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Full Length Research Paper

Segregation of selected agronomic traits in six S_1 cassava families

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Inbreeding of predominantly cross-pollinating crops is expected to result in the generation of progeny with reduced fitness and/or progeny with improved phenotypes. However, this effect is not well documented in cassava (*MANIHOT ESCULENTA* Crantz). In this study, S_1 progeny from six cassava genotypes (I92/00067, TMS 30572, 95/SE-00036, NASE 4, MH95/0469 and Bamunanika) were examined for five traits: fresh root yield (FRY), fresh foliage yield (FFY), harvest index (HI), root dry matter content (DMC) and amylose content in order to study the effects of inbreeding on these traits. Considerable variations were observed among S_1 progeny for FRY (0.0 - 4.3 kg plant^{-1}); FFY (0.2 to 10.2 kg plant^{-1}); HI (0.00 - 0.69); DMC (11.0 - 42%) and amylose content (11.8 to 34.2%). Moreover, in each trait, individual S_1 clones existed that substantially outperformed the non-inbred parents. This was particularly true for amylose content where individual S_1 clones in each family had higher amylose content than their respective non-inbred parent. Nevertheless, with introduction of inbreeding an average reduction of 61, 33.8, 24.6 and 13.2% was observed for FRY, HI, FFY and DMC. These results demonstrate that with introduction of inbreeding in cassava, it is possible to generate improved phenotypes, which should be the focus of breeders.

Key words: Amylopectin content, cassava inbreeding, inbreeding depression, *Manihot esculenta*.

INTRODUCTION

Inbreeding, defined as the mating between individuals related by a shared ancestry, can occur in various forms (Falconer and Mackay, 1996). However, self-fertilisation in which two gametes (from the same individual) participate towards the formation of a new individual is the closest form of inbreeding (Altenburg, 1957; Begg, 1959). Inbreeding occurs naturally in self-pollinating plants, while in cross-pollinating plants self incompatibility mechanisms that take various forms, limit self-fertilisation (Glènmin et al., 2001). In cassava self-fertilisation is limited by the fact that cassava is monoecious with male and female flowers separated by both space and time (IITA, 1990). Female flowers are located on the base of the racemes whereas male flowers are at the top of the inflorescence. Moreover, female flowers generally open 10 to 14 days before male flowers. These mechanisms favor cross-pollination, particularly by insects. Because male and female flowers on different branches or on different plants of the same genotype can open simultaneously, self-pollination can occur (Jennings and Iglesias, 2002; Ceballos et al., 2004). Once inbreeding occurs in cross-pollinated species, it can lead to varying levels of inbreeding depression (loss in fitness), which has been observed in nearly all cross-pollinated species (Wricke and Weber, 1986). This decline in fitness is well illustrated by experiments in maize that were conducted since the early 1900s (Begg, 1959). Genetically, inbreeding depression (ID) is caused by increased expression of homozygous deleterious recessive genes, which are concealed from expression (or full expression) when in a heterozygous form (Begg, 1959). However, inbreeding also presents enormous benefits when advantageous recessive alleles are brought into the homozygous state. Indeed, most successful breeding

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programmes involve inbreeding during at least one stage of cultivar development. The pioneering work on hybrid maize, based on the use of inbred lines in the early 1900s, was a phenomenal initiative (East, 1908), which could be repeated in other cross-pollinated crops.

Cassava is an out-crossing, highly heterozygous plant that has not been subjected to intensive and systematic inbreeding to exploit its benefits, as has been done in maize. Nonetheless, it is encouraging to observe that interest in cassava inbreeding is beginning to gain momentum (Ceballos et al., 2004, 2007; Rojas et al., 2009). Certainly, it would be prudent in cassava to tap into the benefits of inbreeding as witnessed in maize.

Walsh (2005) observed that inbreeding provides an opportunity to exploit both additive and non-additive effects. The author demonstrated that under random mating a single diploid parent only contributes one allele per locus and hence cannot pass on its dominance component to its offspring. To exploit non-additive genetic effects, parents must contribute more than just their additive values, that is, they should pass on coordinated groups of alleles at different loci and/or whole genotypes at single or more loci, a phenomenon that will require that the parents be related (Walsh, 2005). Cassava inbreeding experiments conducted at the International Centre for Tropical Agriculture (CIAT) observed higher yields of some selfed families as compared to the parents, with inbreeding depression varying among families (Kawano et al., 1978). Waxy cassava starch was recently identified in an S_1 inbred clone (AM206-5) at CIAT (Ceballos et al., 2007). It is envisaged that inbreeding in cassava will provide several advantages including: 1) reduction of genetic load which limits attainment of sustainable genetic progress, 2) increased probability of increasing the expression of useful recessive traits and 3) facilitation of the implementation of mutation breeding (Ceballos et al., 2004). These benefits were a major motivation for this study. In this exploratory study, S_1 progeny from six cassava genotypes were examined for starch quality (amylose content) and four agronomic traits: fresh root yield (FRY), fresh foliage yield (FFY), harvest index (HI) and root dry matter content (DMC).

MATERIALS AND METHODS

Generation and field establishment of S_1 families

Six cassava genotypes (I92/00067, TMS 30572, 95/SE-00036, NASE 4, MH95/0469 and Bamunanika) were used as progenitors (S_0) to generate S_1 progeny. With the exception of Bamunanika which is a local variety, the rest are elite genotypes from the International Institute of Tropical Agriculture (IITA). For each genotype 20 stem cuttings were planted at isolation plots at a spacing of 1 m x 0.9 m. The isolation plots were separated by a distance of 100 m from any neighbouring cassava to ensure that only natural self-pollination occurs. A separation of 30 m has been reported to be efficient to ensure genetic isolation in cassava (Kawano et al., 1978). For each selfed genotype, mature fruits were carefully harvested, placed in labelled brown paper bags and left to shatter naturally. Harvested S_1 botanical seeds were not treated, but allowed a two month dormancy breakdown period before being established in nurseries. After two months in the nursery, S_1 seedlings were transplanted to a well-prepared field where they were grown until 10 months, after which they were cloned to generate at least 6 to 10 cuttings (middle section) per seedling. Each S_1 seedling (genotype) was represented by six plants, which were established in the field for evaluation. Because of the modest number of progeny per family (8 to 30), all progeny belonging to the same family, together with the parental genotype, were established in the same block. Each row represented a clone and spacing within rows was 1 m, with between row spacing of 1.5 m to minimise inter-plot interference. A variable number of S_1 seedlings were generated per family and these were evaluated at the National Crops Resources Research Institute (NaCRRI), Uganda, in 2008.

Field evaluations

At harvest, which coincided with 11 months after planting, four innermost plants per clone were uprooted and used for phenotypic assessments. Roots were separated from the vegetative harvestable biomass (leaves, stems and original planting stake) and independently weighed. FRY and FFY (kg plant^{-1}) were computed. HI was computed for each clone following the procedure outlined by Kawano (1990). Estimation of DMC in the root samples was based on the oven dry method. Briefly, collected roots were washed, peeled and chopped into 1 cm thick pieces to a total weight of 200 g (fresh weight). Samples were dried to constant weight in an oven that was maintained at 72°C. Upon attainment of constant weight (48 h), samples were immediately weighed (dry weight). Percentage DMC was computed by dividing the dry weight by the fresh weight and multiplying by 100.

Field evaluations were based on unreplicated single row plots. Unreplicated single-row trials have previously been used to evaluate quantitative traits in cassava (Kawano, 2003; Chávez et al., 2005), results of which have directly contributed to the genetic improvement of cassava. Lack of adequate good quality planting material is the justification for this tradeoff of having more genotypes being evaluated in unreplicated trials as opposed to having fewer genotypes evaluated in replicated trials. The ID phenotypically observed in some progeny significantly limited the number of individuals that generated sufficient and good quality planting material. This study's aim was to obtain initial insights into the effect of inbreeding on key agronomic traits of cassava in order to objectively define future cassava inbreeding activities and thus unreplicated single row field trials were established.

Extraction of starch and determination of amylose content from the S_1 cassava progeny

Harvested cassava roots were used for starch analysis. Each S_1 clone, including parents, was represented by two samples. Cassava starch extraction was carried out using the method described by Benesi (2005). This cassava starch extraction process is simple, rapid and upon settling, the starch is free from any colour, impurities and contamination from proteins or fats, and has been used in previous studies (Ceballos et al., 2007; Sánchez et al., 2009). Using a sensitive balance, 20 mg of the starch flour sample was accurately weighed and dissolved by heating in 1 M sodium hydroxide for 30 min in a water bath maintained at 95°C. When dissolved, this solution was diluted to a concentration of 5 mg ml^{-1} by addition of deionised water. Aliquots of this solution (0.1 ml) were diluted with 5 ml of trichloroacteic acid [0.5% (v/v) concentration] and 0.05 ml iodine solution (0.01 M). The contents were mixed and the absorbance of a sample of this solution was read at 620 nm using a spectrophotometer. Because of the lack of

Table 1. Variation in fresh root yield, fresh foliage yield and harvest index in S_1 cassava progeny

Family	Parent[a]	S_1[b]	Min[d]	Max[e]	Mean	Variance	Skewness	ID[f]
Fresh root yield (kg plant^{-1})								
MH95/0469	4.00	16	0.33	2.40	1.03	0.26	1.58	74.2
NASE 4	3.62	16	0.00	3.25	0.80	0.52	2.81	77.9
TMS 30572	0.89	23	0.00	2.00	0.67	0.26	0.84	24.7
I92/00067	4.75	18	0.33	3.25	1.40	0.68	0.67	70.5
Bamunanika	1.50	28	0.00	0.75	0.16	0.06	1.15	89.3
95/SE-00036	1.14	30	0.00	4.33	0.79	1.28	0.88	30.7
Fresh foliage yield (kg plant^{-1})								
MH95/0469	3.65	16	0.37	4.00	1.53	0.85	1.33	58.0
NASE 4	1.25	16	0.50	4.00	1.11	0.76	2.72	11.2
TMS 30572	2.00	23	0.43	4.33	1.78	1.01	1.04	11.0
I92/00067	3.02	18	0.85	5.55	2.60	1.38	0.74	13.9
Bamunanika	1.66	28	0.45	2.50	1.19	0.26	0.62	28.3
95/SE-00036	1.60	30	0.20	10.2	1.19	5.32	1.85	25.6
Harvest index								
MH95/0469	0.52	16 (5)[c]	0.14	0.66	0.40	0.017	-0.57	23.0
NASE 4	0.74	16 (5)	0.00	0.62	0.41	0.024	-1.11	44.5
TMS 30572	0.31	23 (0)	0.07	0.50	0.28	0.009	0.03	9.6
I92/00067	0.61	18 (2)	0.15	0.57	0.34	0.014	0.33	44.2
Bamunanika	0.48	28 (0)	0.00	0.35	0.11	0.016	0.96	77.0
95/SE-00036	0.42	30 (1)	0.00	0.69	0.40	0.027	-0.49	4.7

[a]Parent represents phenotypic values for respective non-inbreds (S_0 progenitors); [b]S_1 represents individuals evaluated; [c]numbers in parentheses indicate number of progeny with harvest index values > 0.5; [d]Min and [e]Max indicate minimum and maximum values, respectively; [f]inbreeding depression estimated as [(s_0 mean – s_1 mean)/s_0 mean] x 100.

purified cassava starch standards, inferences on amylose in the samples had to be made from a standard curve generated from purified potato starch that contained 100% amylose. Standard curves obtained from purified amylose and amylopectin extracted from potato tubers have previously been used to infer amylose content in cassava (Ceballos et al., 2007). In this study, purified amylose (100%) from potato was serially diluted and used to generate a standard curve for the estimation of the amylose content in the cassava starch samples. The standard curve was generated from different concentrations of amylose: 0, 10, 20, 30, 40, 50, 60, 70 and 80%, by diluting with trichloroacteic acid (0.5%; v/v). Absorbance readings were done as described above. Three readings were taken for each dilution and the mean used.

Data analysis

The number of progeny evaluated varied among families, making the data largely unbalanced. Summary statistics for the agronomic traits FRY, FFY, HI and DMC were computed for each family. For amylose content, the dataset was subjected to analysis of variance using the unbalanced treatment structure in Genstat. Further, linear mixed model analysis for the estimation of variance components using the restricted maximum likelihood (REML) method was done. For this analysis, replicates were considered as fixed, while families and S_1 progeny were considered as random factors. ID was estimated for FRY, FFY, HI and DMC as a percentage of the S_0 average. ID = [(s_0 mean – s_1 mean)/s_0 mean] x 100. Therefore, the lower the ID value, the lower the depression (Rojas et al., 2009).

RESULTS

Data on FRY, FFY and HI for the different S_1 progeny is presented in Table 1. For FRY, it was observed that some S_1 clones in the families TMS 30572 and 95/SE-00036 had FRY values that exceeded by up to 55% of their respective S_0 progenitors. However, in all families, the mean of the S_1 was lower than that of the non-inbred parents. On average lowest average FRY (0.16 kg plant^{-1}) was observed in Bamunanika family and highest (1.4 kg plant^{-1}) in I92/00067 family (Table 1). With exception of families TMS 30572 and 95/SE-00036, all other families had ID associated with FRY > 70% (Table 1). Data for FFY indicated that each of the evaluated families had some S_1 progeny whose values were greater than their S_0 progenitor; indeed, an individual in 95/SE-00036 family exceeded the parent by 84% in FFY (Table 1). In all families, the mean of the S_1 was however lower than that of the non-inbred parents. On average, lowest FFY (1.1 kg plant^{-1}) was observed in NASE 4 and highest (2.6 kg plant^{-1}) observed in family I92/00067. ID associated

Table 2. Variation in root dry matter content in S_1 cassava progeny generated from six parental genotypes.

Family	Parent[a]	S_1[b]	Min[d]	Max[e]	Mean	Variance	Skewness	ID[f]
MH95/0469	32.0	13 (4)[c]	24.0	38.0	31.3	20.2	0.20	2.1
NASE 4	35.0	8(0)	26.0	33.0	30.1	5.26	-0.39	14.0
TMS 30572	41.0	22(11)	20.0	43.0	35.1	32.9	-0.89	14.3
I92/00067	39.0	17 (2)	15.0	40.0	29.7	41.0	-0.96	23.8
Bamunanika	37.0	9(1)	18.0	38.0	28.5	32.5	-0.23	22.9
95/SE-00036	34.0	27(11)	11.0	42.0	33.3	42.8	-1.67	2.0

[a]Parent represents DMC values for respective non-inbreds (S_0 progenitors); [b]S_1 represents individuals evaluated; [c]numbers in parentheses indicate number of progeny with DMC > 35%; [d]Min and [e]Max indicate minimum and maximum DMC respectively. [f]inbreeding depression estimated as [(s_0 mean – s_1 mean)/s_0 mean] x 100.

Table 3. Analysis of variance for amylose content in S_1 cassava families.

Source of variation	Df[a]	SS[b]	MS[c]	Variance component
Replication	1	4.548	4.548	-
Family	5	527.814	105.563*	2.651 (2.196)[d]
Progeny	107	2707.260	25.301*	10.112 (1.772)
Residual	112	577.649	5.158	-

[a]Degrees of freedom; [b]sum of squares; [c]mean squares; [d] figures in parentheses are standard errors associated with the variance components; * P ≤ 5%.

with FFY ranged from 11% in TMS 30572 to 58% in MH95/0469 (Table 1). Both FRY and FFY data were positively skewed. Positive values indicate asymmetrical distributions, when there are a small proportion of unusually high values which result in the mean being higher than the median.

Data for HI indicated that some S_1 individuals in three (MH95/0469, TMS 30572 and 95/SE-00036) of the six families had HI values that exceeded the parental values in the range of 20 to 39% (Table 1). In all families, the mean of the S_1 was however lower than that of the non-inbred parents. The highest average HI (0.41) was observed in progeny derived from the parental genotype NASE 4, while the lowest (0.11) was observed in progeny derived from the parental genotype Bamunanika. Highest variability in HI as reflected by the variance was observed in progeny derived from parental genotype 95/SE-00036, which ranged from 0 to 0.69, while the lowest was observed in progeny derived from TMS 30572, which ranged from 0.07 to 0.50. Progeny derived from parental genotypes 95/SE-00036, NASE 4 and MH95/0469 were negatively skewed. Negative values indicate asymmetrical distributions, when there are a small proportion of unusually low values which result in the mean being less than the median. ID associated with HI ranged from 4.7% in 95/SE-00036 to 77.0% in Bamunanika (Table 1). Overall, highest ID was observed for FRY (61.2%; with Bamunanika being most affected); followed by HI (33.8%; with Bamunanika being most affected) and then FFY (24.6%; with MH95/0469 being most affected).

The data for root DMC of the S_1 progeny in the different families is presented in Table 2 Again, some S_1 individuals in five (MH95/0469, TMS 30572, I92/00067, Bamunanika and 95/SE-00036) of the six families had DMC values that exceeded their respective S_0 progenitors. As with HI, an individual in the 95/SE-00036 family exceeded the parent by a maximum amount of 19%. Again, in all families, the mean of the S_1 was however lower than that of the S_0 progenitors (Table 2).

The highest average DMC (35.1%) was observed in progeny derived from the parental genotype TMS30572, while the lowest average DMC (28.5%) was recorded for the progeny derived from parental genotype Bamunanika. With the exception of progeny from the parental genotype MH95/0469 that had positive skewness (0.20), all other parental genotypes had progeny data that were negatively skewed. The data further indicated (with the exception of S_1 progeny from TMS 30572) that over 60% of the progeny had DMC values less than 35%. ID associated with DMC varied between 2 to 23.8%; progeny of parental genotypes MH95/0469 and 95/SE-00036 had ID for DMC of only 2%. The analysis of variance data for amylose content in the S_1 cassava families is presented in Table 3. Amylose content varied significantly between cassava families and progeny, with most of the variation recorded within progeny. Some S_1 individuals in all of the six families had amylose content values that exceeded the non-inbred parent. Indeed, an individual in the TMS 30572 family exceeded the parent by a maximum amount of 46%. In five of the six families, the mean of the S_1 progeny was however higher than that of the S_0 progenitor (Table 4). The lowest amylose

Table 4. Variation in amylose content in six S_1 cassava families.

Family	Parent[a]	Progeny performance					
		S_1 No[b]	Min[c]	Max[d]	Mean	Variance	Skewness
MH95/0469	19.1	11	17.2	34.2	23.7	29.50	0.75
NASE 4	18.3	15	12.5	22.1	18.1	5.96	-0.53
TMS 30572	14.7	22	12.2	27.4	19.0	16.20	0.45
I92/00067	17.2	21	12.9	25.6	19.2	9.41	0.016
Bamunanika	19.1	16	14.7	26.0	20.2	12.50	0.088
95/SE-00036	16.2	22	11.8	22.8	18.2	10.19	-0.595

[a]Parent represents amylose content of non-inbreds (S_0 progenitors); [b]S_1 No represents number of S_1 individuals evaluated; [c]Min and [d]Max indicate minimum and maximum amylose respectively. The confidence interval associated with the data at 95% ranged from 1.35 to 3.65.

content (11.8%) was recorded in S_1 progeny from 95/SE-00036, while the highest (34.2%) was recorded from S_1 progeny from MH95/0469 (Table 4). With exception of progeny from parental genotype NASE 4 and 95/SE-00036, that had negative skewness, all other progeny had positive skewness for amylose content.

DISCUSSION

A major objective of this study was to determine whether gains could be made through inbreeding in cassava. Considerable variations were observed among S_1 progeny for FRY (0.0 to 4.3 kg plant^{-1}); FFY (0.2 to 10.2 kg plant^{-1}); HI (0.00 to 0.69); DMC (11.0 to 42%) and amylose content (11.8 to 34.2%). Moreover, in each trait examined, individual S_1 clones existed that substantially outperformed their S_0 progenitors. This was particularly true for amylose content where individual S_1 clones in each family had higher amylose content than their respective non-inbred parent. It is this variability that the breeder can harness. This indicates that genetic progress can be achieved through inbreeding for these agronomic traits depending on the breeding objective. Results indicated a general reduction in performance with inbreeding. On average, the mean performance of the S_1 progeny across all the six families for FRY, FFY, HI and DMC was lower than their respective non-inbred progenitors. Average reduction in FRY was 61.2 % (ranging from 24.7 to 89.3); for FFY, 24.6% (ranging from 11.0 to 58%); for HI, 33.8% (ranging from 4.7 to 77%); and for DMC, 13.2% (ranging from 2.0 to 23.8%).

These findings highlight that ID in cassava varies with families and the trait measured as depicted by the range, mean and skewness values of the data. Inbreeding of inherently heterozygous plants results in general loss of vigour, a phenomenon called ID, which is expected to be more severe in early than later generations because during the first inbreeding generation, 50% heterozygosity is lost (Altenburg, 1957; Wricke and Weber, 1986). ID could therefore explain the low phenotypic values obtained in the different families. The observed ID differences among the families could point to varying levels of genetic load in the S_0 progenitors, which appears to be highest in Bamunanika. Nonetheless, to benefit from inbreeding, individuals with higher values (FRY, FFY, HI and DMC) can be crossed among one another, followed by a second round of selfing and selection to further consolidate the fixation of advantageous alleles.

Rojas et al. (2009) estimated ID in cassava using eight families. The authors observed that average ID for FRY was 64% (ranging from 50.6 to 77.8%); for FFY, 37.9% (ranging from 16.4 to 56.5%); for HI, 26.5% (ranging from 16.6 to 43.0%); and 5.3% for DMC (ranging from 0.3 to 8.7%). The current study recorded a slightly higher average reduction for HI (33.8%), DMC (13.2%), and slightly lower values for FRY (61.2%) and FFY (24.6%), when compared to the previous study (Rojas et al., 2009). This could be because totally different germplasm that is, Latin American versus African are being compared and could thus have different levels of tolerance to inbreeding depression and/or genetic load. It is also possible that one of the studies overestimated and/or underestimated the ID estimates, as few families (<10) were compared. This can only be resolved by further detailed studies that compare different cassava populations. Nevertheless, the observation of some S_1 individuals that had higher values than their respective non-inbred parents could suggest that they did not succumb to ID and/or tolerated inbreeding. It is these individuals that the breeders must focus on.

Elsewhere, studies have indicated that although inbreeding does not cause change in gene frequencies, it changes genotypic frequencies in the offspring, which, once changed, affects breeding values and dominance deviations (Wricke and Weber, 1986). This phenomenon could partly explain the relatively high phenotypic values in some inbreds. Walsh (2005) observed that inbreeding provides an opportunity to partially exploit non-additive (dominance and epistatic) variance, that could further explain higher phenotypic values in some inbreds.

Studies conducted in maize established that variance of dominance deviations of inbred lines were 1.6 to 3.3 times higher than the variance of dominance deviations for non-inbred maize individuals for key productivity traits (Edwards and Lamkey, 2002). Moreover, significant specific combining ability that is indicative of dominance variance has been reported for FRY and HI, while significant general combining ability has been reported for DMC (Cach et al., 2006).

It's thus possible that the higher FRY and HI values in some of the S_1s could have resulted from non-additive gene effects, while for DMC, it's possible that increased additive gene effects accounted for the relatively higher values in some of these S_1 inbreds. This is further supported by the fact that additive variance among progeny in cross-pollinated crops increases with inbreeding because additive genetic variance is the major component of the total genetic variance (Hallauer, 1992). It's these outstanding S_1 cassava individuals that breeders must focus on. This is one of the few reports on variation of amylose content in selfed cassava. Our study revealed considerable variation both within and between inbreds, with most of the variation within inbreds (11.8 to 34.2%). Whether or not additive or non-additive gene effects were responsible for this increase in amylose content is unknown. This is an aspect that future studies can establish, as no studies to date have been conducted on the inheritance of amylose in cassava.

In parallel, it will be equally important to know the cause of the decrease in amylose content with inbreeding, as it cannot simply be ascribed to ID because it is not a fitness-related trait. In related studies con-ducted at CIAT that involved generation of several partial inbreds from different genotypes, one S_1 clone (AM206-5) had amylose-free starch, that was the first reported naturally occurring mutation in cassava (Ceballos et al., 2007). Other studies examining amylose content in non-inbred cassava observed 5.2 to 6.5% (Sánchez et al., 2009) and 17.1 to 24.9% (Sanni et al., 2008). Cassava starch with up to 28.8% (Zaidul et al., 2007) and 44% amylose (Aryee et al., 2006) have also been reported. Though these studies used different methodologies and genotypes, they all indicated considerable variation in amylose content in non-inbred cassava. In the present study that involved S_1 inbreds, no amylose-free cassava was identified. However, what is apparent is the high variability of amylose in the S_1s, which could be of benefit to the breeders to increase the competitiveness of cassava starch.

In conclusion, this study presented the first report on cassava inbreeding in Uganda, information of which will be important for the general cassava breeding community; the effects of inbreeding on key agronomic traits have for the first time been quantified on African germplasm. Of particular interest was the generation of vigorous S_1 progeny (with high phenotypic values), which appeared to have benefited from either additive or non-additive genetic effects or a combination of the two. It's these improved individuals that breeders should target.

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