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Genetic Control of Beta-carotene, Iron and Zinc Content in Sweetpotato

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Abstract

Micronutrients deficiency is a major contributor to poor health in developing countries. It can be alleviated by biofortification or enrichment of staple crops with micronutrients. Sweetpotato is a major staple crop in numerous tropical countries and is naturally biofortified. In spite of extensive promotion of orange-fleshed sweetpotato varieties (OFSPs), they are poorly utilized as staple food in most parts of West Africa because of their low dry matter and high sugar content. Beta-carotene is positively correlated with iron and zinc content in sweetpotato. Development of sweetpotato cultivars with end-user preferred traits and higher content of beta-carotene, iron and zinc will alleviate their deficiencies. Knowledge on the genetic control of these traits is critical for their improvement in sweetpotato. This study used diallel mating design to estimate general combining ability (GCA) and specific combining ability (SCA) of storage root beta-carotene, iron and zinc content to determine the genetic control of these traits for sweetpotato breeding. A general model for estimating genetic effect, Gardner and Eberhart analysis II (GEAN II), was used for data analysis. Genetic variability for the traits indicated that they were mostly controlled by additive gene effect. Significant heterosis was found indicating that levels of these micronutrients can be improved in sweetpotato through breeding.

Keywords: beta-carotene content, genetic control, iron content, sweetpotato, zinc content

1. Introduction

Micronutrients are vitamins and minerals required in small amounts that are essential to human health, development, and growth. They include folic acid, iodine, iron, vitamin A and zinc. They play a central role in metabolism and maintenance of tissue function (Shenkin, 2006). Micronutrient deficiencies are a chronic deprivation of these nutrients and constitute a huge public health problem, adversely affecting a third of the world's population (Darnton-Hill et al., 2005; Simon et al., 2013). Nearly 100 million preschool children in the world suffer from vitamin A deficiency (WHO, 2009). Thousands of death of children under five years worldwide are attributed to vitamin A deficiency (Feyrer, Politi, & Wei, 2013), while anemia, which is caused by inadequate intake of iron, affects 1.6 billion people around the globe (De Benoist, Erin, Ines, & Mary, 2008; WHO, 2013). Severe and extensive deficiencies also prevail for zinc (Black et al., 2008). Micronutrients deficiency can be alleviated in several ways including dietary diversification, fortification, supplementation and biofortification (Kumah, 2013). Among these different ways, biofortification which is the genetic enhancement of edible parts of plants with micronutrient concentration is the safest and the most cost effective. Biofortification can be achieved by breeding for farmer and consumer preferred cultivars that have adequate amount of micronutrients.

Sweetpotato (*Ipomoea batatas* (L) Lam) is an important root crop, particularly in the tropical countries such as Uganda, Rwanda and Burundi in Eastern Africa and in Papua New Guinea where annual per capita fresh roots consumption is over 150 kg (Lebot, 2009; Lebot, 2010; Warammboi, Dennien, Gidley, & Sopade, 2011). Sweetpotato is rich in minerals and vitamins (Ray, & Tomlins, 2010), making it a naturally biofortified crop. Improving beta-carotene, iron and zinc content in sweetpotato cultivars with traits preferred by farmers and consumers will go a long way to alleviate these micronutrients deficiency. Sweetpotato breeding objectives, until

recently were exclusively based on heritability of traits (Jones, 1986; Jones, & Dukes, 1980; Jones, Schalk, & Dukes, 1979). But, High estimates of heritability indicate that superior parents tend to produce the best progenies (Rex, 2002), and only additive component of inheritance can be estimated accurately. Therefore, the expected amount of genetic gain realized in subsequent generations of breeding will be obtained only if all the genetic effects are additive (Miller, Williams, Robinson, & Comstock, 1958). In a heterozygous crop like the sweetpotato, non-additive effects are also important and heritability is a poor estimate of non-additive effect. Studies of inheritance in sweetpotato are complicated by its highly heterozygous hexaploid nature and complex segregation ratios. However, because of its ability to be vegetatively propagated, its genetic variation can be partitioned into general combining ability (GCA) and specific combining ability (SCA) using crosses of heterozygous varieties. For this reason, inference can be made on the gene action controlling a given trait based on the relative estimates of GCA and SCA.

North Carolina II (NCII) mating design has been used for trait inheritance studies in sweetpotato (Gasura, Mashingaidze, & Mukasa, 2008; Oduro, 2013; Sseruwu, 2012; Todd, 2013). The gene action controlling production and utilization constraints in sweetpotato has also been studied using diallel mating design (Chiona, 2009; Elisa, Humberto, & Luis, 2000; Mihovilovich, Mendoza, & Salazar, 2000; Mwanga, Yencho, & Moyer, 2002; Shumbusha et al., 2014). The diallel mating design provides more genetic information on a complex crop like sweetpotato. Diallel design in addition to estimating GCA and SCA variance components can also be used to determine cumulative gene effect of breeding populations (Griffing, 1956; Hayman, 1954a, 1954b; Hayman, 1957; Hayman, 1958). Furthermore, it provides information on heterosis effect, which provides a basis for the development of heterotic groups (Gardner, 1982). The objective of this study was to determine the inheritance of storage root beta-carotene, iron and zinc content in sweetpotato for breeding farmer and consumer preferred cultivars that have high amount of these micronutrients to curb their deficiencies.

2. Materials and Methods

2.1 Experimental Sites

Hybridization block was established at the Crops Research Institute of the Council for Scientific and Industrial Research (CSIR-CRI) at Fumesua in the Ashanti region of Ghana in the minor cropping season in 2012. The F_1 progenies produced were evaluated at three locations spanning over three ecozones of Ghana in the minor cropping season in 2013. These were the CSIR-CRI research station at Fumesua in the Ashanti region (forest ecozone), and the National Agricultural Research Stations at Wenchi in the Brong Ahafo region (transition ecozone) and Pokuase in the Greater Accra region (coastal savanna ecozone).

2.2 Genetic Materials Used

Crosses among four parental genotypes, two with low beta-carotene, relatively low iron and low zinc content (Histarch and Ogyefo), and the other two with high beta-carotene, relatively high iron and high zinc content (Apomuden and Beauregard) were made. The parents were three released varieties (Apomuden, Histarch and Ogyefo), and one breeding line (Beauregard) (Table 1). Histarch and Ogyefo are white-fleshed varieties while Apomuden and Beauregard are orange-fleshed. Progeny families and their respective number of seeds are presented in Table 2. The seeds were germinated on moist filter paper in a Petri dish after sand paper scarification, followed by transplanting unto prepared nursery pots in a 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.

2.3 Experimental Layout

The four parental genotypes were crossed using full diallel mating design. Sweetpotato is a highly heterozygous crop which makes each cross between two different parent plants genetically distinct cross and that the variation in the F_1 families produced is equivalent to an F_2 generation in homogenous crop. Twelve families comprising 234 F_1 progenies (123 crosses and 111 reciprocals) (Table 2) were raised in the seedling nursery but due to poor vigour of some genotypes, 196 F_1 progenies out of the 234 were evaluated alongside their parents at the three locations above using an alpha lattice design with two replications. All entries were planted in a single row on ridges at five plants per genotype at spacing of 0.3 m within row and 1m between rows. Four node vines from the middle portion to the tip were used for planting. Genotypes within family were randomised to adjacent plots.

Table 1. Genotypes used in the study and their storage root attributes

Parent	Origin/Status	β-carotene content (mg/100g)DW	Iron content (mg/100g)DW	Zinc content (mg/100g)DW	Storage root Yield (t/ha)	Storage root flesh colour
Apomuden	Release (2005)	33.67	2.56	1.53	19.7	Deep/dark orange
Beauregard	Introduction	24.31	2.12	1.13	37.5	Intermediate orange
Histarch	Release (2005)	9.85	1.49	0.86	24.4	white
Ogyefo	Release (2005)	6.83	1.69	1.01	15.4	White

Table 2. Progeny families and number of seeds per family used

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

[S]F_1 families obtained from crosses above diagonal; F_1 progenies obtained from reciprocals below diagonal.

2.4 Data Collection

Harvesting was done at three and half months after planting on whole plot and one large, one medium and one small storage root were randomly selected for determination of beta-carotene, iron and zinc content. Storage roots selected were 3 cm or more in diameter and without cracks, insect damage or rotten parts (Ekanayake, Malagamba, & Midmore, 1990). The storage roots were washed, peeled and cut into four equal parts longitudinally. Two opposite quarters of the peeled storage roots were selected, sliced into pieces and 50g fresh sample weighed into a polythene envelope. The fresh samples were frozen using deep-freezer and freeze-dried for 72 hours using freeze-dryer. The freeze-dried samples were milled and the milled samples used for the determination of beta-carotene, iron and zinc content using the near-infrared reflectance spectroscopy (NIRS) (Tumwegamire et al., 2011). About 3g of milled sample was placed in a cuvette and placed in a NIRS monochromator model XDS (NIRSystems, Inc., Silver Springs, MD, USA) for scanning and their spectra collected between 400 and 2498nm. Each sample was scanned twice. The average spectrum of each sample was stored and the NIRS results (beta-carotene, iron and zinc content) in an Excel format obtained from computer connected to the NIRS.

2.5 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 four parents were used for the analyses. Analysis of Variance (ANOVA) was first performed on data of all parents and their F_1 derived individuals using the approach of Buerstmayr, Nicola, Uwe, Heinrich and Elisabeth (2007) to determine the mean performance of parents and F_1 progenies. The average cross performance was used to elucidate GCA and SCA using the approach of Gardner and Eberhart (1966) analysis II (GEAN II). Average cross or family performance was obtained as average value from the respective F_1 progenies mean performance. GEAN II is a method of analysing diallel crosses data from heterogeneous parents/populations ("varieties"). This method assumes parents and crosses performance to be fixed effect and environments random effect (Harold, Hugo, Kevin, & Magnie, 2001). The method fit parents and parent cross means, X_{ij} to the linear model $X_{ij} = \mu_v + ½(V_i + V_j) + \sigma h_{ij}$; where, μ_v = mean effect of parents; Vi and V_j = estimates of variety effect for the ith and the jth parents, respectively; and h = estimate of heterosis effect when parent i is crossed to parent j ($\sigma = 0$ when i = j, and 1 when $i \neq j$). Heterosis effect is further partitioned as $H_{ij} = h + h_i + h_j + s_{ij}$; where, h = estimate of average heterosis; h_i and h_j = estimates of variety heterosis (expressed as deviation from h) and indicates general combining ability (GCA); and S_{ij} = estimate of specific heterosis from crossing parents i and j which indicates specific combining ability (SCA). The GEAN II analysis was carried out using SAS 9.2 computer software (SAS, 2002), based on the macros in DIALLEL-SAS05 (Zhang, Kang, & Kendall, 2005). Contrary to the Griffing's Model, GEAN II works with condition if I>J, delete, so data for crosses and reciprocals were not analysed simultaneously (full diallel with parents) but separately (Half diallel with parents). Mid-parent and better parent heterosis were calculated following Fonseca and Patterson (1968) as shown in equation 1 and 2.

$$Ht\ (\%) = ((F_1 - MP) / MP) \times 100) \quad (1)$$

$$Hbt\ (\%) = ((F_1 - BP) / BP) \times 100) \quad (2)$$

Where, Ht = mid-parent heterosis; Hbt = better parent heterosis; MP = mid-parent value; BP = better parent value; $F_{1=}$ F_1 progeny value.

3. Results

3.1 Performance of Parents and F_1 Progenies across Three Environments

Genotype by environment interaction (G x E) was significant (P<0.05) for beta-carotene, iron and zinc content across the reciprocals and only zinc content for the crosses (Table 3). Highly significant differences (P<0.01) were found between the genotypes for beta-carotene, iron and zinc content across the crosses and the reciprocals. There was significant (P<0.05) effect of environment on all the traits except for beta-carotene content for the crosses. While overall heterosis was significant (P<0.05) for beta-carotene and iron content for the crosses and all the traits for the reciprocals, average heterosis was significant (P<0.05) for beta-carotene, iron and zinc content across the crosses and reciprocals. Variety heterosis (which indicates GCA) and SCA were significant (P<0.01) only for beta-carotene content for the crosses but were significant for beta-carotene, iron and zinc content across the reciprocals.

Apomuden performed best as parent for beta-carotene content (37.19mg/100gDW) but, its overall cross performance (14.66 mg/100gDW) was not significantly different from Beauregard (14.86mg/100gDW) and Histarch (10.13mg/100gD) (Table 4). Ogyefo and Histarch had the lowest iron content among the parents with means 1.68 mg/100gDW and 1.49 mg/100gDW. Their means in the overall crosses were 1.64 mg/100gDW and 1.56 mg/100gDW, respectively. The iron content for Apomuden (2.56 mg/100gDW) was the highest followed by Beauregard (2.12 mg/100gDW) but, there was no significant difference in their cross performance with respective means of 1.73 mg/110DW and 1.79 mg/100gDW. The performance of the parents for zinc content was in the same trend as the iron content with Apomuden (1.53 mg/100gDW) obtaining the highest value followed by Beauregard (1.12 mg/100gDW). No significant difference was observed between the cross performance. Significant differences were observed between some crosses and their reciprocals for beta-carotene content. These were Ogyefo x Beauregard and Beauregard x Ogyefo, and Beauregard x Histarch and Histarch x Beauregard (Table 4)

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

Source of variation	Df	**Crosses**			**Reciprocals**		
		Beta-carotene content	Iron content	Zinc content	Beta-carotene content	Iron content	Zinc content
Environment (Env.)	2	23.974^{ns}	1.18**	0.73**	26.08*	1.43**	0.90**
Rep. (Env.)	3	4.696^{ns}	0.05^{ns}	0.02^{ns}	2.87^{ns}	0.03^{ns}	0.02^{ns}
Entry	9	801.825**	0.64**	0.21**	719.56**	0.72**	0.23**
Env. x Entry	18	13.436^{ns}	0.05^{ns}	0.02**	11.24*	0.05*	0.02*
Overall heterosis (h_{ij})	5	305.932**	0.360**	0.1056^{ns}	213.01**	0.36**	0.129*
Average heterosis (h)	1	533.216**	1.141**	0.2310*	686.72**	1.03**	0.210*
Variety heterosis (h_j) (GCA)	3	264.286**	0.233^{ns}	0.1992^{ns}	90.03**	0.30**	0.145*
SCA	2	104.175**	0.001^{ns}	0.0003^{ns}	80.17**	0.02*	0.003*

*Significant at P< 0.05; **Significant at P<0.01; ^{ns} Not significant.

Table 4. Beta-carotene, iron and zinc content of the four parents and their crosses over three environments

Parents	F_1 means				Mean Performance	
	Apomuden	Ogyefo	Beauregard	Histarch	Overall crosses	Parents
Beta-carotene content (mg/100g)DW						
Apomuden		7.9	23.84	13.29	14.66	37.19
Ogyefo	8.79		3.98	4.04	6.82	5.95
Beauregard	22.56	11.55		19.1	14.86	25.64
Histarch	11.59	4.62	8.13		10.13	3.67
Lsd (5%)					5.39	5.39
Iron content (mg/100g)DW						
Apomuden		1.65	1.88	1.61	1.73	2.56
Ogyefo	1.78		1.77	1.47	1.64	1.68
Beauregard	1.91	1.96		1.72	1.79	2.12
Histarch	1.52	1.51	1.51		1.56	1.49
Lsd (5%)					0.35	0.35
Zinc content (mg/100g)DW						
Apomuden		1.05	1.09	0.94	1.03	1.53
Ogyefo	1.1		1.08	0.92	1.05	1.01
Beauregard	1.08	1.16		0.96	1.04	1.12
Histarch	0.9	0.94	0.89		0.93	0.86
Lsd (5%)					0.23	0.23

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

3.2 Estimates of Variety Effect, Variety Heterosis and Average Heterosis for Beta-Carotene, Iron and Zinc Content

Variety effect (v_j) was significant for beta-carotene, iron and zinc content (Table 5). Variety effect (v_j) for beta-carotene ranged from -14.44 mg/100gDW (Histarch) to 19.08 mg/100gDW (Apomuden). Those for iron and zinc content ranged from -0.47 mg/100gDW to 0.59 mg/100gDW and -0.269 mg/100gDW to 0.394 mg/100gDW, respectively. Histarch produced the lowest values and Apomuden the highest values. All the parents showed significant (P<0.01) variety effect for beta-carotene content. Beauregard did not show significant (P>0.05) variety effect for iron and zinc content and Ogyefo for zinc content. Variety heterosis (h_j) which indicates GCA was significant for all the traits, but not all the parents indicated significant values across the traits (Table 5). Values for beta-carotene content ranged from -5.06 (Apomuden) to 7.40 (Histarch). Those for iron content ranged from -0.25 (Apomuden) to 0.22 (Ogyefo). Values for zinc content ranged from -0.175 to 0.145 and these values were given by Apomuden and Ogyefo. Average heterosis was significant (P<0.01) for beta-carotene, iron and zinc content (Table 5).

Table 5. Estimates of variety effect (v_j), average heterosis (h) and variety heterosis (hj) for beta-carotene, iron, and zinc content over three environments

Parents	Traits					
	Beta-carotene (mg/100g)DM		Iron (mg/100g)DW		Zinc (mg/100g)DW	
	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	19.08**	-5.06**	0.59**	-0.25**	0.394**	-0.166*
Ogyefo	-12.16**	-4.00**	-0.28*	0.06^{ns}	-0.121^{ns}	0.072^{ns}
Beauregard	7.53**	1.66^{ns}	0.16^{ns}	0.08^{ns}	-0.004^{ns}	0.055^{ns}
Histarch	-14.44**	7.40**	-0.47**	0.11^{ns}	-0.269**	0.039^{ns}
Std. error	1.19	1.03	0.10	0.09	0.08	0.07
Average Heterosis	-6.09 ±0.88**		-0.28 ±0.08**		-0.127 ±0.06*	
			Reciprocals			
Apomuden	19.08**	-4.87**	0.59**	-0.24**	0.394**	-0.175*
Ogyefo	-12.16**	1.75*	-0.28*	0.22*	-0.121^{ns}	0.145*
Beauregard	7.53**	0.55^{ns}	0.16^{ns}	0.07^{ns}	-0.004^{ns}	0.048^{ns}
Histarch	-14.44**	2.58**	-0.47**	-0.04^{ns}	-0.269**	-0.019^{ns}
Std. error	1.01	0.87	0.11	0.09	0.08	0.07
Average Heterosis	-6.91 ±0.75**		-0.27 ±0.08**		-0.121 ±0.06*	

*Significant at P<0.05; **Significant at P<0.01; ^{ns} Not significant.

3.3 Better Parent, Mid-Parent and Specific Heterosis for Beta-Carotene, Iron and Zinc Content Over Three Environments

Better parent heterosis (h_{ij}) for beta-carotene ranged from -84% for crosses Ogyefo x Beauregard to -22% for crosses Histarch x Ogyefo (Table 6). Mid-parent heterosis ($\hat{h}_{ij}$) ranged from -75% for crosses Ogyefo x Beauregard to 30% for crosses Beauregard x Histarch. Specific heterosis (s_{ij}) was significant (P<0.05) for all the crosses except for crosses Apomuden x Ogyefo, Histarch x Apomuden, Beauregard x Ogyefo, and Beauregard x Histarch (Table 6). Specific heterosis (s_{ij}) was not significant for any of the crosses for iron and zinc content (Table 6). For iron content, better parent heterosis (h_{ij}) ranged from -41% for crosses Histarch x Apomuden to -1% for crosses Beauregard x Histarch. Mid-parent heterosis ($\hat{h}_{ij}$) also ranged from -25% for crosses Histarch x Apomuden to 3% for crosses Beauregard x Ogyefo. Better parent heterosis (h_{ij}) for zinc content had values which ranged from -41% for crosses Histarch x Apomuden to 4% for crosses Beauregard x Ogyefo while mid-parent heterosis ($\hat{h}ij$) ranged from -25% for crosses Histarch x Apomuden to 8% for crosses Beauregard x Ogyefo. F_1 progenies with superior performance over the parents for beta-carotene, iron and zinc content are presented in Table 7. Their beta-carotene content ranged from 13.55 mg/100gDW to 41.71 mg/100gDW. Their iron content ranged from 1.44 to 2.12 mg/100gDW while their zinc content ranged from 0.82 mg/100gDW to 1.26 mg/100gDW.

Table 6. Estimates of heterosis effect for beta-carotene, iron, and zinc content over three environments

Cross	Trait								
	Beta-carotene			Iron			Zinc		
	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 x Ogyefo	-79	-63	1.48^{ns}	-36	-22	0.004^{ns}	-31	-19	0.000^{ns}
$^{\$}$Ogyefo x Apomuden	-76	-59	-2.74**	-30	-16	-0.054^{ns}	-28	-15	-0.015^{ns}
Apomuden x Beauregard	-36	-24	1.92*	-27	-20	-0.011^{ns}	-29	-4	-0.005^{ns}
$^{\$}$Beauregard x Apomuden	-39	-28	2.38**	-25	-18	0.012^{ns}	-29	3	0.000^{ns}
Apomuden x Histarch	-64	-35	-3.39**	-37	-21	0.007^{ns}	-39	-22	0.005^{ns}
$^{\$}$Histarch x Apomuden	-69	-43	0.36^{ns}	-41	-25	0.042^{ns}	-41	-25	0.016^{ns}
Ogyefo x Beauregard	-84	-75	-3.39**	-17	-7	0.007^{ns}	-4	1	0.005^{ns}
$^{\$}$Beauregard x Ogyefo	-55	-27	2.38^{ns}	-8	3	0.042^{ns}	4	8	0.016^{ns}
Ogyefo x Histarch	-32	-16	1.92*	-13	-8	-0.011^{ns}	-9	-2	0.005^{ns}
$^{\$}$Histarch x Ogyefo	-22	-4	2.38**	-10	-5	0.012^{ns}	-7	0	0.000^{ns}
Beauregard x Histarch	-26	30	1.48^{ns}	-1	-5	0.004^{ns}	-14	-4	0.000^{ns}
$^{\$}$Histarch x Beauregard	-68	-45	-2.75**	-29	-17	-0.055^{ns}	-21	-6	-0.016^{ns}
Std. error (crosses)			0.79			0.70			0.51
Std. error (reciprocal)			0.67			0.07			0.05

$^{\$}$Reciprocals; *Significant at P<0.05; **Significant at P<0.01; ^{ns}Not significant

Table 7. List of F_1 progenies that showed superior performance over the parents across three environments

F_1 progenies	Beta-carotene (mg/100g)DW	Iron (mg/100g)DW	Zinc (mg/100g)DW
Apomuden x Beauregard-4	41.71	2.09	1.20
Apomuden	37.19	2.56	1.53
Beauregard x Apomuden-23	33.73	2.01	1.12
Beauregard x Apomuden-4	33.47	2.12	1.26
Beauregard x Histarch-9	32.49	2.07	1.09
Beauregard x Apomuden-19	25.97	1.96	1.13
Apomuden x Ogyefo-18	25.72	2.03	1.21
Apomuden x Histarch-15	25.65	1.77	0.99
Beauregard	25.64	2.12	1.13
Beauregard x Apomuden-17	25.47	1.85	0.96
Beauregard x Histarch-5	24.98	1.59	0.89
Beauregard x Histarch-7	23.20	1.82	1.07
Beauregard x Histarch-4	23.00	1.67	0.91
Beauregard x Apomuden-30	22.49	1.90	1.06
Histarch x Beauregard-21	19.55	1.71	0.90
Histarch x Apomuden-9	19.03	1.44	0.82
Ogyefo x Apomuden-19	18.62	1.96	1.14
Apomuden x Histarch-14	18.16	1.72	0.95
Beauregard x Histarch-6	14.86	1.48	0.86
Beauregard x Apomuden-11	13.55	1.60	0.97
Histarch	3.67	1.49	0.86
Ogyefo	5.95	1.69	1.01
*SEM (P<0.05)	2.63	0.11	0.07
CV (%)	41.1	11.1	11.5

*SEM=Standard error of mean

4. Discussion

The significant mean squares for both variety heterosis (GCA) and specific combining ability (SCA) for beta-carotene, iron and zinc content means that additive and non-additive effects were involved in the expression of beta-carotene, iron and zinc content. However, the substantially greater amounts of the GCA sum of squares for the traits compared with the sum of squares for SCA suggests that additive effects were more important than non-additive effects for beta-carotene, iron and zinc content. This indicates that most of the genetic variation found were additive in nature and majority of the total sum of squares of the traits due to differences among generation performance may be explained by variety effects (vj) and variety heterosis. Consequently, variety effects of the parents were important predictors of the cross performance. This shows predominance effect of additive gene action in beta-carotene, iron and zinc content and suggests that there would be no complications in breeding sweetpotato varieties with high content of beta-carotene, iron and zinc through selection. Oduro (2013),

also found similar result for beta-carotene content on different sweetpotato genotypes. Similar results have also been reported on other traits in sweetpotato (Gasura et al., 2008; Mwanga et al., 2002; Shumbusha et al., 2014; Sseruwu, 2012). Kumah (2013), reported significant effect of GCA and SCA for iron and zinc content in sorghum but found additive gene action conditioning grain zinc content while both additive and non-additive gene effects control grain iron content.

Significant ($P<0.01$) differences between the genotypes show significant genetic differences and indicates that meaningful selection and improvement on beta-carotene, iron and zinc content in sweetpotato is possible. G x E interaction is key in evaluating genotype adaptation and development of genotypes with improved end-product quality (Ames, Clarke, Marchylo, Dexter, & Woods, 1999). Presence of G x E suggest that progress from selection may be complicated since it may be difficult to separate genotypic effects from environmental effects. Significant differences were observed between some crosses and their reciprocals for beta-carotene content. These were Ogyefo x Beauregard and Beauregard x Ogyefo, and Beauregard x Histarch and Histarch x Beauregard. In addition, G x E was not significant for any of the traits for the crosses except zinc content, but G x E was significant for all the traits across the reciprocals. Moreover, overall heterosis was significant for all the traits except zinc content for the crosses, while variety heterosis and SCA were significant ($P<0.05$) for all the traits across the reciprocals and only beta-carotene content for the crosses. These differences between the crosses and their reciprocals may be attributed to maternal or cytoplasmic effects. Maternal or cytoplasmic effects are influences of parents on offspring phenotype occurring through pathways other than inherited DNA. If existing, maternal effect could have inflated the GCA mean squares at the expense of SCA. This has consequences for the interpretation of the results and perhaps for several others that concluded that additive gene action was predominant over non-additive effects. Maternal effects have been reported to influence a number of traits in sweetpotato (Chiona, 2009; Lin et al., 2007; Oduro, 2013).

Significance of overall heterosis indicates opportunity for exploiting heterosis for increase beta-carotene, iron and zinc content in sweetpotato storage roots. Other studies in sweetpotato have shown that there is exploitable heterosis in sweetpotato (Baafi et al., 2016; Grüneberg, Mwanga, Andrade, & Dapaah, 2009). However, among the three kinds of heterosis, average heterosis (h) was the most important. Average heterosis (h) contributed by a particular set of parents used in crosses is the differences between the mean of all crosses and the mean of all parents (Gardner, 1967). The high values of variety heterosis (h_j) of Histarch and Beauregard for beta-carotene and iron content, and Ogyefo and Beauregard for zinc content indicates that these parents have good general combining ability for the respective traits. High variety heterosis (h_j) show differences in occurrence of dominant alleles between parents (Crossa, Gardner, & Mumm, 1987). Negative values may be attributed to unrealized performance expectation of the parents in the progenies. This is because negative values of variety heterosis for breeding varieties/population seem to represent an unfulfilling performance expectation from high variety effect(v_j) and a high average heterosis effect (h) (Harold et al., 2001). Apomuden and Beauregard had the highest beta-carotene, iron and zinc content among the four parents. Parents with higher beta-carotene content had higher iron and zinc content due to the strong positive genotypic correlation among the traits (Baafi, 2014). This indicates that breeding sweetpotato genotypes with high beta-carotene, iron and zinc content will not be too difficult due to the strong positive genotypic association between the traits if suitable parents are used. Apomuden and Beauregard were good parents for the traits and can be inter-crossed to develop elite genotypes with sufficient genetic variability for improvement on beta-carotene, iron and zinc content in sweetpotato.

5. Conclusion

Genetic variability exists for beta-carotene, iron and zinc content in sweetpotato, and much of this genetic variation is additive in nature. This means that beta-carotene, iron and zinc content in sweetpotato are mostly controlled by additive gene effects rather than dominance and epistasis. Significance of overall heterosis indicates some opportunity for exploitation of heterosis for increasing beta-carotene, iron and zinc content in sweetpotato storage roots.These indicates that the parents used can be inter-crossed to develop elite genotypes with sufficient genetic variability for breeding sweetpotato varieties that combined higher amounts of these traits to alleviate malnutrition in Ghana and beyond.

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