POLISH JOURNAL OF NATURAL SCIENCES
Abbrev.: Pol. J. Natur. Sc., Vol 39(1): 15–29, Y. 2024

DOI: 10.31648/pjns.9688

INHERITANCE STUDIES OF GRAIN YIELD IN AFRICAN YAM BEAN (*SPHENOSTYLIS STENOCARPA* (HOCHST EX. A. RICH.) HARMS)

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Key words: additive gene effects, African yam bean, dominance gene effects, epistasis, generation mean analysis, inheritance.

Abstract

African yam bean (AYB) is a tropical underutilized leguminous crop serving as food for man and feeds for animals. Despite its nutritional values, its production is limited by low grain yield. Overcoming this menace through breeding programme requires adequate information on the inheritance pattern of the traits responsible for the low grain yield. Two divergent grain yield potential of AYB accessions collected from the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, were crossed to generate F_1 progenies. The F_1 was advanced to F_2 progenies. Backcrosses to the two parents (BC_1 and BC_2) were generated. The six generations obtained were evaluated in three agroecological environments. Generation mean analysis and scaling tests for grain yield and some grain yield-related traits were estimated and subjected to factorial analysis of variance at $P < 0.01$. The results revealed that at least one of the scaling tests was significant in all the studied traits. The dominance gene effects were larger than additive gene effects in the studied traits. Complementary epistasis was observed in pod weight, number of seed per pod, weight of 100 seeds per pod and seed set percentage while duplicative epistasis was observed in number of locules per pod, number of peduncles per plant, number of pods per peduncles, number of pods per plant, pod weight per plant, seed weight per plant and grain yield. Environmental variances were less than genotypic variances in all studied traits. Pod weight, number of seed per pod, weight of 100 seeds per pod and seed set percentage while duplicative epistasis was observed in number of locules per pod, number of peduncles per plant, number of pods per peduncles, number of pods per plant, pod weight per plant, seed weight per plant and grain yield exhibited high broad sense and low narrow sense heritability. The results further showed that both additive and non-additive gene actions are important in inheriting these traits. The findings obtained in this study suggested that reciprocal recurrent selection should be adopted to obtained higher yield in AYB.

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Introduction

African yam bean (AYB) (*Sphenostylis stenocarpa* [Hochst. ex. A. Rich.] Harms) is a leguminous crop belonging to the family Fabaceae (OLUWOLE et al. 2021, JUDE et al. 2022). Among all the members of the genus *Sphenostylis*. AYB is the most popular and of higher economic value (OJUEDERIE et al. 2016). The crop is of tropical Africa origin (ADEWALE 2011) with a wide genetic diversity. It is a neglected, underutilized, orphan, and under-researched tropical African crop that is on its track to extinction due to the little attention the crop has received from the farmers, the farm produces processors, consumers, and the crop scientists (SHITTA et al. 2016, GBENGA-FABUSIWA 2020). The adaptability of the crop to a wide range of environmental and soil conditions makes it cheap and accessible, serving as a good source of plant protein in food and providing nutritional security (GEORGE et al. 2020, SUMANDIARSA et al. 2021). Figure 1 present the image of AYB plant, roots and seeds.

Fig. 1. Image of AYB: *a*; *b* – AYB plant; *c* – AYB pod; *d* – AYB roots; *e* – AYB seeds
Source: Genetic Resources Centre, International Institute of Tropical Agriculture, Ibadan, Nigeria, access: 25.04.2024

The AYB is cultivated for its highly nutritious edible seeds, leaves, and tubers (AFOLABI et al. 2019, OJUEDERIE et al. 2021). These edible parts of the crop are rich in nutrients that can be compared with other legumes (OLUWOLE et al. 2021). The protein content in the grains varies between 17 and 30 mg/g depending on the accession (GEORGE et al. 2020) which is more than those of pigeon peas, common pea, and chickpea (EKPO 2006, OLUWOLE et al. 2021). The grain and tuber of AYB also has high mineral and vitamin content (BAIYERI et al. 2018, AREMU et al. 2019, NAMANI et al. 2021).

The flour from AYB seeds is used to fortify food that is low in protein content and used as a supplement in livestock feed (NAMANI et al. 2017). The crop is commonly used in replenishing agricultural soil due to it potentiality of fixing nitrogen. Considering the great potential AYB exhibited, its utilization will not only ensure food security but will also sustain agricultural land.

Despite the numerous economic value importance of AYB, the average grain yield of the accessions in farmers' possession over time is low thereby limiting its production and improved varieties with high grain yield attributes (ADEWALE 2011). It becomes necessary to have detailed information of the mode of inheritance of the yield and non-yield trait(s) involves and the nature of gene actions in determining the efficiency of any breeding procedure that can help to attain a maximum genetic improvement in the crop (FOUAD 2020).

Moreover, determining the gene effects governing quantitative traits of the crop is essential. Various biometrical methods have been previously used to obtain information about the inheritance of quantitative traits in crops. For instance, generation mean analysis, a biometrical method can provide the required information on the relative importance of mean effects of the gene(s) i.e. additive effects, dominance deviations, and its effects as a result of non-allelic genetic interactions or epistatic gene effects while estimating genotypic values of the individuals, average genotypic values of families and generations at large (MATHER and JINKS 1982). In this study, generation mean analysis was used to elucidate the mode of inheritance of grain yield and grain yield-related traits in AYB. This was with a view to provide information on the genetic materials required for the improvement of the crop.

Materials and Methods

Source of genetic materials

The genetic materials used for this research were two AYB accessions (TSs 24 and TSs 67) collected from the Genetic Resource Centre (GRC) of the International Institute of Tropical Agriculture (IITA) Ibadan, Nigeria with divergent grain yield potentials. TSs 24 is a high grain yielding while TSs 67 is a low grain yielding accession. Information on the initial evaluation trials conducted at IITA, Ibadan regarding the two accessions on days to 50% flowering were noted to determine the accurate planting time of each accession to ensure proper flowering synchronization to achieve success during hand hybridization.

Obtaining F_1, F_2 and backcross population

Seeds of the two divergent parental lines were planted at the Biological Garden of Elizade University, Ilara-Mokin, and Ondo State, Nigeria. Each of the two parental lines were crossed to generate F_1 progenies. Some seeds from the F_1's and the two parents were planted to advance to F_2 progenies and backcrosses were generated. Backcrosses to P_1 and P_2 were done using F_1 (F_1 was crossed with P_1 and P_2 respectively). Genetic studies were conducted on the six generations generated; P_1, P_2, F_1, F_2, backcross to P_1 (BC_1) and backcross to P_2 (BC_2).

Evaluation of the generation

The parental lines (P_1 and P_2) and F_1 representing the non-segregating population along with F_2, BC_1, and BC_2 representing segregating population were evaluated for grain yield and grain yield-related traits such as pod weight, number of seed per pod, weight of 100 seeds per pod, seed set percentage, number of locules per pod, number of peduncles per plant, number of pods per peduncles, number of pods per plant, pod weight per plant, seed weight per plant and grain yield. These were further used to determine their mode of inheritance. The evaluation was carried out in three agro ecological environments representing three different agro-ecological zones in Nigeria at the Biological Garden, Elizade University, Ilara-Mokin, Ondo State, Nigeria (representing rain forest agro-ecological zone); Ekiti State University Agricultural Teaching and Research Station, Ado-Ekiti, Ekiti State, Nigeria (representing derived savanna agro-ecological zone), and Oke-Ako Farm Settlement, Oke-Ekiti, Ekiti State, Nigeria (representing southern Guinea savannah agro-ecological zone). Seeds of the six generations generated were planted on the field, set out in a Randomized Complete Block Design (RCBD) with three replicates in each of the experimental sites. The number of plants evaluated at each experimental site for each generation were; Experimental site I and II (Rain forest agro-ecological zone and Derived savannah agro-ecological zone) consists of: 21 plants for the non-segregating population P_1 and P_2; 90 and 89 plants for the backcross populations of BCP_1 and BCP_2 respectively.

Experimental site III (Southern Guinea savannah agro-ecological zone) consists of: 21 plants for the non-segregating population P_1 and P_2; 30 plants for the non-segregating population of F_1; 90 plants for segregation population of F_2; 30 plants for the non-segregating population of F_1; 51 plants for segregation population of F_2; 51 plants for the backcross population of BCP_1 and BCP_2.

Pollination procedure

The following steps were involves in emasculation and pollination in AYB flower:

1. Appearance of purple stripe along the flower wing is a sign of flower maturity and the readiness of the flower bud to anthesize within a day.
2. Sterilized forcep was carefully used to remove the petals and the stamen (kneel, banner and wing). When removing the flower petals and stamen with the sterilized forcep, second hand should be used to hold the flower securely and gently to avoid flower dropping from the peduncle.
3. The flower filaments and anthers were gently removed.
4. At this stage, the flowers had been successfully emasculated. The emasculated flowers were set for pollination.
5. For the emasculated flowers that were not ready for hand pollinated immediately, they were covered with small sized pollen bags.
6. A matured flower from a pre-determined plant was removed from its peduncle, tease and use as pollen source or donor.
7. The dehisced anther was rubbed on the emasculated flower. This was done carefully to avoid any form of contamination.
8. The pollinated bags were used to cover the pollinated emasculated flowers immediately.
9. The pollinated flowers were properly labeled and tag for easy identification.
10. The bags were removed a day after pollination.
11. Formation of pods from the hand pollinated flower is a sign of successful pollination.

Agronomic Practices

The experimental plots in the three environments were well-ploughed, harrowed, and ridged mechanically. Planting was carried out in the fourth week of May 2022 for evaluation when the rain was steady. The seeds were sown solely at 1m x 1m spacing at a depth of 2–3 cm. Staking was done two weeks after planting and seedlings were trail to the stakes continually. The plots were kept weed-free throughout the study. No incidence of pest infestation or disease infection was recorded throughout the research.

Data collection

Data were collected on grain yield and some grain yield-related traits (Table 1) using AYB descriptors (Adewale and Dumet 2010).

Table 1

The list and description of the quantitative traits collected

S/N	Traits	Abbreviation	Measurement definitions	Unit
1	number of pods per peduncle	PodPed.$^{-1}$	the mean number of pods per peduncle of 10 randomly selected plants from the same plot	counting; visual assessment method
2	number of peduncles per plant	Ped.Pl. $^{-1}$	the mean number of peduncles from 10 randomly selected plant sample at harvest from the same plot	counting; visual assessment method
3	number of locules per pod	Loc.Pod^{-1}	this is the mean number of seed cavities in 10 randomly selected pods from the same plot	counting; visual assessment method
4	number of seeds per pod	Seedpod^{-1}	this is the mean number of seeds from 10 randomly selected pods in the same plot	counting; visual assessment method
5	pod weight	Pw	this is the average weight of 10 randomly selected pods at harvest from the same plot using digital weighing balance	[g]
6	number of pods per plant	PodPl.$^{-1}$	this is the mean number of pods from 10 randomly selected plants in the same plot at harvest	counting; visual assessment method
7	pod weight per plant	PwPl.$^{-1}$	this is the mean weight of total pods produced by 10 randomly selected plants from the same plot using digital weighing balance	[g]
8	seed weight per plant	SwPl.$^{-1}$	this is themean weight of seeds produce per plant of produced 10 randomly selected plant from the same plot using digital weighing balance	[g]
9	100-seed weight	100-SW	the weight of 100 randomly selected seeds taken from total seed yield obtained from the same plot using electronic weighing balance	[g]
10	seed Set Percentage	SSP	the mean ratio of seed number and loculi number/ pod multiplied by 100; measured on 10 randomly selected pods	[%]
11	grain yield per hectare	GY^{-1}	the weight of total dried seeds obtained from the same plot using weighing balance.	[kg ha^{-1}]

Statistical analyses

Data obtained were subjected to factorial analysis of variance (ANOVA) using IRRI PBTools software, version 1.4. (IRRI 2014) by the Biometrics and Breeding Informatics, PBGB Division, International Rice Research Institute, Los Baños, Laguna based generation mean analysis. Estimates of the four scaling tests (A, B, C, and D) and Generation mean analysis were determined according to the method suggested by HAYMAN (1958) and JINKS and JONES (1958). The significances of scaling test A and B, C and D indicate the presence of J (additive x dominance interaction), l (dominance x dominance interaction) and i (additive x additive interaction). The significance of one of the four scales for a trait reveals that epistatic digenic interaction that could contributed to the inheritance in the traits.

Biometrical methods

Most biometrical methods presumed the absence of epistasis in drawing inferences from genetic studies, whereas its presence cannot be underestimated (SHARMA 1988). Most of these biometrical methods failed to estimate gene interaction effects. However, generation mean analysis (GMA) as a biometrical method proposed by HAYMAN and MATHER (1955), and JINKS and JONES (1958) is capable of handling the limitations of other biometrical methods efficiently (SHARMA 1988). GMA provides the opportunity to detect the presence or absence of epistasis (non-allelic interaction) and determined the type of epistasis that is involved if present (SHARMA 1988).

Results

Estimate of scaling tests for grain yield and grain yield-related traits

Estimates of scaling tests for grain yield and some grain yield-related traits in AYB across the three environments were presented in Table 2. Scaling test A for the combined agro ecological environments shows that the traits are significantly different ($P < 0.01$) for the number of locules per pod, the number of peduncles per plant, the number of pods per peduncle, pod weight per plant, seed weight per plant, weight of 100 seeds and grain yield. Scaling test B indicated that four such as number of peduncles per plant, number of pods per plant, weight of 100 seeds, and grain yield were significantly different ($P < 0.01$). For scaling test C, the traits studied were not significant for the number of pods per plant, pod weight per plant, pod weight, and seed weight per plant whereas other traits were significant. Moreover, for scaling test D, all the traits were significant for all the studied traits except for seed weight per plant and weight of 100 seeds.

Table 2

Estimates of scaling test for grain yield and other related agronomic traits in six generations of AYB across the three environments

Traits (units)	Scaling test			
	A	B	C	D
LocPod^{-1}	-6.4 ±0.53**	-0.23 ±0.59	-4.17 ±1.05**	-1.23 ±0.42**
PedPl^{-1}	-1.89 ±0.25**	-2.02 ±0.29**	1.71 ±0.5**	2.81 ±0.21**
PodPed^{-1}	-1.39 ±0.08**	0.11 ±0.09	-0.42 ±0.16**	-0.43 ±0.06**
PodPl^{-1}	-1.22 ±0.89	-10.01 ±1.21**	0.83 ±1.90	-6.03 ±0.75**
PwPl^{-1} [g]	-30.74 ±4.38**	6.06 ±5.89	-5.14 ±9.33	-9.77 ±4.15**
PW [g]	0.07 ±0.12	0.21 ±0.21	-0.42 ±0.28	0.35 ±0.14*
SeedPod^{-1}	-0.02 ±0.40	-0.08 ±0.48	-4.52 ±0.84**	1.85 ±0.34**
SSP [%]	-0.03 ±0.42	-0.72 ±00.47	-4.53 ±0.83**	1.89 ±0.35**
SwPl^{-1} [g]	-17.68 ±6.31**	5.38 ±5.43	-3.6 ±9.78	-4.35 ±3.67
100SW [g]	2.97 ±0.68**	4.19 ±0.95**	6.96 ±1.35**	0.1 ±0.48
GY [kg hac^{-1}]	-150.02 ±15.90**	-674.7 ±4.22**	1302.52 ±86.31**	238.81 ±43.92**

*, ** Significant at $P < 0.05$ and $P < 0.01$ level of probability respectively

Explanations: locPod^{-1} – number of locules per pod; PedPl^{-1} – number of peduncles per plant; PodPed^{-1} – number of pods per peduncle; PodPl^{-1} – number of pods per plant; PwPl^{-1} – pod weight per plant; PW – pod weight; SeedPod^{-1} – number of seeds per pod; SSP – seed set percentage; SwPl^{-1} – seed weigh per plant; 100SW – 100-seed weight; GY – grain yield ha^{-1}.

Estimates of gene effects for grain yield and some grain yield-related traits in AYB

Table 3 shows the estimates of gene effects for grain yield and some grain yield-related traits across the three agro ecological environments. The mean and the additive gene effects were highly significant ($P < 0.01$) in all the studied traits. The result also revealed that the dominance gene effect was significant ($P < 0.01$) for the traits studied except for the number of seeds per pod, seed set percentage, and weight of 100 seeds. Additive x additive gene interaction was also significant for all the studied traits except for seed weight per plant and weight of 100 seeds. Additive x dominance interactions were not significant ($p > 0.05$) for the number of peduncles per plant, seed set percentage, seed weight per plant, and weight of 100 seeds. Furthermore, the dominance x dominance gene interaction was highly significant for all the studied traits except seed weight per plant.

Table 3

Estimates of gene effects for grain yield and other related agronomic traits in six generations of AYB across the three environments

Traits	Gene effects						
	m	*d*	*h*	*i*	*j*	*l*	epistasis type
LocPod^{-1}	22.74 ±0.18**	-0.17 ±0.21**	7.42 ±0.96**	2.46 ±0.84**	6.17 ±0.72**	-9.09 ±1.35**	D
PedPl^{-1}	9.71 ±0.08**	-1.09 ±0.12**	7.20 ±0.47**	5.62 ±0.43**	-0.13 ±0.33**	-9.53 ±0.70**	D
PodPed^{-1}	2.66 ±0.02**	0.05 ±0.03**	0.89 ±0.14**	0.86 ±0.12**	1.5 ±0.10	-2.14 ±0.21**	D
PodPl^{-1}	19.67 ±0.30**	-8.45 ±0.44**	13.20 ±1.62**	12.06 ±1.50**	-8.79 ±1.28**	-23.29 ±2.6**	D
PwPl^{-1} [g]	113.5 ±1.67**	-38.65 ±2.46**	46.37 ±8.62**	19.54 ±8.30*	36.8 ±6.40**	-44.22 ±13.58**	D
PW [g]	4.79 ±0.05**	-1.25 ±0.1**	2.07 ±0.30**	-0.7 ±0.29**	0.14 ±0.22**	0.98 ±0.48**	C
SeedPod^{-1}	17.85 ±0.15**	-3.51 ±0.17**	5.82 ±0.78	-3.7 ±0.69**	-0.78 ±0.57**	2.88 ±1.09**	C
SSP [%]	17.80 ±0.16**	3.47 ±0.18**	10.01 ±0.78	-3.78 ±0.70**	-0.7 ±0.58	3.04 ±1.11**	C
SwPl^{-1} [g]	94.79 ±1.45**	-35.83 ±2.25**	41.74 ±9.31**	8.7 ±7.35	23.06 ±7.53	-21 ±13.29**	D
100SW [g]	22.96 ±0.17**	-2.76 ±0.33**	8.9 ±1.09	-0.2 ±0.97	1.22 ±0.98	7.36 ±1.91**	C
GY [kg hac^{-1}]	1460.69 ±21.57**	-581.67 ±8.19**	592.10 ±87.85**	477.62 ±84.43**	524.5 ±16.33**	-347.28 ±92.33**	D

*, ** Significant at $P < 0.05$ and $P < 0.01$ level of probability respectively

Explanations: locPod^{-1} – number of locules per pod; PedPl^{-1} – number of peduncles per plant; PodPed^{-1} – number of pods per peduncle; PodPl^{-1} – number of pods per plant; PwPl^{-1} – pod weight per plant; PW– pod weight; SeedPod^{-1} – number of seeds per pod; SSP – seed set percentage; SwPl^{-1} – seed weigh per plant; 100SW – 100-seed weight; GY – grain yield/ha^{-1}; *m* – mid point; *d* – additive effect; *h* – dominance effect; *i* – additive X additive gene interaction; *j* – additive X dominance gene interaction; *l* – dominance X dominance gene Interaction; D – duplicate type of epistasis; C – complementary type of epistasis

Estimates of components of variance and other allied genetic parameters for grain yield and grain yield-related traits in AYB

Estimates of components of variance and other allied genetic parameters for grain yield and grain yield-related traits in AYB across the three agro ecological environments are shown in Table 4. The values observed due to environmental variance were less than values obtained from additive and dominance variances in grain yield attributes. Environmental, additive, and dominance variances had the same value (0.01) for the number of pods per peduncle. The weight of 100 seeds were 0.24, 0.16, and 1.17 g for environmental, additive, and dominance genetic variances, respectively. This indicated that the value for environmental variances is greater than additive variance but less than dominance variance for this trait. A similar trend was observed in all the studied traits except for the number of pods per peduncle and grain yield. Pod weight recorded the same value (0.01) for environmental and additive variances. The result indicated that dominance genetic variance was higher than the additive genetic variance in all the studied traits.

Table 4

Genetic parameters for grain yield and other related agronomic traits in six generations of AYB across the three environments

Traits	σ^2E	σ^2D	σ^2H	DD	σ^2P	σ^2G	Hns [%]	Hbs [%]
100SW [g]	0.24	0.16	1.17	2.64	1.58	1.34	10.68	84.83
LocPod^{-1}	0.13	0.02	0.45	4.39	0.61	0.48	3.84	77.97
PedPl^{-1}	0.02	0.01	0.08	2.53	0.12	0.10	10.97	81.42
PodPed^{-1}	0.01	0.01	0.01	2.89	0.01	0.01	8.68	81.54
PodPl^{-1}	0.39	0.20	1.61	2.78	2.22	1.82	9.40	8229
PwPl^{-1} [g]	7.72	6.57	32.90	2.23	47.20	39.47	13.92	82.62
PW [g]	0.01	0.01	0.03	1.62	0.05	0.05	24.90	90.59
SeedPod^{-1}	0.08	0.01	0.26	4.11	0.35	0.27	4.32	77.57
SSP [%]	0.09	0.02	0.27	3.55	0.37	0.29	5.77	78.69
SwPl^{-1} [g]	14.28	5.91	60.52	3.19	80.72	66.43	14.80	82.29
GY [kg hac^{-1}]	0.54	796.56	1592.05	1.13	2389.16	2388.62	0.33	99.97

Explanations: locPod^{-1} – number of locules per pod; PedPl^{-1} – number of peduncles per plant; PodPed^{-1} – number of pods per peduncle; PodPl^{-1} – number of pods per plant; PwPl^{-1} – pod weight per plant; PW – Pod weight; seedPod^{-1} – number of seeds per pod; SSP– seed set percentage; SwPl^{-1} – seed weigh per plant; 100SW – 100-seed weight; GY – grain yield/ha^{-1}; σ^2E – environmental variance; σ^2D – additive variance; σ^2H – dominance variance; DD – degree of dominance; σ^2P – phenotypic variance; σ^2G – genotypic variance; Hns [%] – narrow sense heritability in percentage; Hbs [%] – broad sense heritability in percentage.

Discussion

The estimate of the degree of dominance shows that none of the studied trait's values is less than 1. Grain yield recorded the highest value for phenotypic and genotypic variances. Furthermore, the variation observed for narrow sense heritability ranged from 3.84% for the number of locules per pod to 33.00% for grain yield. A range of 77.57 (number of locules per pod) to 90.59% (pod weight) was observed for broad-sense heritability.

The levels of significance observed in A, B, C, and D scaling tests show the presence of non-allelic interactions in the studied traits (SHARMA 1988). This reveals that epistatic digenic interaction contributed to the inheritance of all the studied traits. The scaling test results revealed that the additive-dominance model is insufficient for describing the mode of inheritance for grain yield and other studied traits in AYB. Most of the traits of interest to plant breeders show polygenic inheritance (ACQAACH 2012). This implied that the inheritance of these studied traits is complex and polygenic in nature (SHAHROLIN et al. 2013). This finding suggests that epistasis should be considered when proposing a successful improvement programme for all these traits in AYB. This finding is in conformation with the result of GUPTA et al (2017) for different traits in cowpea and grain yield in soybean by ABOU-SEN (2020).

The estimated mean (*m*) reveals the contribution owing to the overall mean coupled with locus effects and interaction of fixed loci. The level of significance in mean (*m*) values for grain yield and other studied traits across the three agro ecological environments is an indication that the traits were inherited quantitatively. JAGTAP (1986) reported that whenever the additive effects are more than the non-additive effects, it is suggested that selection would be effective in early segregation generation. On the other hand, if the non-additive effect is more than the additive portion, improvement of the traits involves selection through later generations. The results in this study revealed that dominance gene effects were larger than additive gene effects in some traits including grain yield in some environment(s) while additive gene effects were higher for some traits as well. This is an indication that both dominance and additive genes are important in the inheritance of these studied traits. Moreover, the estimates of dominance [*h*] effects that were significant for grain yield and in more than 90% of the studied traits across the three agroecological environments showed the importance of dominance gene action. The significance of both additive [*d*] and dominance [*h*] gene action in the inheritance of grain yield and some other studied traits across the three agroecological environments is an indication that both additive and dominance effects are essential in the genetics of these traits.

The type of epistasis in existence is determined by the dominance [*h*] effect and dominance x dominance [*l*] gene interaction effects. When the dominance [*h*] effect and dominance x dominance [*l*] gene interaction effects were in the opposite direction, a duplicate type of epistasis is said to be in existence. If the dominance [*h*] effect and dominance x dominance gene interaction effects were in the same direction, a complementary type of epistasis is involved (SHAMA 1988, SAID 2014, MISTRY et al. 2016). The different types of epistasis observed in grain yield and other studied traits could be because of environmental factors such as temperature, soil factors, relative humidity, water and wind. Complementary epistasis type was observed in pod weight, number of seeds per pod, seed set percentage, and weight of 100 seeds while other studied traits displayed duplicative epistasis. A duplicative type of epistasis hinders trait improvement through selection, thus high magnitude of dominance [*h*] and dominance x dominance [l] gene interaction effects would not be expected (MISTRY et al. 2016). Bi-parental mating is suggested for duplicate types of epistasis. Likewise in the presence of complementary type epistasis, improvement can be made through selection in F_3 onward (THAKARE et al. 2017).

There is preponderance of dominance variances in all the studied traits across the three agro ecological environments. Therefore, breeding for these traits should be based on hybridization (SAID 2014). The environmental variance values were lower than genotypic variance values in all the studied traits. This suggests that the inheritance of these traits is more determined by genetic factors rather than environmental factors, hence selection would be the best breeding approach to improve these studied traits (BARAKAT 1996, ALPHONSU et al. 2011, OYIGA and UGURU 2011). The number of pods per peduncle had the least environmental variance while seed weight per plant had the highest environmental variance although still lower compare to genetic variances. This suggests that environmental factors have a greater influence on seed weight per plant than every other studied trait. This shows that post-flowering environmental factors might influence grain filling.

When the degree of dominance equal to 0, it indicated that dominant gene action is totally absence. When the degree of dominance is equal to unity (1), this shows that complete dominance genetic action is in control. However, if it is greater than 0 but lesser than 1, it shows that partial dominance action is in existence. Moreover, whenever the degree of dominance is greater than 1, over-dominant genetic action is in existence (ELIA et al 1997, AGBOWURO 2016). In this study, the degree of dominance values was greater than unity (1) in all the studied traits in the combined environment. This shows the presence of over-dominance gene action in the inheritance of the studied traits. Therefore, early selection of these traits must be avoided. The selection should be delayed to the third or fourth generation to give room to the loss of non-additive genetic variance. After a series of inbreeding, the additive genetic variance can be estimated (SAID 2014).

The heritability percentage obtained for all the study traits in this study is greater than 60%. This indicated that reasonable progress can be made in improving these traits through selection. Similar findings were reported in Cowpea by SAID (2014). Narrow sense heritability in percentage was low for all the studied traits ranged from 0.33 for grain yield to 24.90 for pod weight according to ROBINSON et al. (1955) classification. Low narrow sense heritability in the study could be because of large epistatic effects. This was also buttressed by the findings of HAKIZINMANA et al. (2004). The differences observed between narrow and broad sense heritability reveals the contribution of non-additive effects (dominance and/ or epistasis) in the genetic makeup of the studied traits. Heritability for self-pollinated crops l is not important as narrow-sense heritability which is measured by additive variance directly. The differences recorded between the genotypes for the studied traits show that selection could be effective for making improvements in grain yield. This therefore implied that both additive and non-additive genetic actions are vital for improving grain yield in AYB.

Conclusion

The level of significance observed in scaling tests A, B, C, and D for grain yield and related grain yield traits studied in AYB reveals the presence of epistasis. This shows that epistasis should be considered when proposing a successful improvement programme for all these traits in AYB. The significance of both additive [*d*] and dominance [*h*] in the inheritance of the studied traits is an indication that both additive and dominance effects are essential in the genetics of these traits. The existence of the duplicative type of epistasis was exposed in some traits while complementary epistasis type was revealed in some other traits as well. Broad sense heritability values are higher is greater than narrow sense heritability in all the studied traits. Low narrow sense heritability values recorded for the studied traits are an indication that the non-additive gene is in control while high broad sense heritability shows that these traits are governed by additive genes with large heritable variance. Hence, recurrent reciprocal selection method should be adopted.

Accepted for print 15.05.2024

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