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HERITABILITY, COMBINING ABILITY AND INHERITANCE OF STORAGE ROOT DRY MATTER IN YAM BEANS

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ABSTRACT

Storage root dry matter content (RDM) is central to the improvement of consumer and industrial attributes of root crops. Yam bean (*Pachyrhizus* species) is a legume root crop newly introduced in Uganda, but its adoption may be constrained by low RDM. The objective of this study was to investigate the magnitude of variance for general combining ability (GCA) and specific combining ability (SCA) effects, heritability estimates and inheritance of RDM in yam beans. Progenies of sixteen crosses, generated using the North Carolina (NCII) mating scheme, were evaluated in F₁ and F₂ field experiments, with three replications at the National Crops Resources Research Institute (NaCRRI), Namulonge in Central Uganda, during the first cropping seasons of April, 2013 and 2014, respectively. Significant (p<0.001) mean squares for general combining ability (GCA), and specific combining ability (SCA) were observed in F₁ and F₂ generations, demonstrating additive and non-additive genetic inheritance of RDM. High Baker's ratio in F₁ (0.76) and F₂ (0.78), and large $\sigma^2_{GCA}/\sigma^2_{SCA}$ (3.13) indicate predominance of additive gene effects. Narrow sense heritability was high in both F₁ (0.74) and F₂ (0.75), implying that RDM can be improved in yam beans through selection. The results provide a basis for selection of suitable parents for hybridisation and breeding programmes to develop high dry matter yam bean varieties in Uganda.

Key Words: Baker's ratio, gene action, *Pachyrhizus* species

RÉSUMÉ

La teneur en matières sèches du stock racinaire (MSR) est essentiel en terme d'amélioration des qualités des cultures racinaires pour les consommateurs et d'industriels. Le haricot-igname (espèce *Pachyrhizus*) est une culture racinaire légumineuse nouvellement introduite en Ouganda, mais son adoption pourrait être handicapée par sa teneur basse en matières sèches racinaires. Cette étude avait pour objectif d'étudier le niveau de la variance pour les effets de la capacité de combinaison générale et la capacité de combinaison spécifique, estimations de l'héritabilité et l'héritage de MSR dans les haricots ignames. Les progénies de seize croisements générés à l'aide du système de croisement de la Caroline du Nord (NCII), ont été évalués dans des essais en champs de F₁ et F₂ avec trois répétitions à l'Institut National de Recherche sur les Ressources Végétales (NaCRRI), Namulonge en Ouganda, pendant les premières saisons culturales d'Avril 2013 et 2014, respectivement. Les carrés moyens significatifs (P<0,001) de capacité générale de combinaison et capacité spécifique de combinaison étaient observés dans les

générations F_1 et F_2 démontrant ainsi un héritage génétique additif et non additive de MSR. Le rapport élevé de Baker en F_1 (0,76) et F_2 (0,78), et $\sigma^2_{GCA}/\sigma^2_{SCA}$ (3.13) large indiquent la prédominance des effets de gènes additifs. Une étroite héritabilité d'ordre de F_1 (0.74) et F_2 (0.75) était observée, ce qui implique que MSR peut être amélioré dans le haricot-igname par voie de sélection. Les résultats constituent une base pour la sélection des parents appropriés pour les programmes d'hybridation et d'amélioration génétique pour développer des variétés de haricot-ignames à haute teneur en matières sèches en Ouganda.

Mots Clés: Ratport de Baker, action génique, espèce *Pachyrhizus*

INTRODUCTION

Yam bean (*Pachyrhizus* sp.) is a storage root-forming legume of neo-tropical origin (Sørensen, 1996), but was recently introduced in East and Central Africa for food production (Heider *et al.*, 2011). The crop belongs to the genus *Pachyrhizus* Rich. ex DC; subtribe *Diocleinae*, tribe *Phaseoleae* and the *Fabaceae* legume family (Sørensen, 1988). The genus consists of five species of which two, namely *P. ferrugineous* (Piper) Sørensen and *P. panamensis* Clausen are still wild; and *P. erosus* (L.) Urban, *P. ahipa* (Wedd.) Parodi and *P. tuberosus* (Lam.) Spreng are in cultivation (Lackey, 1977; Ingham, 1990). All *Pachyrhizus* species are propagated by true seed, diploid ($2n=2x=22$), self-compatible and permit successful interspecific hybridisation (Sorensen, 1990; Grüneberg *et al.*, 2003).

Yam bean is traditionally a minor and underutilised crop (Sørensen, 1996; Jacobsen *et al.*, 2015), mainly because of low storage root dry matter (RDM) content that limits its food and industrial use (Rizky *et al.*, 2013; Agaba *et al.*, 2016). Nonetheless, the crop has attracted scientific and nutritional interest because its storage roots contain vitamins and micronutrients, such as iron and zinc (Noman *et al.*, 2007; Dini *et al.*, 2013), 56 to 58% starch (Forsyth *et al.*, 2002) and 8 to 18% proteins (Velasco and Grüneberg, 1999; Zanklan *et al.*, 2007) on dry weight basis. Yam bean may offer nutritional benefits to local populations, where micro-nutrient deficiencies are rampant such as communities in the new introduction areas of East and Central Africa. The crop is suitable for low-input agriculture on small farm holdings (Zanklan *et al.*, 2007;

Rodríguez-Navarro *et al.*, 2009) because of its capability to improve soil fertility through Rhizobium-Bradyrhizobium-facilitated nitrogen-fixation (Castellanos *et al.*, 1997), minimal pest incidences due to insecticidal rotenone in seeds and shoot (Grüneberg *et al.*, 1999; Lautié *et al.*, 2013), relatively short growth cycles, and wide geographic adaptation even in semi-arid conditions (Diouf *et al.*, 1998; Belford *et al.*, 2001). Yam bean gives high and stable yields of up to 80 t ha⁻¹ of edible storage roots (Sørensen, 1996; Karuniawan, 2004); making its yield potential comparable to other root and tuber crops, such as cassava (*Manihot esculenta* Crantz) and sweetpotato (*Ipomoea batatas*) (Zanklan *et al.*, 2007).

Storage root dry matter content in root crops is important for consumption and industrial processing (Tumwegamire *et al.*, 2011), yet most yam bean varieties have low RDM which limits adoption (Zanklan *et al.*, 2007; Agaba *et al.*, 2016). Potential for improvement of RDM lies in hybridisation with the high RDM cultivar of *Pachyrhizus tuberosus* called the chuin (Ørting *et al.*, 1996; Grüneberg *et al.*, 2003; Zanklan *et al.*, 2007). The chuin is known for high RDM (26 to 36%) and can be cooked or processed like cassava to “gari”, a food staple for millions of people in West Africa (Zanklan *et al.*, 2007; Padonou *et al.*, 2013).

Through hybridisation and selection, the chuin may improve dry matter content of *P. erosus* accessions with high yields, wide adaptation, and drought tolerance (Belford *et al.*, 2001) and the *P. ahipa* accessions, with early maturity and erect or semi-erect growth habit (Zanklan *et al.*, 2007). While studying the possibility of incorporating high dry matter

from the chuin into the broader yam bean gene pool, Grüneberg *et al.* (2003) observed fertile and vigorous interspecific hybrids between *P. tuberosus*-chuin and *P. erosus* and *P. ahipa* accessions.

The improvement of storage RDM has been identified as a major breeding goal for yam beans (Grüneberg *et al.*, 2003; Zanklan *et al.*, 2007), but the crop remains genetically under-exploited; with a general lack of genetic studies on dry matter content. A recent study by Jha and Singh (2014) reported positive and significant combining abilities (GCA and SCA effects) for quantitative traits in Mexican yam bean (*Pachyrhizus erosus* L. Urban) such as root yield, root length and root girth. However, these results have not been corroborated across the cultivated yam bean species and no progress has been made to study inheritance of RDM in yam beans. This study, therefore, was conducted to estimate variance components, combining ability and heritability so as to infer the inheritance of RDM in yam bean as a basis for improvement through selection.

MATERIALS AND METHODS

Experimental sites. The field study was carried out at the National Crops Resources Research Institute (NaCRRI) at Namulonge in Central Uganda. It is located at 0° 32'N and 32° 35'E, 1150 metres above sea level, and experiences a mean annual temperature of 22.2 °C and a bimodal rainfall pattern with a mean of 1270 mm. Namulonge is characterised by red ferralitic soils with low pH (4.9-5.0) (Tumwegamire *et al.*, 2011)

Development of breeding populations. Nine yam bean accessions, with varying RDM, were crossed to generate F₁ progenies (Table 1). Three high dry matter cultivars belonging to *P. tuberosus*-chuin were used as male parents and crossed with six low dry matter female parents; three of which were *P. ahipa*

and three *P. erosus* accessions. The crosses were done following North Carolina II (NC II) mating design, with no reciprocals in accordance with Comstock and Robinson (1952) to generate a mixture of 16 full- and half-sib F₁ families.

Field evaluations. The seeds of each of the 16 F₁ progenies and their 9 parents were planted under field conditions at Namulonge, during the first rains of April, 2013. Plots consisted of two ridges, each measuring 3 metres long and 1 metre apart. Seeds were sown on ridges by hand at a spacing of 0.3 metre between plants. Plots were arranged in a randomised complete block design (RCBD) and replicated twice due to limited seed.

The experiments were kept weed free and no reproductive pruning of flowers was done or fertilisers or agrochemicals applied during the crop growth cycle. From the F₁ experiment, seeds were allowed to mature and were harvested on single plant basis, dried and planted in an F₂ experiment during the first rains of 2014. However, two crosses, namely 209022 x 209015 and 209031 x 209015, did not produce F₁ seed and were, therefore, excluded from the evaluations (Table 1).

Data collection. The F₁ and F₂ experiments were harvested six months after planting in 2013 and 2014, respectively. Three storage roots were randomly selected from each genotype and taken to the NaCRRI nutrition quality laboratory for determination of RDM. The sampled roots were washed thoroughly using flowing tap-water to minimise soil contamination, then peeled and sectioned into multiple longitudinal slices. The slices were mixed together and a sample of 100 g fresh weight was packed in polythene bags and vacuum-freeze dried at -31°C for 72 hours, using a vacuum freeze drier, YK-118-50, True-Ten Industries, Korea, 1995. The freeze dried samples were weighed immediately after leaving the freeze drier and their dry weight

TABLE 1. CIP code names and characteristics of parents and crosses evaluated in F₁ and F₂ under field conditions at NaCRRRI, Namulonge in Central Uganda

CIP code names		Species	Plant type	^b RDM Classification
Crosses	Parents			
209076	209004	<i>P. ahipa</i>	Erect	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209077	209004	<i>P. ahipa</i>	Erect	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209079	209022	<i>P. ahipa</i>	Erect	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209078	209004	<i>P. ahipa</i>	Erect	Low RDM
	209015	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209080	209022	<i>P. ahipa</i>	Erect	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209082	209031	<i>P. ahipa</i>	Erect	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209083	209031	<i>P. ahipa</i>	Erect	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209085	209016	<i>P. erosus</i>	Spreading	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209086	209016	<i>P. erosus</i>	Spreading	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209087	209016	<i>P. erosus</i>	Spreading	Low RDM
	209015	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209088	209018	<i>P. erosus</i>	Spreading	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209089	209018	<i>P. erosus</i>	Spreading	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209090	209018	<i>P. erosus</i>	Spreading	Low RDM
	209015	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209091	209019	<i>P. erosus</i>	Spreading	Low RDM
	209013	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209092	209019	<i>P. erosus</i>	Spreading	Low RDM
	209014	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM
209093	209019	<i>P. erosus</i>	Spreading	Low RDM
	209015	<i>P. tuberosus - chuini cultivar</i>	Spreading	High RDM

^aCIP = International Potato Center; ^bRDM = storage root dry matter content; Low RDM < 20%; High RDM > 25%

recorded. RDM was calculated as the average difference between flesh and dry weight estimates (Wilken *et al.*, 2008).

Statistical and genetic analyses. Mean performance of the crosses and parents were obtained based on the general analysis of variance model in GenStat 14th edition (VSN International Ltd, Hemel Hempstead, UK) (Payne *et al.*, 2011). The means of crosses

were further processed using the general combining ability model in which male and female parents were fitted as fixed factors and the residual taken as an estimate of SCA effects (female x male interaction). GCA effects were estimated from the parameter estimates for parents from the ANOVA of North Carolina II design (NCII); while the SCA effects were calculated as the difference between the observed and predicted means of RDM in

crosses. The significance of GCA and SCA effects were tested using a standard t-test. The estimates of narrow sense heritability (NSH), broad sense heritability (BSH) and Baker's ratio were calculated from the GCA and SCA variance components analysis following Falconer *et al.* (1996);

$$\text{NSH} = \left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} \right] / \left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} + \sigma^2_e \right],$$

Where:

σ^2 = Sample variance,

$[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}}]$ = Additive gene effects,

$[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} + \sigma^2_e]$ = Phenotypic effects, and

σ^2_e = Error variance

While BSH, which estimates the proportion of phenotypic variation due to total genetic effects:

$$\text{BSH} = \left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} \right] /$$

$$\left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} + \sigma^2_e \right],$$

Where:

$$\left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} \right] =$$

Total genetic effects, and

$$\left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} + \sigma^2_e \right] =$$

Phenotypic effects

Then Baker's ratio (BR) was calculated as:

$$\text{BR} = \left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} \right] / \left[\sigma^2_{\text{GCA(Female)}} + \sigma^2_{\text{GCA(Male)}} + \sigma^2_{\text{SCA}} \right]$$

The gene action controlling inheritance of RDM in yam bean was inferred from the relative magnitudes of GCA and SCA. Baker's ratio was used to estimate the relative significance of additive and non-additive gene effects (Baker, 1978). In the estimation of genetic parameters using NCII ANOVA, we assumed no maternal effects and epistasis (Kearsey and Pooni, 1998) in the inheritance of RDM in yam beans.

RESULTS

Analysis of variance. The mean squares of crosses were highly significant ($P < 0.001$) in both F_1 and F_2 generations (Table 2). Also, the mean squares for male general combining ability (GCA_{male}) were significant ($P < 0.01$) for RDM in both F_1 and F_2 generations. However, the GCA estimates for female parents were not consistent across F_1 and F_2 generations, giving significant ($P < 0.001$) mean squares only in F_2 . Moreover, the mean squares for female GCA affects were four times higher than for the male parents in the F_2 generation (Table 2). The interaction mean squares between male and female parents (SCA effects) were highly significant ($P < 0.001$) in both F_1 and F_2 generations. The variance components for GCA effects were higher than SCA effects giving a predictability ratio ($\sigma^2_{\text{GCA}}/\sigma^2_{\text{SCA}}$) higher than unity for males in F_1 , as well as females in F_2 (Table 2). The predictability ratio for GCA_{male} were three times as large as the SCA effects ($\sigma^2_{\text{GCA}}/\sigma^2_{\text{SCA}} = 3.13$) in F_1 generation. However, the combining ability of both parents was not consistent because the predictability ratio for female parents and male parents in F_1 and F_2 , respectively, were lower than unity.

Heritability and Bakars' ratio. The RDM showed high narrow sense heritability estimates namely, 0.74 in F_1 and 0.75 in F_2 generation. Similarly, the broad sense heritability estimates were high (0.97) across F_1 and F_2 generations. Baker's ratio estimates for RDM were also consistently high at 0.76 and 0.78 in F_1 and F_2 , respectively (Table 2).

TABLE 2. Mean squares, combining abilities, heritabilities and Baker's ratios for RDM in F₁ and F₂ yam bean progenies evaluated at Namulonge in Central Uganda

Source of variation	df	F ₁ Population		F ₂ Population	
		Mean squares	F test	Mean squares	F test
Crosses	15	22.23***	9.18E-08	22.79***	2.85E-13
GCA _{female}	5	0.91	0.757449	39.37	6.56E-13
GCA _{male}	2	72.25***	2.39E-08	10.54**	0.001394
SCA	8	23.05***	5.99E-07	14.44***	1.02E-07
Residual	23	1.745		1.38	
CV%		6.16		6.63	
Variance components					
σ^2 GCA _F		0.52		28.53	
σ^2 GCA _M		41.40		7.64	
σ^2 SCA		13.21		10.46	
σ^2 GCA _F / σ^2 SCA		0.04		2.73	
σ^2 GCA _M / σ^2 SCA		3.13		0.73	
NSH		0.74		0.75	
BSH		0.97		0.97	
Bakers' ratio		0.76		0.78	

df = degrees of freedom; CV = coefficient of variation; GCA = General combining ability; SCA = specific combining ability; NSH = Narrow sense heritability; BSH = Broad sense heritability; σ^2 = variance; F = Female; M = Male; ** and *** significant at P<0.01 and <0.001, respectively

Combining ability effects. On the basis of the estimated GCA effects (Table 3), male parent 209014 contributed positive and significant GCA effects (P<0.001) in F₁ and F₂ generation while female parents; 209016 and 209018 showed significant and positive GCA effects only in F₂ generation. Negative and significant GCA effects were recorded for male parent 209013 in both F₁ and F₂, as well as female parent, 209022 in F₂ generation.

SCA effects were highly significant (P<0.001) for crosses 209022 x 209013 and 209022 x 209014 in F₁ generation, but these crosses did not produce F₂ seed and could not be evaluated in the F₂ experiment (Table 4). Crosses that gave positive SCA effects across F₁ and F₂ included 209004 x 209014, 209016 x 209013, 209018 x 209013, 209018 x 209015 and 209019 x 209013 (Table 4). Conversely,

the cross 209019 x 209014 had negative SCA effects in both F₁ and F₂ generations.

Performance of parents and progenies.

The RDM values for crosses in F₁ generation varied from 10.32% in 209022 x 209013 to 34.11% in 209022 x 209014 (Fig. 1). However, the best performing cross (209022 x 209014) in F₁ generation did not produce F₂ seed and was eliminated from further analysis.

The cross 209004 x 209014 with RDM of 25.43% was the next best, and consistently performed better than the respective means in F₁ and F₂ populations. Whereas crosses, 209016 x 209013 and 209016 x 209014 had less RDM than the population mean of 21.43% in F₁ generation, the same crosses rebounded with higher

TABLE 3. General combining ability (GCA effects) for RDM in the F₁ and F₂ yam bean progenies evaluated at Namulonge in Central Uganda

Parent	GCA effects	
	F ₁ Population	F ₂ Population
209013	-3.701***	-1.137***
209014	3.169***	1.683***
209015	0.799	-0.397
209004	0.376	0.373
209016	-0.924	3.323***
209018	0.116	3.163***
209019	-0.124	-0.887
209022	1.056	-10.307***
209031	-0.224	-0.817
SE	1.159	2.985

SE = Standard error; *** Significant at P<0.001

TABLE 4. Specific combining ability (SCA) effects for RDM in F₁ and F₂ yam bean progenies evaluated at Namulonge in Central Uganda

Crosses	SCA estimates	
	F ₁ Population	F ₂ Population
209004 x 209013	0.086	-2.197
209004 x 209014	0.46	0.499
209004 x 209015	-0.546	1.698
209016 x 209013	1.423	3.59
209016 x 209014	-2.134	0.716
209016 x 209015	0.711	-4.306
209018 x 209013	2.22	1.383
209018 x 209014	-2.627	-2.711
209018 x 209015	0.407	1.328
209019 x 209013	3.09	0.327
209019 x 209014	-2.517	-1.607
209019 x 209015	-0.573	1.281
209022 x 209013	-8.462***	-
209022 x 209014	8.462***	-
209031 x 209013	1.643	-3.103
209031 x 209014	-1.643	3.103
S.E	1.868	0.959

S.E = standard error; *** significant at P<0.001

RDM values at 23.5 and 22.4% respectively, in comparison to the mean of 17.73% in the F₂ generation. Crosses, 209004 x 209015, 209018 x 209014, 209018 x 209015 and 209031 x 209014, had higher dry matter values than their respective generation means across F₁ and F₂ populations. The cross 209022 x 209013 had the lowest RDM at 10.32 and 5.89% in F₁ and F₂ generations, respectively. The evaluated parents could be classified into two groups, namely high dry matter genotypes (209013, 209014 and 209015) with a range of 29.32 to 33.21% and the low dry matter group (209004, 209016, 209018, 209019, 209022 and 209031) with RDM of 7.83 to 15.72% (Fig. 1).

DISCUSSION

Genetic variability and inheritance of RDM.

The combining ability analysis revealed significant variances for both GCA and SCA effects demonstrating that both additive and non-additive gene effects play vital roles in the expression of RDM in early generations of yam bean breeding. The results revealed the presence of significant genetic variation between crosses and among both male and female parents indicating potential for selection of high dry matter lines to improve RDM in yam beans. GCA mean squares were three and two times higher than SCA mean squares for males and females in F₁ and F₂, respectively (Table 2) which suggested preponderance of additive gene action in the inheritance of RDM. Nonetheless, significant SCA mean squares for RDM in F₁ and F₂ indicated non-allelic interaction among the parents and demonstrated inconsistency of males over different female parents across the two generations.

High narrow sense heritability suggested that the performance of the progenies could be succinctly predicted from the parents and confirmed potential for selection of superior

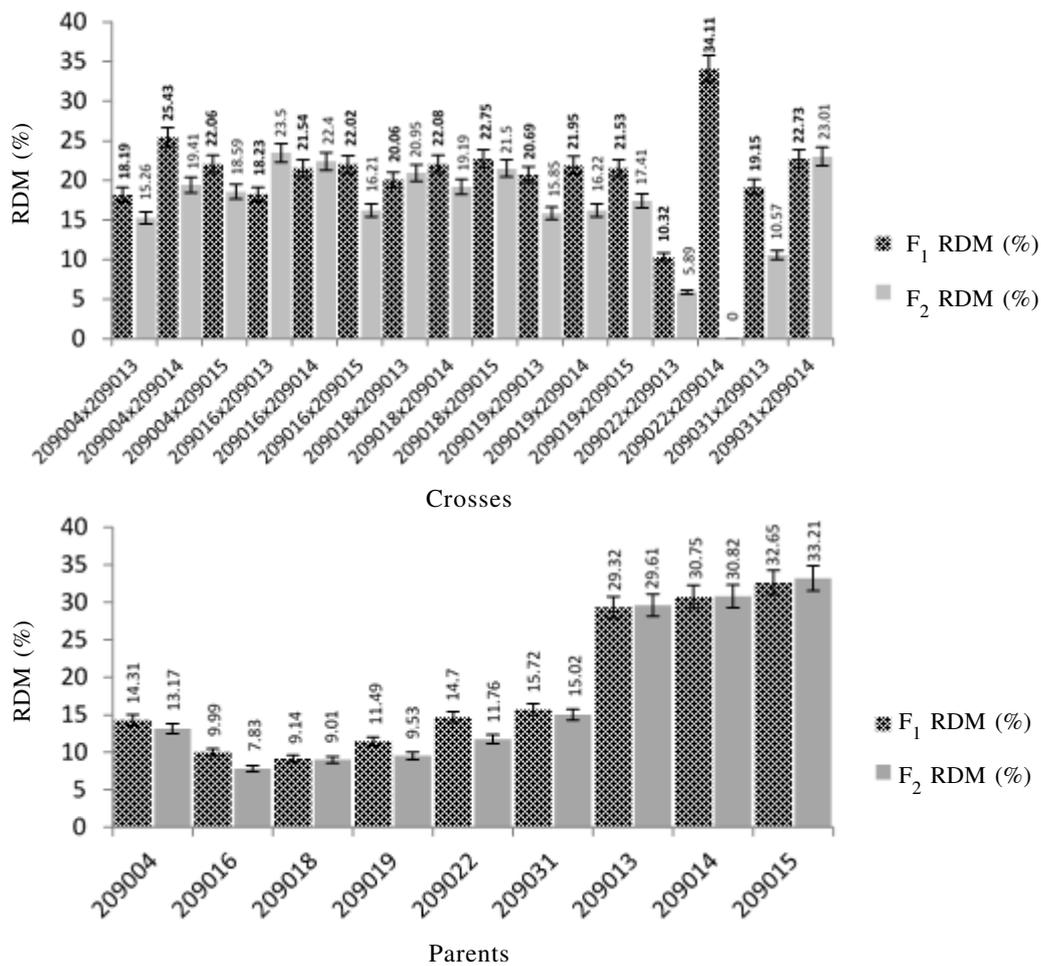


Figure 1. Storage root dry matter content of parents and crosses in F₁ and F₂ yam bean populations evaluated at Namulonge in Central Uganda.

genotypes with significant response to selection for RDM in early generations of yam bean breeding. The broad sense heritability was similarly high indicating the genetic potential of the parents to largely pass on the RDM trait to subsequent generations. This result is in agreement with the findings by Grüneberg *et al.* (2003) which demonstrated that introgression of high RDM from the chuin into the remaining cultivated yam bean gene pool was possible resulting in fertile and vigorous progenies. High heritability estimates for RDM and associated traits in yam beans have been

reported elsewhere (Sørensen, 1996; Agaba *et al.*, 2016).

The high estimates for Baker's ratio in F₁ and F₂ generations (Table 2) indicated the importance of additive genetic effects in the inheritance of RDM in yam bean which suggests that the genes controlling RDM can easily be fixed in advanced generations. A ratio that is closer to unity enhances the argument for predominance of additive genes in the inheritance of the trait. High Baker's ratio reveals the relative importance of GCA to SCA effects in the genetic determination of RDM

in yam beans, and shows that progeny performance can be predicted based on GCA effects of parents. This observation is supported by the argument that the ratio of additive to non-additive variance in a population gives an indication of relative importance of GCA and SCA estimates in predicting progeny performance (Owolade *et al.*, 2009).

High predictability ratios ($\sigma_{GCA}^2/\sigma_{SCA}^2$) confirmed the prevalence of additive gene effects in the inheritance of RDM. Bi *et al.* (2015) argued that a large ratio between GCA and SCA effects reveals the relevance of additive gene effects while a small value signifies the presence of dominant and/or epistatic gene effects. This finding rationalises our earlier notion that additive gene effects are more influential than non-additive gene effects in the inheritance of RDM in yam beans.

The presence of additive gene effects indicates a high chance for predicting the performance of progenies based on phenotypic scores of the parents. The action of additive gene effects in the inheritance of RDM is supported by the arguments of Grüneberg *et al.* (2003), that improvement of root dry matter content in the yam beans is possible through inter- and intra- specific hybridisation. However, gene effects in the present study might have been overestimated because combining ability studies from one location tend to have high genetic effects and capture less environmental variance. Such results cannot be generalised beyond the particular test environment. Consequently, increasing sample size, replication and testing of progenies across multi-locations might improve genetic parameter estimates for RDM in yam beans.

Combining abilities. Significant GCA effects were observed for several parents in this study (Table 3) suggesting the presence of additive gene effects in the expression of RDM among the parents. The positive GCA effects obtained identified most of the current parents with potential for use in breeding programmes to develop high RDM yam bean varieties. Female

parents; 209016 and 209018 had high GCA effects which made them good combiners for improvement of RDM in yam beans. The male parent, 209014 had significant GCA effects which identified it as the only good combiner for improvement of RDM among the three *P. tuberosus*-chuins used. According to Kearsley and Pooni (1998), the magnitudes of GCA and SCA estimates shows the importance of additive and non-additive gene effects in the inheritance of quantitative traits and offer vital genetic information about potential genetic progress in breeding programmes. Therefore, a breeder may use the current parents (209014, 209016 and 209018) to improve RDM in yam beans through interspecific hybridisations. These parents might constitute vital sources of high RDM genes for initiating a breeding programme to improve RDM among the yam bean germplasm in Uganda. The results further identified the parents with positive but non-significant GCA estimates either in F_1 or F_2 (209015, 209004, and 209022) as suitable genotypes for inclusion in yam bean breeding programmes. Conversely, parents with negative significant GCA effects, namely, 209013 and 209022 are less desirable in the development of high dry matter yam beans because such parents might be poor combiners for RDM.

Crosses with positive SCA effects in F_1 and F_2 (Table 4) represent promising families to select for high RDM genotypes in future yam bean breeding programmes. It was observed that crosses with positive and significant SCA effects also gave high values of RDM compared to the population means in F_1 and F_2 generations. Such associations between SCA effects and mean performance of the crosses have been reported in yam beans (Jha and Singh, 2014), suggesting that environmental factors such as drought would influence RDM of root crops. This finding is supported by the observations of Zanklan *et al.* (2007) which revealed high root dry matter content in yam beans grown under water stressed conditions at Niaouli compared to the irrigated location

at Songhai in Benin. The crosses that failed to produce F_2 seed in this study demonstrated the inherent low rate of successful crossings and high rates of flower abortions associated with interspecific hybridisation among *Pachyrhizus* species (Grüneberg *et al.*, 2003).

Previously, significant GCA and SCA effects and predominance of additive genes for inheritance of root traits such as root length, girth yield and earliness in yam beans were reported by Jha and Singh (2014). Even though Jha and Singh (2014) did not investigate the dry matter trait, it could be hypothesised that inheritance of RDM would not significantly deviate from the other quantitative root traits in yam beans.

Dry matter in parents and progenies. The mean RDM content of parents and crosses in the evaluated yam bean germplasm (Fig. 1) falls within the ranges reported elsewhere (Sørensen, 1996; Grüneberg *et al.*, 2003; Zanklan *et al.*, 2007). However, the yam bean parents used in this study can be categorised into the low RDM genotypes (*P. erosus* and *P. ahipa*) and high dry matter genotypes that belong to *P. tuberosus* - chuin cultivar. The chuin is the only high dry matter cultivar among the four groups of *P. tuberosus* known as Ashipa, Yushpe, and Jíquima cultivars (Sørensen, 1996). Recent molecular characterisation has shown a clear separation between chuin and Ashipa cultivar groups (Santayana *et al.*, 2014). The use of the chuin in this study demonstrated high transmissibility of the RDM trait in yam beans, and the results demonstrated high potential for crop improvement and integration of the yam bean into new farming systems in Africa as envisaged by Zanklan *et al.*, 2007 and Heider *et al.*, 2011. This finding revealed that the evaluated yam bean germplasm has potential for improvement of storage root dry matter content (RDM) which could accelerate adoption of the crop in Uganda where high dry matter trait is preferred among root crops for consumption and industrial applications.

CONCLUSION

This study demonstrates that the evaluated yam bean germplasm has potential for improvement of storage root dry matter content (RDM) in yam beans. It is also clear that the inheritance of RDM in yam beans is conditioned by both additive and non-additive gene effects; although additive gene action is predominant and associated with high Baker's ratios and narrow-sense heritabilities across F_1 and F_2 generations. The predominance of GCA over SCA variance suggest that stringent early generation selection would be effective to improve RDM in the current yam bean germplasm. The identified suitable parents and crosses should enhance selection of breeding strategies for high genetic gain in the development of high dry matter varieties in future yam bean breeding programmes.

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