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INHERITANCE OF ROOT DRY MATTER CONTENT IN SWEETPOTATO

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ABSTRACT

There has been much emphasis on breeding for increased sweetpotato storage root yield, but less on dry matter yield, and its inheritance. High dry matter content (DMC) is associated with consumer preferences, and is important for the processing industry. This study was conducted to determine the type of gene action controlling DMC and to assess genotype by environment (G x E) interaction effect on DMC in sweetpotato. Five parental clones varying in DMC were hand-crossed in a half-diallel design to generate ten families. Ten genotypes of each family were planted in a trial at Namulonge (swamp and upland environments) and Serere in Uganda in 2009 and 2010. Highly significant ($P<0.001$) differences were found both between genotypes and between families for DMC. High significant general combining ability (GCA) ($P<0.001$) and specific combining ability (SCA) ($P<0.01$) were obtained, meaning that the differences among families for high DMC were due to both GCA and SCA. The relative importance of GCA and SCA was 0.59, indicating that additive gene action was slightly more predominant than non-additive gene action in predicting progeny performance for high DMC. Broad sense heritability (H) estimates for DMC were 0.70 and 0.73, respectively on genotype and family means across environments basis, suggesting that DMC was moderately influenced by the environment. Rapid selection for best genotypes would be possible, since progenies can be predicted from the phenotype of the parents. Parent SPK (GCA = 1.02) was the best combiner. The effect of location was less significant compared to seasons, suggesting the need to evaluate genotypes for several seasons, but in few locations to save resources.

Key Words: General combining ability, half-diallel, *Ipomoea batatas*, Uganda

RÉSUMÉ

Plusieurs efforts ont été fournis dans le cadre d'augmenter le rendement de la patate douce, mais peu d'efforts visant le rendement sec et son héritabilité. La matière sèche est associée aux préférences des consommateurs et elle est importante dans l'industrie de transformation. Cette étude a été menée dans le but de déterminer le type de l'action génétique contrôlant la matière sèche, ainsi que d'évaluer l'effet d'interaction génotype x environnement sur la matière sèche sur la patate douce. Cinq différents parents en terme de matière sèche ont été croisés en moitié diallèle et dix familles sont obtenues. Les semences sont plantées dans les boites en bois dans les serres à Namulonge, Uganda. Dix génotypes pour chacune des familles sont plantées dans l'essai à Namulonge (environnement marrais et hautes terres) et Serere en bloques complètement randomisées, avec deux répétitions, durant la période Octobre 2009-Mars 2010. Pour déterminer la matière sèche, une quantité de 200 g pour chacune des génotypes a été séchée à 65^0C jusqu'à ce que le poids soit constant. Les données sont analysées en utilisant le logiciel Genstat. Aptitude générale à la combinaison (AGC) et aptitude spécifique à la combinaison (ASC) sont calculées selon Modèle I, Méthode 4 selon la description de Griffing (1956). Hautes significative ($P< 0,001$) différences sont trouvées aussi bien entre génotypes que familles pour la matière sèche. Hautes significatives

AGC (P<0,001) et ASC (P<0,01) sont trouvées, signifiant que les différences observées entre les familles pour la matière sèche sont dues à la fois à AGC et ASC. L'importance relative de l'AGC et ASC était 0,59, ce qui indique que l'action génétique additive était un peu plus importante que l'action génétique non-additive en prédicant la performance des progénitures pour la matière sèche. L'héritabilité en large sens (H) pour la matière sèche était de 0,70 et 0,73 en se basant respectivement sur la moyenne du génotype et celle de la famille sur tous les environnements, suggérant que la matière sèche était modérément influencée par l'environnement. Ceci indique que la sélection rapide des génotypes serait possible, car les progénitures peuvent être prévenues en se basant sur le phénotype des parents. Parent SPK (GCA=1,02) était la meilleure combinant dans cette étude. L'effet des locations était moins significatif comparable aux saisons, suggérant l'importance d'évaluer les génotypes sur plusieurs saisons, mais dans les moins de locations dans le cadre d'économiser les ressources.

Mots Clés: Aptitude générale à la combinaison, moitié diallèle, *Ipomoea batatas,* Uganda

INTRODUCTION

Sweetpotato (*Ipomoea batatas* L. (Lam)) ranks seventh in the world, on dry matter basis, among the food crops (FAO, 2008). In sub-Saharan Africa, it is the third most important crop with nearly 90% of the total output coming from eastern and southern Africa (Ewell and Mutuura, 1994). Uganda (2,554,000 t), Tanzania (1,379,000 t), and Rwanda (826,000 t) are among the largest sweetpotato producing countries in sub-Saharan Africa (FAO, 2008).

Most sweetpotato varieties currently cultivated in SSA have a dry matter (DM) content that is too low (25-30%) to be used as raw material in the processing industry, which prefers DM >35% (Lu and Sheng, 1990). Moreover, high DM is one of the important attributes that affects consumer preferences in most of SSA (Tumwegamire *et al.*, 2004). For long-term population improvement, a diallel crossing pattern combined with recurrent mass selection is recommended as an effective way to combine favourable genes and alleles in parental genotypes (Huaman and Zhang, 1997).

Heritability is a measure of the correspondence between phenotypic values and breeding values. High estimate does not explain how good materials are, only that superior parents tend to give the best progeny (Rex, 2002). Heritability estimates help to predict the performance of the offspring based on the performance of their parents, using a particular combination of breeding materials and techniques of evaluation. Jones (1986) and Courtney (2007), respectively, found that DM narrow sense heritability estimates in sweetpotato, were 0.65 and 0.92. On the other hand, Wanda *et al*. (1987) estimated broad-sense heritability of DM content to be 0.97.

Most of the DM in sweetpotato (85 to 90%) is carbohydrates (Wanda *et al.,* 1987), thus factors that affect the total carbohydrate fraction are essentially the same as those that influence DMC. The carbohydrate fraction consists of starch, sugars, pectin, cellulose and probably hemicellulose. Sweetpotato starch, which contains 79 to 83% amylopectin, is the major carbohydrate, accounting for 65 to 80% of the total dry matter (Muhanna and Rees, 2004). The concentration of fructose, glucose and total sugar within sweetpotato roots is negatively correlated with root DMC.

The objective of this study was to determine the inheritance of root DM content in sweetpotato, in order to facilitate improvement of the crop for energy value, processing quality and desirability by farmers.

MATERIALS AND METHODS

The experiment was conducted in a screenhouse and experimental fields of the National Crops Resources Research Institute (NaCRRI) at Namulonge and the National Semi-Arid Agricultural Research Institute (NaSAARI) at Serere, in Uganda. Namulonge is located at 1,150 meters above sea level (masl) and at 0° 32'N, 32° 35'E. It experiences an average high temperature of 28.4°C, and mean annual bimodal rainfall of 1,270 mm (Smit *et al*., 1997). At Namulonge, two environments were selected for the study, namely the swamp and upland.

Serere is located in north-eastern Uganda, 33°27' E, 1°32'N, and 1,140 masl. The area receives annual bi-modal rainfall ranging from 800

to 1,150 mm. Mean maximum and minimum temperatures are 33°C and 17°C, respectively (Kabi *et al.*, 2001).

Parental material. Five parental sweetpotato clones varying in DMC and other attributes were crossed in a half-diallel design.These five clones had previously been evaluated for DMC at NaCRRI, with three having high DMC, namely New Kawogo (NKA), SPK004 (SPK) and Kyabafuruki (KYA) (Mwanga *et al.*, 2009); and two having low DMC (Jewel (JEW) and Huarmeyano (HUA)) (Mwanga and Bohac, 2004). Among the five parents, only JEW was orange-fleshed. Though self-fertilisation occurs only rarely in sweetpotato (Poole, 1955), we emasculated the female parents to eliminate such a possibility. In each of two replications, five clonal plants from each of ten genotypes representing each of the ten full-sib families were evaluated, totaling 100 genotypes.

Development of F1 plant material. True seeds from each selected family were germinated in a screenhouse. True seeds were scarified by soaking in concentrated (98%) sulfuric acid for 30 minutes, to break dormancy imposed by the seed coat. Scarified seeds were sown 1 cm deep in sterile soil, in seed-boxes of 150 cm by 90 cm and spaced 15 cm x 3 cm.

Field experiment. Ten well-established plants, representing each family, were chosen randomly, and five 30-cm cuttings of each genotype, planted in two replications in the field. Experiments were planted at Namulonge, in both upland and swamp environments, and at Serere during October – Novemeber 2009 (the second rainy season) and March of 2010. A split-plot arrangement, with two replications was used, with families arranged as main plots, in a randomised complete block design. Genotypes within each family were randomised as sub-plots. Each entry in a replication was represented by a single row containing 5 plants. Parental material was also included in the setups.

Plant spacing within rows was 30 cm, and 80 cm between rows. Planting and management practices were similar in all locations, and weeding was carried out using hand-hoes whenever necessary, until harvest. Roots were harvested five months after planting. One plant at both ends of each row was left as a guard plant, giving a harvest area of 0.72 m^2 per sub-plot.

Data collected. Data were collected on root characteristics, namely marketable and non-marketable root number and weight. Roots classified as marketable were those over 3 cm in diameter and without cracks, insect damage or rotten parts (Ekanayake *et al.,* 1990).

Root characteristics and vine weight were evaluated at harvest. Sweetpotato storage root DMC was determined using the method of Benesi *et al*. (2004). Three undamaged roots from each genotype were randomly selected just after harvesting. The medial sections of selected roots for each genotype were sliced thinly, and then manually mixed together. A duplicated fresh sample of 200 g each (w1) was placed in an open-top paper bag and oven-dried at 65°C for 72 hours to constant weight. The oven-dried samples were weighed immediately (w2) and DM (%) was calculated gravimetrically.

Data analysis. Data were subjected to general analysis of variance (ANOVA) using GenStat,12.2 Edition software. Since there was at least one missing genotype recorded in the data from each location, unbalanced ANOVA was used. Only when significant differences among families were established, was the second step of diallel analysis performed (Singh and Chaudhary, 1979). Fisher's Protected Least Significance Difference test (LSD) at $P< 0.05$, was used to separate means. The progeny means of DMC were subjected to diallel analyses using GenStat. General combining ability (GCA) and specific combining ability (SCA) variance components were computed according to the fixed-effects Model I, Method 4 (only one set of F1's; with parents and reciprocals excluded) as described by Griffing (1956). Correlations between traits were performed using EXCEL programme.

RESULTS

Dry matter content. There was a very large, highly significant interaction of season (S) x location (L) ($P<0.001$) which overshadowed the

individual main effects of S and of L (Table 1). Highly significant differences for DMC were found between genotypes (P<0.001) and families (P<0.001). Genotypes interacted significantly with all environmental factors (S, L, S x L), but G x L had smaller interactions than G x S and G x S x L. There was a significant interaction between families and environments (F x E (P<0.01) and F x S x L (P<0.05)), but no significant interactions were found for F x L and F x S.

Both GCA x E and SCA x E were significant. The two crosses with SPK, NKA x SPK (32.5%) and SPK x HUA (32.6%), had the highest means of all the crosses. The lowest performing family was JEW x HUA with a DMC of 28.0%. The progeny denoted [9] from a cross NKA x HUA, was the overall best with a DMC of 35.2% (Table 2). Across seasons, family NKA x SPK was the best performer for DMC (32.7%) (Table 4). Although, the cross Jew x Hua was the lowest in performance in the Serere location, the best performing genotype for DMC (42%) came from the same family (data not shown).

Heritability for DMC. Based on variance components, broad-sense heritability and broad-

TABLE 1. ANOVA for combining ability of DMC in sweetpotato, combined across three locations, two seasons, 2009B and 2010A

Source	DF (with missing plots)	Mean squares	F-test	Variance components
Season (S)	1	228.56	0.04ns	-
Locations (L)	2	5830.30	0.95ns	-
S x L	2	6118.74	484.84***	-
Rep (R) /(S x L)	6	12.62	3.87***	-
Families (F)	9	286.27	4.41***	1.84
GCA	4	376.94	5.45***	0.85
SCA	5	202.53	3.29**	1.17
F x Environments (E)	45	31.80	1.85**	0.73
F x S	9	35.64	1.26ns	0.12
F x L	18	33.06	1.17ns	0.12
F x S x L	18	28.21	2.03*	0.72
GCA x E	20	36.01	2.09**	0.31
GCA x S	4	51.66	2.85ns	0.18
GCA x L	8	50.73	3.61*	0.30
GCA xS x L	8	13.48	0.78ns	-0.06
SCA x E	25	28.43	1.65*	0.56
SCA x S	5	21.07	0.47ns	-0.39
SCA x L	10	20.27	0.50ns	-0.51
SCA x S x L	10	40.24	2.34*	1.15
F x [R/(S x L)]=MPE	54	6.25	1.92***	6.25
Genotypes (G) /F	90	47.39	3.33***	2.76
G/ F x E	423	14.23	4.37***	5.48
G/ F x S	89	18.85	1.73**	1.32
G/ F x L	179	14.81	1.36*	0.98
G/F x S x L	155	10.91	3.35***	3.82
Residual(=SPE)	488	3.26		3.26
Total	1120	36.09		

*, **, ***Significant at the 0.05, 0.01 and 0.001 probability levels respectively; ns not significant
MPE= Main plot error; SPE= Sub-plot error; SPE= sub-plot error; GCA= variation due to general combining ability; SCA= variation due to specific combining ability

TABLE 2. Within cross variability for sweetpotato dry matter content (%) across environments in Uganda

Genotype	Jew x Hua	Nka x Jew	Hua x Kya	Nka x Hua	SPK x Jew	SPK x Hua	SPK x Kya	Nka x Kya	Nka x SPK	Jew x Kya
1	34.5	23.5	33.0	31.9	31.5	33.5	31.3	31.6	32.2	29.7
2	28.3	27.8	29.4	32.1	28.0	31.5	31.1	34.6	32.8	32.0
3	26.8	29.3	31.5	31.9	26.3	30.5	31.1	31.0	31.2	32.6
4	32.3	23.9	28.9	35.0	29.9	31.9	33.3	29.0	35.1	31.7
5	24.4	31.0	29.7	31.9	30.8	34.9	28.9	32.8	30.0	33.6
6	27.9	31.0	32.2	29.8	32.9	33.0	31.1	31.7	31.8	32.5
7	27.2	31.4	30.4	34.8	34.5	34.3	30.8	31.2	31.9	31.4
8	23.5	28.0	30.4	29.4	29.2	31.0	32.7	33.3	32.7	33.3
9	26.6	33.2	29.1	35.2	32.4	32.5	34.3	32.2	34.3	31.1
10	28.6	25.6	32.6	28.7	28.0	32.9	31.4	32.1	33.1	33.4
Mean	28.0	28.5	30.7	32.1	30.3	32.6	31.6	32.0	32.5	32.1
Min	23.5	23.5	28.9	28.7	26.3	30.5	28.9	29.0	30.0	29.7
Max	34.5	33.2	33.0	35.2	34.5	34.9	34.3	34.6	35.1	33.6

Coefficient of variation (CV%) = 6; $LSD_{0.05}$ = 1.44

sense coefficient of determination (BS-CGD) estimates across environments was 0.70 for genotype means, and 0.73 for family means, respectively. As stated before, only variance components for interpreting inheritance were calculated:

Baker's ratio $(2\sigma^2_{GCA}/(2\sigma^2_{GCA} + \sigma^2_{SCA}))$ was 0.59.

Relationship between DMC and some other variables. Significant differences were found between genotypes for marketable root weight (MRW), but not families for this trait (Table 3). Highly significant interactions were found for G x L, G x S and G x L x S (P<0.001). The means for marketable root weight are shown in Table 4.

Significant differences between genotypes (P<0.001) and families (P<0.05) were found for non-marketable root weight. The interactions were significant for G x L (P<0.01), G x S (P<0.01) and G x L x S (P<0.05) for this parameter. Families interacted significantly with seasons (F x S, P<0.001), locations (F x L, P<0.05), but not with the combination S x L.

General Combining Ability and SCA. GCA and SCA values and their level of significance are presented in Table 5. The high DMC parent SPK showed significant (P<0.01) positive GCA effects (1.02); while the low DMC parent had significant (P<0.001) negative GCA effects (-1.66). A combination of low x high DMC parents (JEW x KYA) resulted in a highly significant (P<0.001) positive SCA effect (2.01). A cross between two high DMC parents SPK x KYA, produced progenies with negative SCA effects (-1.13).

DISCUSSION

General and specific combining ability for root DMC. The significant differences for DMC found among families (Table 1) were due to both GCA and SCA. The magnitudes of the GCA (0.85) and SCA (1.17) variance components suggest that both additive and non-additive gene action are important in controlling DMC. The relative importance of GCA and SCA reported here (0.59, based on Baker's ratio) suggests that GCA was slightly more important than SCA in progeny family performance for high DMC. This indicates that additive gene action was slightly more influential than non-additive gene action. This study conforms to the observations of Sakai (1964), who reported larger additive than non-additive genetic variance for DMC in sweetpotato. Cach *et al.* (2006) also reported quite similar results in cassava, where GCA was large and significant for DMC, compared with SCA. These results suggest that, in crossing high by high DMC parents, progeny should have high

TABLE 3. Marketable root weight (MRW) means (kg/sub-plot†) for each environment, 2009B and 2010A

Family	Serere 2009B	Serere 2010A	Serere (both)	Swamp 2009B	Swamp 2010A	Swamp (both)	Upland 2009B	Upland 2010A	Upland (both)	Combined 2009B	Combined 2010A	Across environments
JEW x HUA	0.5	0.3	0.4	0.1	0.1	0.1	0.3	0.2	0.3	0.3	0.2	0.3
NKA x JEW	0.7	0.7	0.7	0.3	0.4	0.3	0.1	0.3	0.2	0.3	0.5	0.4
HUA x KYA	0.8	0.1	0.5	0.3	0.1	0.2	0.6	0.2	0.4	0.6	0.2	0.4
NKA x HUA	0.8	0.5	0.7	0.2	0.2	0.2	0.3	0.2	0.2	0.4	0.3	0.4
SPK X JEW	0.6	0.2	0.4	0.1	0.2	0.2	0.3	0.2	0.2	0.3	0.2	0.3
SPK x HUA	0.5	0.4	0.5	0.1	0.2	0.1	0.5	0.2	0.4	0.3	0.3	0.3
SPK X KYA	1.0	0.2	0.6	0.1	0.1	0.1	0.4	0.2	0.3	0.5	0.2	0.3
NKA X KYA	0.7	0.4	0.5	0.1	0.3	0.2	0.2	0.4	0.3	0.3	0.3	0.3
NKA X SPK	0.5	0.1	0.3	0.2	0.1	0.2	0.9	0.3	0.6	0.5	0.2	0.4
JEW X KYA	0.7	0.6	0.7	0.1	0.3	0.2	0.4	0.4	0.4	0.4	0.4	0.4
G. mean	0.7	0.4	0.5	0.2	0.2	0.2	0.4	0.3	0.3	0.4	0.3	0.3
C V %	32.4	39.3		62.5	35.2		45.6	54.4		24.4	29.9	28.6
s.e	0.24	0.13		0.1	0.08		0.18	0.13		0.12	0.08	0.09
sed	0.34	0.18		0.1	0.11		0.25	0.18		0.22	0.11	0.13
$LSD_{0.05}$	0.69	0.37		0.2	0.23		0.53	0.38		0.44	0.23	0.25

CV = coefficient of variation; s.e = standard error; s.e.d = standard error of the difference; $LSD_{0.05}$ = Least Significant Difference. †A sub-plot consisted of 3 middle plants for each genotype (0.72 m^2)

TABLE 4. Diallel mean for dry matter content (%) for each season B and A at Serere and Namulonge (swamp and upland) in Uganda

Family	Serere 2009B	Serere 2010A	Serere Both	Swamp 2009B	Swamp 2010A	Swamp Both	Upland 2009B	Upland 2010A	Upland Both	Seasonal means		
										2009B	2010A	Across seasons
JEW x HUA	34.9	24.7	29.8	21.1	26.4	23.7	28.0	32.7	30.3	28.0	27.9	28.0
NKA x JEW	35.4	27.1	31.3	20.3	26.3	23.3	30.4	34.0	32.2	28.7	29.1	28.8
HUA x KYA	35.7	27.0	31.4	23.5	30.3	26.9	32.7	35.4	34.1	30.6	30.9	30.7
NKA x HUA	37.3	29.4	33.3	22.0	32.8	27.4	34.0	37.0	35.5	31.1	33.0	32.1
SPK X JEW	35.0	26.6	30.8	20.3	31.3	25.8	33.8	37.5	35.6	29.7	31.8	30.6
SPK x HUA	36.6	30.5	33.5	22.9	32.8	27.9	34.3	38.5	36.4	31.2	34.0	32.6
SPK X KYA	36.4	26.5	31.5	26.1	31.6	28.8	33.5	36.5	35.0	32.0	31.5	31.7
NKA X KYA	37.6	28.7	33.2	24.0	30.5	27.3	33.1	36.9	35.0	31.6	32.1	32.0
NKA X SPK	37.1	29.5	33.3	24.3	32.5	28.4	34.1	38.7	36.4	31.8	33.6	32.7
JEW X KYA	36.2	30.8	33.5	25.7	31.4	28.5	34.5	33.7	34.1	32.1	32.0	32.2
Grand mean	36.2	28.1	32.1	23.0	30.6	26.8	32.8	36.1	34.5	30.7	31.6	31.1
$LSD_{0.05}$	2.9	3.0		2.9	3.4		2.9	3.1		2.6	2.7	2.1
C V %	4.1	5.5		8.2	6.8		6.2	4.6		5.9	5.7	5.8

c.v = Coefficient of variation, LSD_{005} = Least significant difference

TABLE 5. Estimates of GCA effects (in bold) and SCA (off diagonal) effects for sweetpotato DMC across environments in Uganda

Parent	NKA	SPK	JEW	HUA	KYA
New Kawogo (NKA)	**0.32^{ns}**	0.18^{ns}	-1.03^{ns}	1.01^{ns}	-0.17^{ns}
Kakamega (SPK)		**1.02****	0.14^{ns}	0.82^{ns}	-1.13*
Jewel (JEW)			**-1.66*****	-1.12*	2.01***
Huarmeyano (HUA)				**-0.36^{ns}**	-0.71^{ns}
Kyabafuruki (KYA)					**0.68^{ns}**

*, **, *** Significant at the 0.05, 0.01 and 0.001 probability levels respectively; ^{ns} not significant. Standard error, GCA = 0.38; SCA = 0.52

DMC values with means close to the mid-parent value.

Dry matter content (DMC) genotype. Root DMC values for family means ranged from 23.5% for both the JEW x HUA and NKA x JEW families to 35.2% for NKA x HUA (Table 2). These values are within the ranges of DMC for the current sweetpotato genotypes in Eastern Africa, as reported by Brabet *et al*. (1998). The results show that the two low DMC parents, JEW and HUA, contributed negatively to the lowest DMC genotype mean (23.5%), among all crosses.

Highly significant differences for DMC were found between both genotypes within families and between families. These results concur with those of Kanju (2000) who studied sweetpotato in South Africa. The variance component for genotypes within families was higher (2.76) than that for families (1.84), indicating that selection of specific genotypes within families for high DMC is very important.

Two families involving the high DMC parent SPK had the highest means of all the crosses (NKA x SPK with 32.7%, SPK x HUA with 32.6%). Genotype 9 from a high by low DMC cross, NKA x HUA (Table 2), was the best genotype averaged across the six environments, with a mean of 35.2%; followed by genotype 4 from family NKA x SPK (35.1%). Based on the average performance of genotypes within families, the lowest performing genotype overall was from the family NKA x JEW, with a DMC mean of 23.5% (Table 2).

Genotype 1 from JEW x HUA, a cross from a low by low parental DMC, ranked seventh in performance (34.5%), indicating that it is possible to get good genotypes from crosses involving two parents with low DMC. Furthermore, cross JEW x KYA was the best performer for MRW, with a combined mean of 0.4 kg sub-plot^{-1}.

Orange-fleshed sweetpotatoes are important in addressing vitamin A deficiency in developing countries, and are being promoted especially in Eastern Africa (Tumwegamire *et al.*, 2004). Jewel, therefore, could be a good parent for obtaining progeny with orange flesh as well as moderate to high DMC.

The coefficient of variation for MRW was generally high, especially for the swamp 2009 B season (62.5%) and the upland 2010 season (54.4%) (Table 3), indicating large plot-to-plot variability (Table 3). This agrees with the statement of Andrade *et al*. (2009) that sweetpotato experimental trials have a very large plot error for yield traits. The same authors have reported cv values of 35-45% in plots with 15 plants, and cv values of 25% in plots with more than 60 plants. This shows that the cv plot error can be improved through using relatively large samples of plants.This indicates that plot to plot variability was very high for this trait. In some cases, there were no roots at all, or only non-marketable roots were present

Performance of genotypes. Differences were not large among family means for DMC averaged over locations and seasons (Table 4). Namulonge swamp gave the lowest mean for DMC (26.8%); while the highest locational mean was Namulonge upland (34.5%). Seasons, 2009B and 2010A resulted in nearly equal DMC means of 30.7 and 31.6%, respectively, although there were strong interactions of seasons with locations (environments). Parent SPK was involved in two

of the three best families for DMC, which agreed with the GCA value for this parent (Table 4).

General and specific combining ability effects for DMC. Based on GCA values (Table 5), the high DMC parent SPK had the highest positive and significant GCA effects (GCA = 1.02, P<0.01). However, its specific cross with another high DMC parent, KYA, produced progenies with significant negative SCA effects (SCA = -1.13, P<0.05). This implies that the non-additive gene action arising from the combination of parents, SPK and KYA, resulted in the cross performing below the expectation based on GCA effects. The reason for this is not clear, though since sweetpotato is highly heterozygous and hexaploid, favourable gene combinations can be broken down in progeny from a cross of parents selected for a desirable trait.

The orange-fleshed root parent, JEW, had negative and high GCA effects (GCA = -1.66, P<0.001) (Table 5). Though this parent had negative GCA effects, it produced progeny with a positive and highly significant SCA when crossed with parent KYA (SCA = 2.01, P<0.001). Similar results have been reported by Chiona (2009) on β-carotene content in sweetpotato in Zambia. These results imply that parents should not be discarded based on their negative GCA effects, since they can express their performance in specific crosses and in specific genotypes.

Estimates of heritability. Since genotypes were random representatives of families, calculation of heritability estimates is appropriate, and the broad-sense heritability estimate for DMC was 0.70 for genotype means across environments. With regard to families, parents were considered fixed, implying that it is appropriate to report the broad-sense coefficient of genetic determination (BS-CGD), which was 0.73 for family means across environments. These estimates are relatively high compared to the range 0 to 1, suggesting that the trait was only moderately influenced by the environment. This implies that rapid selection would be possible since good progeny can be predicted from the phenotype of the parents. Jones (1980) and Chiona (2009) reported nearly equal estimates for narrow sense heritability (h^2) for root DMC. The heritability estimates reported here suggest that rapid selection would be possible, since clonal reproduction allows for the preservation and utilisation of superior genotypes, regardless of the relative contributions of additive or non-additive types of gene action.

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