, 1998). For the maize varieties adapted to and tolerant to *Striga* in western Kenya, there is no published report on the role of different gene action modes involved in their tolerance to the noxious weed. Therefore we conducted a generation mean analysis with the objective to estimate the magnitude of gene effects influencing tolerance to *Striga hermonthica* in a cross between Maseno university resistant maize inbred line MSP1/P2 and the susceptible inbred line 5057 from the IITA. Information about gene effects including additive, dominance gene effects (a and d) and the three types of non allelic gene interactions, that is, additive x additive (aa), additive x dominance (ad) and dominance x dominance (dd) are very important in designing an effective gene deployment strategies in a resistance improvement program. Generation mean analysis is a simple and a useful technique for estimating these genetic effects as well as epistasis. The nature of epistasis is also useful in deciding breeding procedures to be adopted for the improvement of quantitative characters.

2. Materials and Methods

2.1 Site Description

The field studies were done at Maseno University of Kenya and at Nyahera in Kenya. Maseno university site is *Striga* free and lies along the Equator at latitude 0°, longitude 34°30'E at an altitude of 1515 metres above sea level. The soils at Maseno are well drained, extremely reddish brown and friable clay. The soils vary in color, consistence and texture. They are classified as dystric nitosols (Jaetzold et al., 1982). It experiences mean minimum and maximum annual temperatures of 15.4 °C and 29.9 °C respectively with an annual rainfall of between 1100-1500mm (Jaetzold et al., 1982). Nyahera, a *Striga* hot spot, lies at latitude 34°53.452'E, longitude 0°35.977'N at an altitude of 1490 metres above sea level. The soils are well drained, shallow to moderately deep dark yellowish brown to reddish brown, friable, stony sandy clay loam to gravelly sandy clay. They are classified as ferralitic, humic and dystric cambisols (Jaetzold et al., 1982). The average annual rainfall is 1650mm per annum (Jaetzold et al., 1982). The two sites have a bimodal type of rainfall where the first peak falls between April and August (Long rains season) and the second peak between September and December (short rains season). The short rains season, however are sometimes unreliable.

Maseno site being *Striga* free was used to make crosses during the short rains of 2011 and the long rains of 2012. Evaluations were done at Nyahera under *Striga* infestation in the short rains of 2012 and the long rains of 2013.

2.2 Maize Population Development

Striga resistant maize inbred line developed by Maseno University, MSMP1/P2 was crossed to *Striga* susceptible inbred line 5057 from the International Institute of Tropical agriculture (IITA). The F₁ generations were selfed to produce F₂ generations, and F₁ generations were crossed to both parents [resistant parent (P₁) and susceptible parents (P₂)] to produce backcrosses of F₁ for each parent (BC₁P₁) and (BC₁P₂) generations, respectively. Experimental units comprised populations of the six generations with details as follows: P₁ = MSMP1/P2, P₂ = 5057, F₁ = MSMP1/P2 × 5057, F₂ = MSMP1/P2 × 5057 (selfed), BC₁P₁ = (MSMP1/P2 × 5057) × MSMP1/P2; BC₁P₂ = (MSMP1/P2 × 5057) × 5057.

2.3 Field Evaluation and Experimental Design

The six generations, P₁, P₂, F₁, F₂, BC₁P₁ and BC₁P₂ were evaluated under *Striga* sick plots at Nyahera during the short rains (September to December) of 2012 and long rains (April to August) of 2013. Experimental plots were ploughed and harrowed twice. Seeds were hand - sown one seed per hill. Field evaluations for entries were grown in a randomized complete block design in three replications. The experimental units were four row plots for the P₁, P₂, and F₁ generations, a six row plot for the BC₁P₁ and BC₁P₂ generations, and an eight row plot for the F₂ progeny generation. The length of the rows including 1 meter alleys was 5.1 meters with 0.75 meters between rows. Four, six and eight rows were used to reduce intergenotypic competition between plots of different generations and to sample adequately genotypic variability within generations. A compound fertilizer was applied at the rates of 60 kg N, 60 kg P, and 60 kg K ha⁻¹ at the time of sowing. Additional 60 kg N ha⁻¹ was applied as top dressing 4 weeks later after sowing. Hand hoe weeding was carried out prior to *Striga* emergence and thereafter weeds were hand pulled.

2.4 *Striga* Severity Assessment and Assessment for Other Components of Resistance

In each experiment, 15 plants from homogenous generations (P₁, P₂ and F₁), 30 plants from backcross generations [(BC₁P₁) and (BC₁P₂)] and 60 plants from F₂ generations were assessed for *Striga* severity, emerged *Striga*, plant height and ear height in each replicate.

2.4.1 *Striga* Severity Assessment

Each of the plants sampled for assessment were tagged. *Striga* damage syndrome was scored per plant using the scale of 1-5; where 1 = no damage, indicating normal plant growth and high level of tolerance, and 5 = complete collapse or death of the maize plant, that is, highly sensitive/intolerant. Emerged *Striga* counts and *Striga* damage rating at 8 and 10 weeks were recorded per plant.

2.4.2 Plant Height and Ear Height (cm)

These were measured as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear respectively.

2.5 Data Analysis

Generation means were calculated for each of the 6 generations on an individual plant basis using OPSTAT software. To determine the mode of inheritance of resistance/tolerance to *Striga*, Gamble's (1962) notation was used, where [m] = F₂ mean; additive gene effects [a] = B₁CP₁ - BC₁P₂; dominance gene effects [d] = -0.5P₁ - 0.5P₂ + F₁ - 4F₂ + 2BC₁P₁ + 2BC₁P₂; additive x additive gene effects [aa] = -4F₂ + 2BC₁P₁ + 2BC₁P₂; additive x dominance gene effects [ad] = -0.5P₁ + 0.5P₂ + BC₁P₁ - BC₁P₂ and dominance x dominance gene effects [dd] = P₁ + P₂ + 2F₁ + 4F₂ - 4B₁CP₁ - 4B₁CP₂.

The model for a generation mean, Y, is:

$$Y = m + aa + \beta d + \alpha 2aa + 2\alpha\beta ad + \beta 2dd$$

Where, Y, the observed generation mean; m, F₂ mean; a, additive gene effects; d, dominance gene effects; aa, additive x additive epistatic gene effects; ad, additive x dominance epistatic gene effects and dd, dominance x dominance epistatic gene effects. α and β represent the coefficients for the genetic effects for the particular generation being estimated (Hayman, 1958; Mather & Jinks, 1982). The estimates of least effective factors (gene) were obtained using Castle / Wright formula (Weber, 1950).

3. Results

3.1 *Striga* Data

3.1.1 Emerged *Striga* Counts

There were significant differences ($P < 0.05$) among the maize generations for emerged *Striga* count at 8 weeks after planting (Table 1). The mean *Striga* count was 1.1. The highly resistant generation with low (zero) *Striga* emergence was P_1 . The maize generation with the highest number, 3.1, was the susceptible parent P_2 .

Significant differences ($P < 0.05$) were observed in the emerged *Striga* count amongst the maize generations for emerged *Striga* at 10 weeks after planting (Table 1). The mean *Striga* count was 2.3. The generation with the highest number, 6.2, was the susceptible parent P_2 . The resistant parent P_1 had the least count of 0.4.

3.2 Maize Response to *Striga* Infection

3.2.1 *Striga* Damage Rating at 8 Weeks after Planting

Significant differences ($P < 0.05$) were observed amongst the maize generations for *Striga* damage rating at 8 weeks after planting (Table 1). *Striga* damage ratings ranged from 1.1 to 2.7. The mean rating was 1.6. The susceptible parent P_2 had the highest damage rating of 2.7 on the scale of 1-5, whereas the resistant parent P_1 had the lowest damage score of 1.1. This was however not significantly different from F_1 , BC_1P_1 and BC_1P_2 generations. The susceptible parent damage score rating of 2.7 was significantly different from the rest of the generations.

3.2.2 *Striga* Damage Rating at 10 Weeks after Planting

There were significant differences ($P < 0.05$) among the maize generations for *Striga* damage rating at 10 weeks (Table 1). The mean rating was 2.3. The susceptible parent P_2 had the worst score of 3.6 whereas the resistant parent, P_1 had the best score of 1.1. F_1 generation was similar to BC_1P_1 but significantly different from P_1 , P_2F_2 and BC_1P_2 . Among the segregating generations, F_2 had the highest score followed by BC_1P_2 and BC_1P_1 respectively. The means for *Striga* counts and *Striga* damage ratings for B_1CP_2 generations were skewed towards the susceptible parent P_2 whereas the BC_1P_1 generations were skewed towards the resistant parent P_1 .

3.2.3 Plant Height

There were significant differences ($P < 0.05$) among the generations for plant height (Table 1). Plant heights ranged from 82.3 to 134.4 cm. The mean plant height amongst the generations was 99 cm. The resistant parent P_1 had the highest figure of 134.4 cm whereas the susceptible parent P_2 had the lowest value of 82.3 cm. This however was not significantly different from the height of the segregating F_2 and BC_1P_2 generations at 84.7 and 85.9 cm respectively.

3.2.4 Ear Height

There were significant differences amongst the generations for ear height. The mean ear height was 43.6 cm. The ear heights ranged from 34.5 to 60.3 cm. The resistant Parent P_1 had the highest ear placement at 60.3 centimeters whereas the susceptible Parent, P_2 had the ear placement at 36.1 centimeters. The back cross to the susceptible parent BC_1P_2 had the lowest ear placement of 34.5 cm. The ear heights for the susceptible parent P_2 , F_2 and backcross to the resistant parent BC_1P_1 were however not significantly different.

Table 1. Means of *Striga* counts, *Striga* damage ratings, plant and ear height of P₁, P₂ and F₁, F₂, B₁CP₁, B₁CP₂ generations

Generation	Variable					
	<i>Striga</i> Count		<i>Striga</i> Damage Rating		PH	EH
	8 weeks	10 weeks	8 weeks	10 weeks		
P ₁	0.0 ^c	0.4 ^e	1.1 ^c	1.1 ^e	134.4 ^a	60.3 ^a
P ₂	3.1 ^a	6.2 ^a	2.7 ^a	3.6 ^a	82.3 ^d	36.1 ^{bc}
F ₁	0.1 ^c	1.5 ^{cd}	1.4 ^c	1.7 ^d	109.8 ^b	50.9 ^{ab}
F ₂	1.4 ^b	2.0 ^{bc}	1.8 ^b	2.8 ^b	85.9 ^d	42.1 ^{bc}
BC ₁ P ₁	0.3 ^c	0.7 ^{de}	1.3 ^c	1.7 ^d	96.8 ^c	37.5 ^{bc}
BC ₁ P ₂	1.5 ^b	2.8 ^b	1.1 ^c	2.1 ^c	84.7 ^d	34.5 ^c
Mean	1.1	2.3	1.6	2.2	99.0	43.6
CV (%)	1.1	0.9	0.4	0.4	0.2	0.2
SE±	0.5	0.9	0.3	0.4	8.2	4.1
Std	1.2	2.1	0.6	1.0	20.1	10.1
Mid-parent (m)	1.5	3.1	1.9	2.4	108.1	48.2

Note. Means followed by the same letter within columns do not differ significantly according to DMRT.

P₁ = resistant Parent (MSMP1/P2); P₂ = Susceptible parent (5057); BC₁P₁ = Backcross to resistant parent; BC₁P₂ = Backcross to susceptible parent. PH = Plant height; EH = Ear height; SE±, Standard error of the mean; Std, Standard deviation.

3.3 Correlation between *Striga* Damage Rating and Plant Height of the Maize Generations

Figures 1 and 2 are the correlation plots of *Striga* damage rating and plant height of the maize generations of the cross between P₁ (MSMP1/P2) and P₂ (5057). The correlation was negative ($r = -0.56$) and the coefficient of the relationship (R^2) was 0.3 at 8 weeks after planting (WAP). The same negative correlation scenario ($r = -0.75$) and ($R^2 = 0.57$) was observed at 10 WAP.

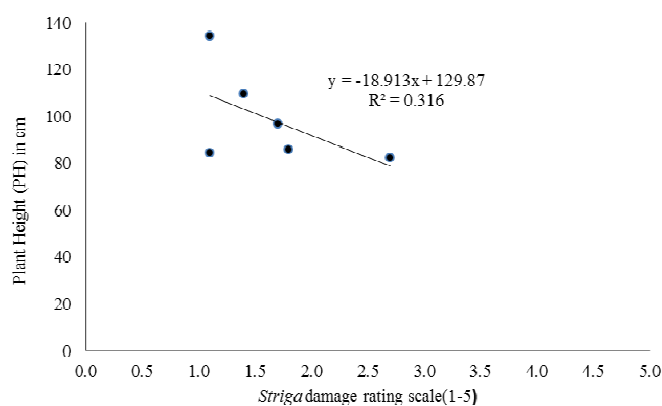


Figure 1. Linear correlation between plant height of the generations and *Striga* damage rating at 8 weeks after planting

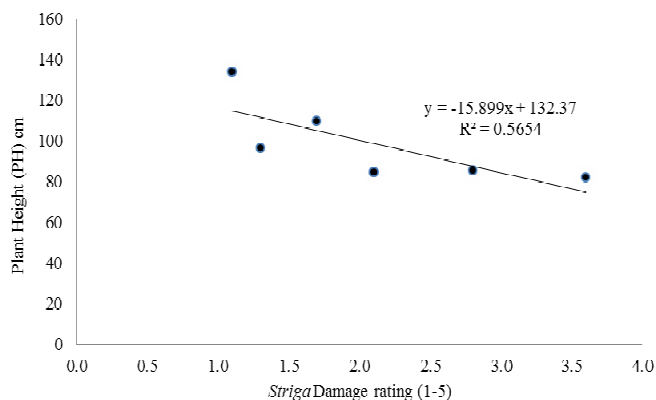


Figure 2. Linear correlation between plant height of the generations and *Striga* damage rating at 10 weeks after planting

3.4 Correlation between *Striga* Damage Rating and Ear Height of the Maize Generations.

The estimates of linear correlation was negative ($r = -0.48$ and $r = -0.56$) at 8 and 10 WAP respectively (Figures 3 and 4). The coefficient of determination (R^2) was 0.23 and 0.31 respectively.

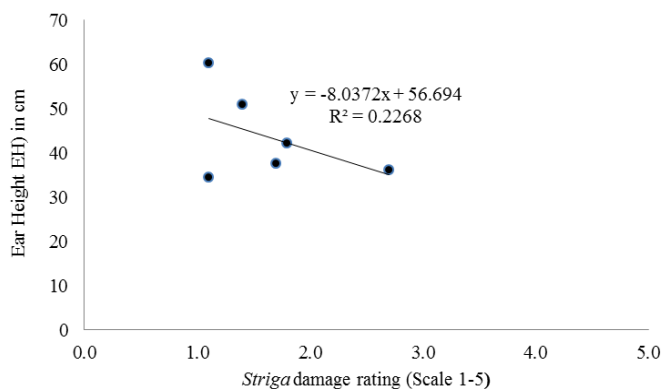


Figure 3. Linear correlation between Ear height of the generations and *Striga* damage rating at 8 weeks after planting

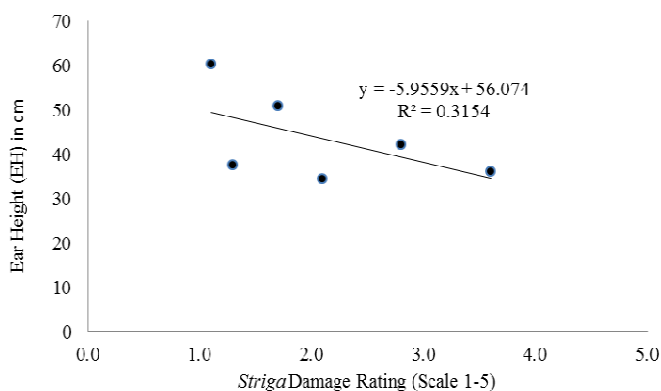


Figure 4. Linear correlation between Ear height of the maize generations and *Striga* damage rating at 10 weeks after planting

3.5 Estimates of Genetic Components

Estimates of the six parameters, i.e. additive (a), dominance (d), additive x additive (aa), additive x dominance (ad), dominance x dominance (dd) and F_2 means (m) are presented in Table 2. The results indicated that the mean effects (m) were highly significant for the variables.

Table 2. Estimates of genetic components of mean for various traits of the cross P_1 (MSMP1/P2) \times P_2 (5057) of maize under *Striga* infestation

Variable	m	[a]	[d]	[aa]	[ad]	[dd]
<i>Striga</i> Count 8	1.35±0.12**	-1.15±0.13**	-3.33±0.57*	-1.90±0.55*	0.83±0.40*	1.80±0.79*
<i>Striga</i> Count 10	1.95±0.12**	-2.15±0.29**	-2.53±0.85*	-0.77±0.74 ^{ns}	1.50±0.82 ^{ns}	3.27±1.50*
<i>Striga</i> Damage Rating 8	1.77±0.12**	0.63±0.11**	-1.93±0.52**	-1.40±0.51**	2.93±0.26**	2.27±0.68**
<i>Striga</i> Damage Rating 10	2.75±0.11**	-0.82±0.08**	-4.85±0.50**	-4.23±0.48**	0.87±0.22**	5.63±0.62**
Plant Height (cm)	85.85±2.46**	12.08±2.25**	21.10±12.11 ^{ns}	19.70±10.81 ^{ns}	-27.97±7.79**	53.47±17.24**
Ear Height (cm)	42.1±1.86**	2.95±1.38*	-21.72±8.39**	-24.43±7.92**	-18.27±4.17**	78.63±10.77**

Note. m: F_2 means; ns, **, * = non-significant, Significant at 1% and 5% probability level, respectively; [a], [d], [aa], [ad], [dd] = net directional effects of loci contributing to additive, dominance, additive x additive, additive x dominance, and dominance x dominance components, respectively.

From the experiment, all kinds of gene effects are significant ($P < 0.05$), except additive x additive, additive x dominance for emerged *Striga* count at 10 weeks after planting and dominance, additive x additive effects for plant height which were not significant. Among the interactions, dominance x dominance interactions (dd) are larger than (aa) and (ad) except for *Striga* damage rating at 8 weeks after planting while among the main effects, dominance (d) is greater than the additive (a) component. The (d) and (dd) are in opposite directions except for plant height hence the nature of epistasis is duplicate. The (d) is negative, whereas (dd) is positive.

The additive gene effects (a) were positive and highly significant for *Striga* damage rating at 8 weeks. This was the same for plant height and ear height. Meanwhile negative significant values for these parameters were detected for emerged *Striga* count at 8, 10 weeks after planting as well as for *Striga* damage rating at 10 weeks.

With regard to dominance gene effects (d) negative values were observed for *Striga* count 8, *Striga* count 10, *Striga* damage rating at 8, *Striga* damage rating at 10 weeks and Ear height. Positive and non-significant gene effects were observed for plant height.

With respect to additive x additive type gene action, positive and non-significant effects were observed for plant height. Negative and non-significant effects were observed for *Striga* count at 10 weeks. Negative and significant effects were observed for *Striga* count at 8 weeks. *Striga* damage rating at 8 and 10 weeks and ear height, also exhibited significant additive and dominance gene effects.

Additive x dominance gene effects (ad) were found to be positive and significant for *Striga* count 8 and *Striga* damage rating at 8 and 10 weeks. Emerged *Striga* count at 10 weeks was positive and non-significant. Plant and Ear heights had negative and highly significant effects.

Concerning the dominance x dominance type of gene action, (dd), positively significant and highly significant effects were detected for all the variables.

3.6 Estimates of the Number of Genes.

The estimated number of genes controlling various traits in both crosses is presented in Table 3. Considering Castle-Wright's formula for estimation and crosses the number of genes responsible for emerged *Striga* and *Striga* damage rating as well as ear height was below one, whereas the number controlling plant height was approximately 3.0.

Table 3. Estimates of the number of genes for the various traits in the cross $P_1 \times P_2$

Trait	Formular (Castle-Wright's)
<i>Striga</i> count at 8 weeks	0.781
<i>Striga</i> count at 10 weeks	-4.553
<i>Striga</i> damage rating at 8 weeks	0.629
<i>Striga</i> damage rating at 10 weeks	0.685
Plant Height (cm)	2.627
Ear Height (cm)	0.284

4. Discussion

The mean *Striga* emergence and *Striga* damage ratings for the *Striga* resistant parent was significantly lower than the susceptible parent P_2 . This result shows that plant resistance to *Striga* was manifested and expressed by a lower number of emerged parasitic plants and less damage sustained by the host. It also suggests that screening progenitors was effective in differentiating the resistant from susceptible inbred lines. These results are consistent with the observations reported in maize (Kim et al., 1999) and sorghum (Oliver et al., 1991; Arnaud et al., 1999).

The means for emerged *Striga* counts at 8 and 10 weeks after planting and *Striga* damage rating at 10 weeks after planting for BC_1P_1 were skewed towards the resistant parent P_1 . This indicates that several genes could be involved in *Striga* resistance/tolerance. When backcross to the susceptible parent (BC_1P_2) was performed, population distribution skewed towards the susceptible parent P_2 (5057). In general, backcrossing to susceptibility increases frequency of alleles for susceptibility. Backcrossing to resistant parent increases alleles for resistance hence skews towards resistant direction. However, the presence of transgressive segregants that perform better or worse than parents do exist in this study. Transgressive segregants were observed in BC_1P_2 population which resulted in more resistant plants than the susceptible parent P_2 (5057) for the *Striga* damage rating at 8 weeks.

Plant and Ear heights were negatively correlated with *Striga* damage rating which accounted for 30 and 57 percent of the variance in plant height at 8 and 10 weeks. On the other hand, *Striga* damage rating accounted for 23 and 30 percent of the variance in Ear height at 8 and 10 weeks. This is not unusual since susceptibility to *Striga* is manifested by decreased plant and ear height and the converse is true (Nagawa, 1991; Reda & Kabebe, 1994; Mbase, 1994). This scenario is supported by Akanvou et al. (1997) who reported a negative genetic correlation between plant height, *Striga* count, *Striga* rating and ear height. According to Akanvou and Doku (1998) negative association are expected since *Striga* reduces yield through its adverse effects on the physiology of the infested plants.

Estimates of the six parameters, i.e. additive (a), dominance (d), additive x additive (aa), additive x dominance (ad) and dominance x dominance and F_2 means (m) presented in Table 2 indicate that the mean effects (m) were highly significant for the variables indicating that all the variables except plant height, are qualitatively inherited. *Striga* resistance in maize, reported to date, appears to be qualitative and recessive in nature (Lane et al., 1997; Oswald & Ransom, 2004; Gethi & Smith, 2004) qualities that may further ensure its stability (Rispaill et al., 2007). Other reports also suggest that *Striga* resistance is controlled by relatively few genes with additive effects (Shinde & Kulkarni, 1982; Vasudeva Rao et al., 1982). On the contrary Lane et al. (1997); Ejeta (2007); Hausmann et al. (2004) reported that resistance/tolerance to *Striga* was quantitatively inherited.

Higher mean values of dominance effects over additive effects, significant dominant genetic effects (d) for *Striga* emergence and *Striga* damage rating suggested a preponderance of non-additive genetic effects in the inheritance of *Striga* tolerance. This is in agreement with Kim (1994), who reported the importance of both additive and non-additive effects for *Striga* emergence in a di-allele study. This is also in agreement with Akanvou et al. (1997), who reported the preponderance of non-additive genetic effects for *Striga* emergence. On the contrary, Gethi and Smith (2004), reported that additive gene effects were more important than non-additive gene effects in the expression of all the resistance traits measured.

Gene interaction is considered to be complementary when the (d) and (dd) estimates have the same signs and to be duplicating when the signs differ (Mather & Jinks, 1982). Gene interactions in this study were of duplicate type except for plant height which was complementary. This is contrary to Azizi et al. (2006), who reported duplicate type of non-allelic interaction for plant height in maize. The presence of duplicate type of gene

interaction confirms the importance of dominance effects.

The additive gene effects (a) were positive and highly significant for *Striga* damage rating at 8 weeks, plant height and ear height. Meanwhile negative and significant values were detected for emerged *Striga* count at 8, 10 weeks after planting and *Striga* damage rating at 10 weeks. The results indicate that selection for *Striga* tolerance, plant and ear height are important in early generations. The negative and significant values mean that the materials that were used in the study have decreasing alleles for *Striga* tolerance and selection to improve it could be effective. One such effective way is to use the recurrent selection methods that capitalize on additive gene action for the screening of segregating families (Badu-Apraku et al., 2013). This should facilitate the accumulation of resistance/tolerance genes to develop germplasm with multigenic resistance/tolerance that could be effective and durable over time (Berner et al., 1995; Menkir & Kling, 2007; Badu-Apraku et al., 2012).

With regard to dominance gene effects (d) negative values were observed for *Striga* count 8, *Striga* count 10, *Striga* damage rating at 8, *Striga* damage rating at 10 weeks and Ear height. This means that the alleles responsible for low values for *Striga* tolerance and ear height were dominant over the alleles controlling high values. Positive and non-significant gene effects were observed for plant height indicating the presence of dominant gene effect in the inheritance of plant height.

With respect to additive x additive (aa) type gene effects, positive and non-significant effects were observed for plant height. This means that early selection for plant height might be effective for *Striga* breeding. Negative and non-significant effects were observed for *Striga* count at 10 weeks. Negative and significant effects were observed for *Striga* count at 8 weeks, *Striga* damage rating at 8 and 10 weeks as well as ear height. This means that early generation selection for *Striga* tolerance simultaneous with ear height might not be an effective strategy in a *Striga* breeding program.

Additive x dominance type gene effects (ad) were found to be positive and significant for *Striga* count 8 and *Striga* damage rating at 8 and 10 weeks. Emerged *Striga* count at 10 weeks was positive but non-significant. Plant and Ear heights had negative but highly significant effects. Negative sign of interaction suggest an interaction between increasing and decreasing alleles, thus providing evidence of dispersion of genes in the inbred parents (Mather & Jinks, 1982). Yi-Hong Wang et al. (2014) reported that both additive and dominant gene action are involved in *Striga* resistance under conditions of *Striga* infestation.

Concerning the dominance x dominance (dd) gene action, positive and highly significant effects were detected for all the variables. Positive and significant results confirm the important role of dominance x dominance gene interactions in the genetic system which controls *Striga* emergence, *Striga* tolerance, plant and ear heights.

For estimation of the number of effective factors, differences between parents and variation in F₂ and backcrosses are needed. The Castle/Wright formula (Weber, 1950) was used to estimate the number of effective factors. With regard to *Striga* count, *Striga* damage rating and ear height an estimate of genes number was below one. These values should be considered as one and probably more. This may be due to the existence of interaction between pertinent non-allelic genes. With regard to plant height estimates of the effective factors when using Castle/Wright was 3.0 suggesting that the parental varieties differed in three pairs of genes. Thus, the number of effective factors might not be the actual number of genes due to the existence of interaction of non-allelic between the pertinent genes and dominance. This result is in accordance with that reported by Swamy Rao (1979) who reported that plant height was under the control of polygenes. The more than one gene responsible for the trait plant height, in the cross, stipulates polygenic inheritance of this trait in maize. The genes controlling quantitative traits could be linked and therefore segregate as a group or as an effective factor (Milus & Line, 1986).

The negative Castle-Wright estimates for *Striga* count at 10 weeks are probably due to violations of the assumptions of the Castle-Wright estimator. The Castle-Wright equation assumes fixed differences between the parents, additive gene action, unlinked loci, and equality of allelic effects (Lynch & Walsh, 1998). The assumption most likely violated is that of additive gene action, especially since dominance calculation indicates partial dominance for the trait examined (Table 3).

5. Conclusion

The estimates of number of genes involved and mode of gene action is important in deciding the breeding procedure for maize improvement under *Striga* infestation. A method that involves accumulation of favorable genes for the improvement of the trait under selection would be ideal. When inherited through additive gene action the favorable genes are expected to make equal contribution to the improvement of the trait.

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