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Genetic control of dry matter, starch and sugar content in sweetpotato

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ABSTRACT

Sweetpotato (*Ipomoea batatas* L. (Lam)) is a nutritious food security crop for most tropical households, but its utilisation is very low in Ghana compared to the other root and tuber crops due to lack of end-user-preferred cultivars. Knowledge on the genetic control of important traits such as dry matter, starch and sugar content of sweetpotato storage roots in a breeding population is critical for making breeding progress in developing sweetpotato varieties preferred by farmers and consumers. This study used diallel mating design to elucidate general combining ability and specific combining ability, to determine the gene action controlling storage root dry matter, starch and sugar content in sweetpotato and the heterotic potential of the traits to facilitate the crop's improvement for increased utilisation. A general model for estimating genetic effects, GEAN II, was used to analyse the data. Genetic variability was seen for dry matter, starch and sugar content of sweetpotato and much of this genetic variation was additive in nature. The study also revealed significant heterosis in sweetpotato which offers opportunity for breeding non-sweet, high dry matter sweetpotato varieties that are preferred by farmers and consumers in Ghana.

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Additive effect; breeding; GCA; genetic variability; heterosis; non-additive effect; SCA

Introduction

Sweetpotato (*Ipomoea batatas* L. (Lam)) is in the botanical family *Convolvulaceae*. It is the only crop plant of major economic importance for food among the approximately 50 genera and more than 1000 species of the family (Thottappilly 2009), which may be due to the Agrobacterium infection which occurred in evolutionary times of the crop (Kyndta et al. 2015). It is a nutritious food, low in fat and protein, but rich in carbohydrates (Betty 2010). The potential of sweetpotato in food security and global well-being has been well recognised (Van Hal 2000). It is a staple food for millions of people and the seventh most abundant crop globally after wheat, rice, maize, potato, barley and cassava (Bouvelle-Benjamin 2007). However, its utilisation is very low in Ghana compared to the other root and tuber crops such as cassava, yam and cocoyam. Consumers in Ghana prefer non-sweet sweetpotatoes with high dry matter content (Sam & Dapaah 2009; Baafi et al. 2015). Conversely, locally available clones have very sweet taste, which limit their consumption as a staple food (Missah & Kissiedu 1994). Recently introduced orange-fleshed varieties, which possess the vitamin A precursor to combat vitamin A deficiency at relatively cheaper cost, have low dry matter content that is not preferred. Lack of varieties with end-user-preferred traits has been the main reason for the low utilisation of sweetpotato in Ghana. There is a need to develop farmer- and consumer-preferred sweetpotato varieties to increase the crop's utilisation in Ghana.

Sweetpotato breeding until recently was exclusively based on estimates of heritability of the traits concerned (Jones et al. 1979; Jones & Dukes 1980; Jones 1986). Estimates of heritability indicate that superior parents tend to pass on desirable additive genes to their progeny (Rex 2002). The expected amount of superiority is realised in subsequent generations only if the genetic effects are additive (Miller et al. 1958). In cross-pollinating crops such as the sweetpotato, combinability, or the ability of a parent to pass on desirable genes to a hybrid progeny, is more important. Knowledge on the gene action influencing high dry matter, high starch and non-sweetness therefore becomes critical in sweetpotato improvement or cultivar development.

Mating designs that estimate general combining ability (GCA) and specific combining ability (SCA) of quantitative traits are important in breeding heterozygous crops (Hayman 1954a; Griffing 1956; Fry 2004). The North Carolina II (NCII) mating design has been used to study inheritance in sweetpotato (Gasura

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et al. 2008; Sseruwu 2012; Oduro 2013; Todd 2013), but the diallel mating design may provide more genetic information on a complex crop such as the sweetpotato. Diallels, in addition to estimating GCA and SCA variance components from a set of randomly chosen parental lines, can also be used to obtain estimates of genetic effects for a fixed set of parental lines from multiple environment experiments (Zhang & Kang 1997). Diallel cross is used for determining cumulative gene effects of breeding populations (Hayman 1954a, 1954b; Griffing 1956; Hayman 1957, 1958), and also provides information on heterosis. Heterosis provides a basis for the formation of genetic pools (Gardner 1982). The mode of inheritance for some production and utilisation constraints in sweetpotato has been studied using diallels (Elisa et al. 2000; Mihovilovich et al. 2000; Mwanga et al. 2002; Chiona 2009; Shumbusha et al. 2014).

Griffing (1956), Method 4 has been used for inheritance studies in sweetpotato (Elisa et al. 2000; Mwanga et al. 2002; Courtney et al. 2008; Chiona 2009; Shumbusha et al. 2014) but, Gardner and Eberhart (1966) proposed an alternative analysis (GEAN II) for diallel crosses from heterogeneous parents. GEAN II is useful in evaluating n varieties and their $n(n-1)/2$ F_1 crosses. Variation among entries (genotypes) is apportioned into entries (genotypes) and mid-parent heterosis (Gardner & Eberhart 1966; Hallauer & Miranda Fo 1988; Murray et al. 2003). Heterosis is further subdivided into variety heterosis which indicates GCA, average heterosis and specific heterosis which indicates SCA (Murray et al. 2003). This analysis assumes parents and crosses performance to be fixed effects and environments random effects (Harold et al. 2001). The approach fits parents and parent cross means, X_{ij} to the linear model $X_{\mathrm{ij}} = \mu_v + ½(V_i + V_j) + \sigma h_{\mathrm{ij}}$, where μ_v = mean effects of parents, V_{i} and V_{j} = estimates of variety effects for the ith and the jth parents, respectively; and h = estimate of heterosis effects when parent i is crossed to parent j ($\sigma = 0$ when $\mathrm{i} = \mathrm{j}$, and 1 when $\mathrm{i} \neq \mathrm{j}$). Heterosis effects only existing in crosses are further partitioned as $H_{\mathrm{ij}} = h + h_i + h_j + s_{\mathrm{ij}}$, where h = estimate of average heterosis; h_{i} and h_{j} = estimates of variety heterosis (expressed as deviation from h) and indicates GCA; and S_{ij} = estimate of specific heterosis (SCA) from crossing parents i and j. GEAN II has successfully been used for studying heterosis and estimating GCA and SCA in variety diallels of maize (Crossa et al. 1987; Ali et al. 2001; Harold et al. 2001; Lee et al. 2003).

Table 1. Genetic materials used and their characteristics.

Parents	Dry matter content (%)	Starch content (%)	Sugar content (%)
Apomuden	27.0	47.04	28.97
Beauregard	32.0	63.27	22.90
Histarch	45.0	72.70	10.43
Ogyefo	42.0	71.37	11.67

This study used diallel mating design to estimate GCA and SCA effects, to elucidate the gene action controlling storage root dry matter, starch and sugar content in sweetpotato and heterotic potential of the traits to facilitate the crop's improvement for increased utilisation.

Materials and methods

Experimental sites

A hybridisation block was established at the Crops Research Institute (CRI) of the Council for Scientific and Industrial Research (CSIR) at Fumesua in the minor cropping season in 2012. The F_1 progenies produced were evaluated at three locations spanning over three major agroecological zones of Ghana in the minor cropping season in 2013. These were the CSIR-CRI research station at Fumesua (forest ecozone), and the national agricultural research stations at Wenchi (transition ecozone) and Pokuase (coastal savanna ecozone). The mean annual rainfalls are 2200 mm (forest ecozone), 1300 mm (transition ecozone) and 800 mm (coastal savanna ecozone) (SRID [Statistics, Research and Information Directorate] 2001). The soils in the forest and transition ecozones are generally loamy and are distinguished from those of the savanna ecozones by the greater accumulation of organic matter (MoFA [Ministry of Food and Agriculture] 1998).

Genetic materials used

Crosses were made among four parent genotypes, two with low sugar, high dry matter and high starch content (Histarch and Ogyefo) and, two with high sugar, low dry matter and low starch content (Apomuden and Beauregard) (Table 1). Histarch and Ogyefo are white-fleshed varieties while Apomuden and Beauregard are orange-fleshed varieties. Progeny families and their respective number of seeds are shown in

Table 2. Progeny families and number of seeds used.

Parents	Histarch	Ogyefo	Apomuden	Beauregard
Histarch		30	30	22
Ogyefo	20		22	6
Apomuden	13	30		13
Beauregard	13	4	31	

Table 2. The seeds were germinated on moist filter paper in a Petri dish after sand paper scarification. Germinated seeds were then transplanted to prepared nursery pots in the screen house for the establishment of seedling nursery. Vine cuttings from each genotype were hardened and multiplied in the field after eight weeks in seedling nursery for the establishment of the trials.

Experimental layout

The four parents were crossed using the full diallel mating scheme. Sweetpotato is a highly heterozygous crop making each cross between two different parent plants genetically distinct such that variation in the F_1 is equivalent to an F_2 generation in a homogenous crop. Twelve families consisting of 234 F_1 progenies (123 crosses and 111 reciprocals) were raised in the seedling nursery but due to poor vigour of some genotypes, 196 F_1s (100 crosses and 96 reciprocals) were evaluated, alongside their parents, using alpha lattice design with two replications. All entries were planted on ridges of single-row plots with five plants per genotype at a planting distance of 0.3 m within row and 1 m between rows. Four node vines from the middle portion to the tip were used for planting. Genotypes within family were randomised to adjacent plots.

Data collection

Harvesting was done on whole plot at three and half months after planting and one large, one medium and one small, storage root were randomly selected for determination of dry matter, starch and sugar content. Storage roots selected were approximately 3 cm or more in diameter and without cracks, insect damage or rotten parts (Ekanayake et al. 1990). The storage roots were washed, peeled and cut into four equal parts longitudinally. Two opposite quarters of the peeled storage roots were sliced into pieces and 50 g fresh sample weighed into a polythene envelope. The fresh samples were frozen using deep-freezer after which it was freeze-dried for 72 hours using freeze-dryer. The dry weights of the freeze-dried samples were recorded. The freeze-dried samples were milled and the milled samples used for the determination of the starch and sugar content using the near-infrared reflectance spectroscopy (NIRS). Dry matter content was calculated as the ratio of the weight of dry sample to that of the fresh sample expressed as a percentage.

Data analysis

F_1 progenies with missing data were eliminated from the analysis. Data for 156 F_1 progenies (80 crosses and 76 reciprocals) out of the 196 and their 4 parents were used for the analyses. Analysis of Variance was first performed on data of all parents and their F_1-derived individuals using the approach of Buerstmayr et al. (2007) to determine the mean performance of parents and the F_1 progenies using Genstat (Genstat 2007). The mean performance of the F_1 progeny families was used for estimation of GCA and SCA employing the Gardner and Eberhart (1966) approach. The analysis was done using SAS 9.2 computer software (SAS 2002), based on the macros in DIALLEL-SAS05 (Zhang et al. 2005). Contrary to the Griffing's Model, Gardner and Eberhart (1966) analysis II works with condition if $I > J$, delete, so data for crosses and reciprocals were not analysed simultaneously (full diallel with parents) but separately (as Half diallel with parents).

Results

Performance of parents and F_1 progenies across three environments

The mean squares for dry matter, starch and sugar content across crosses and their reciprocals are shown in Table 3. The environment effects were significant ($p < .05$) for starch and sugar content and non-significant ($p > .05$) for dry matter content across crosses and reciprocals. The genotypes (entry) showed significant ($p < .01$) differences across the crosses and their reciprocals. The genotype by environment interaction (G × E) effects for all the traits were not significant ($p > .05$) across the crosses and only for dry matter and starch content across reciprocals. Both the overall heterosis and variety heterosis (GCA) were significant ($p < .01$) for all the traits across the crosses and their reciprocals. On the other hand average heterosis effects were significant ($p < .05$) only for starch content for the crosses, and starch and sugar content ($p < .01$) across the reciprocals.

SCA was significant ($p < .01$) for only starch and sugar content only for the reciprocals.

For dry matter content, Histarch and Ogyefo performed well as parents (43% and 40%) but Histarch did not differ significantly ($p > .05$) from the other parents in cross performance except Beauregard (Table 4). The poorest performing parent was Apomuden (26%). There were significant differences for the overall cross performance for starch content. Histarch and Ogyefo were the best performing parents (73%

Table 3. Mean squares for the four parents and their crosses across three environments.

		Crosses			Reciprocals		
Source of variation	Df	Dry matter content	Starch content	Sugar content	Dry matter content	Starch content	Sugar content
Environment (Env.)	2	0.0005^{ns}	37.50*	51.77**	0.0019^{ns}	43.69**	29.21**
Rep. (Env.)	3	0.0002^{ns}	2.19^{ns}	8.20^{ns}	0.0005^{ns}	3.37^{ns}	10.10**
Entry (genotypes)	9	0.0193**	408.02**	294.76**	0.0214**	426.35**	288.60**
Env. × Entry (genotype)	18	0.8000^{ns}	5.81^{ns}	8.61^{ns}	0.0005^{ns}	4.48^{ns}	6.40**
Overall heterosis (h_{ij})	5	0.0017*	107.11**	74.38**	0.0036**	158.11**	88.99**
Average heterosis (h)	1	0.0014^{ns}	41.85*	5.48^{ns}	0.0001^{ns}	75.05**	37.64**
Variety heterosis (h_j)	3	0.0032**	107.70**	132.78**	0.0049**	206.65**	113.12**
SCA	2	0.0014^{ns}	17.40^{ns}	13.453^{ns}	0.0015^{ns}	47.88**	34.01**

*$p < .05$.
**$p < .01$.
^{ns}Not significant.

and 71%). For sugar content, Ogyefo and Histarch had the lowest content among the parents (15% and 15%). They were also essentially the lowest in the overall crosses means (19% and 19%). Apomuden produced the highest sugar content (37%) among the parents. Significant differences were observed between some crosses and their reciprocals. These were Beauregard × Histarch and Histarch × Beauregard (dry matter content), Ogyefo × Beauregard and Beauregard × Ogyefo (starch content), and Beauregard × Histarch and Histarch × Beauregard (sugar content).

Estimates of variety effects, average heterosis and variety heterosis for dry matter, starch and sugar content

Variety effect (v_j) was significant for dry matter, starch and sugar content (Table 5). Variety effect (v_j) ranged from −0.09% (Apomuden) to 0.09% (Histarch) for dry matter content, from −17.75% (Apomuden) to 9.50% (Histarch) for starch content and from −7.58% (Ogyefo) to 14.77% (Apomuden) for sugar content. All parents had significant ($p < .01$) variety effects for all the traits except Beauregard which did not show significant ($p > .05$) variety effect for starch and sugar content. Variety heterosis (h_j) which indicates GCA was significant for all the traits (Table 5) with dry matter content ranging from −0.03 (Ogyefo) to 0.03 (Apomuden), starch content ranging from −4.79 (Beauregard) to 6.32 (Apomuden) and sugar content ranging from −4.81 (Apomuden) to 4.69 (Beauregard). Average heterosis was significant for all the traits except dry matter content (Table 5).

Better parent and mid-parent heterosis for dry matter, starch and sugar content over three environments

For dry matter content, better parent heterosis ranged from −26% for the crosses between Beauregard and Histarch to −5% for crosses between Ogyefo and Histarch

Table 4. Dry matter, starch and sugar content across parents and progeny families over three environments in Ghana during 2013 minor season.

	F_1 progeny family means					
Parents	Apomuden	Ogyefo	Beauregard	Histarch	Overall	Parental means
Dry matter content (%)						
Apomuden		33	28	36	39	26
Ogyefo	33		33	41	36	40
Beauregard	28	31		32	32	31
Histarch	38	40	40		38	43
Lsd (5%)					6	6
Starch content (%)						
Apomuden		66	57	66	64	45
Ogyefo	65		67	72	67	71
Beauregard	57	61		62	62	63
Histarch	69	71	70		68	73
Lsd (5%)					5	5
Sugar content (%)						
Apomuden		19	29	21	23	37
Ogyefo	20		19	15	19	15
Beauregard	28	23		25	24	22
Histarch	18	16	17		19	15
Lsd (5%)					4	4

$^{S}F_1$ means for crosses above diagonal.
F_1 means for reciprocals below diagonal.

Table 5. Estimates of variety effects, average heterosis and variety heterosis for dry matter, starch and sugar content in three environments in Ghana during 2013 minor season.

	Traits					
	Dry matter content (%)		Starch content (%)		Sugar content (%)	
Parents	Variety effects (v_j)	Variety heterosis (h_j)	Variety effects (v_j)	Variety heterosis (h_j)	Variety effects (v_j)	Variety heterosis (h_j)
Crosses						
Apomuden	−0.09**	0.03**	−17.75**	5.97**	14.77**	−4.81**
Ogyefo	0.05**	0.01^{ns}	8.18**	0.96^{ns}	−7.58**	−1.47^{ns}
Beauregard	−0.04**	−0.02**	0.08^{ns}	−4.79**	−0.42^{ns}	4.69**
Histarch	0.09**	−0.01^{ns}	9.50**	−2.13**	−6.77**	1.59^{ns}
Std. error	0.01	0.01	1.04	0.90	1.03	0.89
Average Heterosis		−0.01 ± 0.01^{ns}		1.71 ± 0.77*		−0.62 ± 0.76^{ns}
Reciprocals						
Apomuden	−0.09**	0.02**	−17.75**	6.32**	14.77**	−4.44**
Ogyefo	0.05**	−0.03**	8.18**	−3.87**	−7.58**	2.74**
Beauregard	−0.04**	−0.01^{ns}	0.08^{ns}	−4.35**	−0.42^{ns}	3.47**
Histarch	0.09**	0.02**	9.50**	1.90**	−6.77**	−1.77*
Std. error	0.01	0.01	0.88	0.76	0.79	0.68
Average Heterosis		0.02 ± 0.01^{ns}		2.28 ± 0.66**		−1.62 ± 0.59**

*$p < .05$.
**$p < .01$.
^{ns}Not significant.

(Table 6). Mid-parent heterosis ranged from −14% for crosses Beauregard × Histarch and Beauregard × Ogyefo to 9% for crosses Histarch × Apomuden. Specific heterosis (s_{ij}) which indicates SCA was significant ($p < .05$) for only crosses Ogyefo × Apomuden and Histarch × Beauregard. For starch content, better parent heterosis ranged from −15% for crosses Beauregard × Ogyefo and Beauregard × Histarch to −1% for crosses Ogyefo × Histarch while mid-parent heterosis ranged from −10% for crosses Beauregard × Ogyefo to 17% for crosses Histarch × Apomuden. Crosses Ogyefo × Apomuden, Beauregard × Apomuden, Apomuden × Histarch, Ogyefo × Beauregard, Histarch × Ogyefo and Histarch × Beauregard showed significant ($p < .05$) specific heterosis (SCA) for starch content (Table 6). For sugar content, better parent heterosis was computed based on the low sugar content parent (Table 6) and ranged from 3% for crosses Ogyefo × Histarch to 63% for crosses Beauregard × Histarch. Mid-parent heterosis for sugar content ranged from −29% for crosses Histarch × Apomuden to 35% for crosses Beauregard × Histarch. Specific heterosis (SCA) was significant ($p < .05$) for crosses Ogyefo × Apomuden, Beauregard × Apomuden, Histarch × Ogyefo and Histarch × Beauregard (Table 6). A list of F_1 progenies that showed superior performance are presented alongside their parents in Table 7. Their sugar content ranged from 12.93% to 14.88% and starch content from 71.37% to 75.57%, while their dry matter content ranged from 40% to 46%.

Discussion

Significant mean squares for both variety heterosis (GCA) and SCA for starch and sugar content (Table 3) indicated that additive and non-additive effects were involved in the expression of starch and sugar content. However, the SCA accounted for a less of the total sum of squares compared to the variety heterosis (GCA) for dry matter, starch and sugar content suggesting that additive effects were more important than non-additive effects for all the traits. This implies that most of the genetic variation observed were additive in nature and majority of the total sum of squares of the traits due to differences among generation performance could be explained by variety effects (v_j) and variety heterosis (GCA). Variety effects depend on the performance of parents (Harold et al. 2001), and it is the difference between the mean of a parent and the mean of all parents (Gardner 1967). Thus, variety effects for the parents were important predictors of the cross performance. This predominance of additive effects in determining dry matter, starch and sugar content suggest that there would be no complications in breeding these traits since the traits can be improved through selection. Oduro (2013)found additive effects more important than non-additive effects for dry matter, starch and sugar content on different sweetpotato genotypes. Similar results have been reported for dry matter content (Shumbusha et al. 2014), and other traits in sweetpotato (Mwanga et al. 2002; Gasura et al. 2008; Sseruwu 2012).

The significant ($p < 0.01$) differences between the genotypes (entries) (Table 3) demonstrate significant genetic diversity and indicate that meaningful selection and improvement on dry matter, starch and sugar content in sweetpotato is possible. In addition, the divergence indicates that parents selected for the study were very contrasting for dry matter, starch and

Table 6. Estimates of heterosis effects for dry matter, starch and sugar content over three environments.

	Trait								
	Dry matter content (%)			Starch content (%)			Sugar content (%)		
Cross	Better parent (h_{ij})	Mid-parent ($\hat{h}_{ij}$)	Specific heterosis (s_{ij})	Better parent (h_{ij})	Mid-parent ($\hat{h}_{ij}$)	Specific heterosis (s_{ij})	Better parent (h_{ij})	Mid-parent ($\hat{h}_{ij}$)	Specific heterosis (s_{ij})
Apomuden × Ogyefo	−18	0	−0.012^{ns}	−7	14	−0.82^{ns}	35	−24	0.69^{ns}
$^{\$}$Ogyefo × Apomuden	−18	0	0.013*	−8	12	2.24**	42	−20	−1.82**
Apomuden × Beauregard	−10	−3	0.009^{ns}	−10	4	−0.56^{ns}	34	−0.7	0.56^{ns}
$^{\$}$Beauregard × Apomuden	−10	−3	−0.007^{ns}	−10	5	−1.59**	30	−4	1.50**
Apomuden × Histarch	−16	3	0.003^{ns}	−9	12	1.38*	38	−19	−1.22^{ns}
$^{\$}$Histarch × Apomuden	−12	9	−0.006^{ns}	−5	17	−0.65^{ns}	22	−29	0.32^{ns}
Ogyefo × Beauregard	−18	−8	0.003^{ns}	−7	−1	1.38*	35	8	−1.22^{ns}
$^{\$}$Beauregard × Ogyefo	−23	−14	−0.006^{ns}	−15	−10	0.65^{ns}	59	27	0.32^{ns}
Ogyefo × Histarch	−5	−3	0.009^{ns}	−1	−0	−0.56^{ns}	3	0.2	0.53^{ns}
$^{\$}$Histarch × Ogyefo	−7	−5	−0.007^{ns}	−3	−2	−1.59**	9	6	1.50**
Beauregard × Histarch	−26	−14	−0.012^{ns}	−15	−9	−0.82^{ns}	63	35	0.69^{ns}
$^{\$}$Histarch × Beauregard	−7	8	0.013*	−4	3	2.24**	10	−9	−1.82**
Std. error (direct crosses)			0.01			0.69			0.68
Std. error (Reciprocal crosses)			0.01			0.57			0.53

$^{\$}$Reciprocals.
*$p < .05$.
**$p < .01$.
^{ns}Not significant.

sugar content. Significant differences have been reported for dry matter, starch and sugar content of different sweetpotato genotypes (Gasura et al. 2008). Studies conducted elsewhere have shown that substantial variation in flavour and sweetness exists in sweetpotato (Mclaurin & Kays 1992; Morrison et al. 1993) while sugar content in sweetpotato is reported to be cultivar-dependent (Ravindran et al. 1995; Aina et al. 2009). G × E interaction is important in evaluating genotype adaptation and development of genotypes with improved end-product quality (Ames et al. 1999). The non-existent of G × E for dry matter and starch content (Table 3) suggest that progress from selection for these traits can be realised since genotypic effects can be separated from environmental effects. Significant G × E for sugar content (Table 3) may complicate selection and breeding progress for sugar content. Oduro (2013) reported significant G × E for dry matter, starch and sugar content on 11 sweetpotato genotypes studied. The differences in this result and that of Oduro (2013) may be attributed to differences in sweetpotato genotypes used and the environments used for the evaluation. Significant differences were observed between some crosses and their reciprocals (Table 4). These were Beauregard × Histarch and Histarch × Beauregard (dry matter content), Ogyefo × Beauregard and Beauregard × Ogyefo (starch content), and Beauregard × Histarch and Histarch × Beauregard (sugar content). These differences may be attributed to maternal effects. Maternal effects are influences of parents on offspring phenotype occurring through pathways other than inherited DNA. If present, maternal effect could have increased the GCA mean squares at the expense of SCA. This has implications for the interpretation of the results and perhaps for several others that overwhelmingly concluded that additive gene action was predominant over non-additive effects for dry matter, starch and sugar content in sweetpotato. This agrees with Oduro (2013), who reported that maternal effects probably influenced the expression of dry matter, starch and sugar content in sweetpotato. Maternal effects have been reported to influence a number of traits in sweetpotato (Lin et al. 2007; Chiona 2009).

The high values of the variety heterosis (h_j) (GCA) of Apomuden for dry matter and starch content, and Beauregard for sugar content (Table 5) indicate that

Table 7. List of F_1 progenies that showed heterosis over three environments.

F_1 progeny	Dry matter content (%)	Starch content (%)	Sugar Content (%)
Histarch × Apomuden-11	44	75.57	12.93
Ogyefo × Histarch-14	46	74.48	13.01
Histarch × Beauregard-14	42	71.37	13.45
Histarch × Beauregard-10	40	72.81	13.66
Ogyefo × Histarch-3	42	73.58	13.78
Histarch × Ogyefo-34	43	72.77	13.83
Histarch × Ogyefo-24	41	72.57	13.86
Histarch × Apomuden-1	40	73.96	14.10
Histarch × Ogyefo-4	42	72.59	14.28
Ogyefo × Apomuden-16	40	72.91	14.36
Ogyefo	39	71.37	14.36
Ogyefo × Histarch-9	45	72.24	14.39
Ogyefo × Histarch-20	41	72.45	14.67
Histarch × Beauregard-2	41	71.43	14.73
Histarch × Ogyefo-30	41	72.31	14.88
Histarch	43	72.70	15.17
Beauregard	31	63.27	21.51
Apomuden	26	45.44	36.71
*SEM ($p < .05$)	2.00	2.03	1.79
CV (%)	8.7	5.7	15.9

*SEM = Standard error of mean.

these varieties had high GCA for the respective traits. High variety heterosis (h_j) (GCA) indicates differences in frequencies of dominant alleles between them and the other parents (Crossa et al. 1987). The negative values obtained for the variety heterosis (h_{ij}) (GCA) (Table 5) may be attributed to unrealised performance expectation of the parents in the F_1 progenies. Negative values of variety heterosis for breeding varieties/population seem to represent an unfulfilling performance expectations due to a high variety effects (v_j) and a high average heterosis effect (h) (Harold et al. 2001). Apomuden and Beauregard had the highest sugar content as reflected by their positive values for variety effects (v_j) (Table 5). Ogyefo and Histarch had the highest dry matter and starch content and this is also reflected by their positive values for variety effects (v_j). This indicates that Ogyefo and Histarch contributed positively to increase dry matter and starch content, and decreased sugar content in the F_1 progenies. Apomuden and Beauregard on the other hand contributed to increase sugar content in the F_1 progenies. Significance of the overall heterosis (Table 3) indicates some opportunity for exploitation of heterosis for breeding non-sweet, high dry matter sweetpotato varieties that are preferred by farmers and consumers in Ghana. Heterosis for dry matter, starch and sugar content is present in sweetpotato progenies between certain varieties (Grüneberg et al. 2009; Baafi et al. 2016). In this study, only reciprocal crosses Ogyefo × Apomuden and Histarch × Beauregard showed significant specific heterosis for dry matter, starch and sugar content (Table 6). It thus also suggests that heterosis for dry matter, starch and sugar content is present in sweetpotato progenies between not just certain varieties but more specifically for specific crosses. This shows the advantage of full diallel mating design over the others in sweetpotato breeding. Crosses Ogyefo × Apomuden and Histarch × Beauregard produced progenies Ogyefo × Apomuden-16 and Histarch × Beauregard-14, respectively (Table 7). Ogyefo × Apomuden-16 had dry matter, starch and sugar content of 40%, 72.91% and 14.36% while its parents Ogyefo and Apomuden had dry matter, starch and sugar content of 39%, 71.37%, and 14.36%, and 26%, 45.44% and 36.71%, respectively (Table 7). Histarch × Beauregard-14 had dry matter, starch and sugar content of 46%, 74.48%, and 13.01% compared to its parents Histarch (dry matter 43%, starch 72.70%, and sugar content 15.17%) and Beauregard (dry matter 31%, starch 63.27%, and 21.51%). These progenies showed superior performance over their parents for dry matter, starch and sugar content except Ogyefo × Apomuden-16 which showed similar performance in sugar content as Ogyefo. Sweetpotato progenies with superior performance were reported by Baafi et al. (2016). While those superior progenies were obtained from non-contrasting parents (high dry matter, high starch and low sugar parents), superior progenies obtained in this study were from contrasting parents. Histarch and Ogyefo are low sugar, high dry matter, and high starch content genotypes while Apomuden and Beauregard are high sugar, low dry matter and low starch content genotypes (Table 1). This indicates that it is possible to breed non-sweet, high dry matter sweetpotato varieties that have good utilisation qualities from contrasting parental genotypes also through exploitation of heterosis. This means that the parents used in this study can be inter-crossed to develop elite genotypes with sufficient genetic variation for breeding non-sweet, high dry matter sweetpotato varieties that have very good cooking quality for increased utilisation of the crop in Ghana.

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No potential conflict of interest was reported by the authors.

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