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INTER-RELATIONSHIPS AMONG TRAITS AND PATH ANALYSIS FOR YIELD COMPONENTS OF CASSAVA: A SEARCH FOR STORAGE ROOT YIELD INDICATORS

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ABSTRACT

Research aimed at selecting varieties of cassava (*Manihot esculenta* Crantz) with potential for high storage root yields through identification of stable yield components that can be used as selection criteria was carried out at three locations of different altitudes in Uganda. Multiple regression and simple phenotypic correlation coefficients revealed that storage root number and storage root weight were important components in storage root yield across locations. The path analysis identified leaf area, storage root number, storage root girth and storage root weight as the main yield components with root number (0.53) and storage root weight (0.45) having the highest values of direct path coefficient. Probably due to environmental influence, only 43% of the total variation of the storage root yield relationship was explained by the path coefficient analysis.

Keys Words: *Manihot esculenta,* multiple regression, phenotypic correlation, yield components

RÉSUMÉ

Une recherche visant à sélectionner des variétés potentielles à haut rendement en tubercules du manioc (*Manihot esculenta* Crantz) par identification des composantes stables de rendement qui peuvent étre utilisées comme critères de selection a été conduite dans trois localités de differentes altitudes en Uganda. La régression multiple et les simples coéfficients de correlation phénotypique ont revélé que le nombre de tubercules et le poids moyen des tubercules étaient des principales composantes du rendements des tubercules à travers tous les sites. L'analyse dès chemins a indiqué quatre caractères: la surface folière, le nombre des tubercules, le diamètre des tubercules et le poid moyen des tubercules comme composantes importantes avec le nombre des tubercules et le poids moyen des tubercules ayant 0.53 et 0.45 comme coefficient de chemin direct respectivement. Due probablement à une grande influence environnementale, seulement 43% de la variation totale du rendement des tubercules ont été expliqués par l'analyse des coefficients de chemin.

Mots Clés: *Manihot esculenta,* régression multiple, correlation phénotypiques, composantes du rendement

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is one of the most important sources of food energy in several tropical countries. Since its introduction into Africa, cassava has spread through sub-Saharan Africa to become one of the dominant starchy staples in the diet of the people. Africa produces 80 million tonnes of cassava annually, translating into an estimated 300 calories per day for 200 million people (Nweke and Enete, 1999). Cassava can produce reasonably well under marginal conditions of climate and soils where other crops cannot (Iglesias *et al.*, 1997). Its high productivity per unit of land and labour, advantageous flexible harvesting date, ability to recover from pest attack and reputation as a famine reserve make this root crop a basic component of the farming systems in many areas of Africa (Nweke and Enete, 1999). As a consequence, any improvement of the efficiency in selecting and identifying cassava genotypes suitable to the different environments would have great potential in terms of human nutrition.

Storage root yield , the main goal of a cassava breeding programme, is a complex quantitativily inherited trait and difficult to improve directly. Although progress has been made in terms of storage root yields (Kawano *et al.*, 1987), the problem of identifying appropriate indicators of yield during selection process still remains. Hahn and Hozyo (1984) suggested that yield in cassava has three components: the number of storage roots per unit area, the average root weight and the percentage of dry matter content of storage roots. However, attempts to identify the index of selection using simple correlation analysis did not confirm dry matter to be an important indicator of the storage root yield (Mahungu, 1983, 1994a; Ntawuruhunga, 1992; Varma and Matura, 1993). Kawano *et al.* (1987) reported that selection for dry matter content could be conducted without serious impact on other yield components. Kang (1994) suggested that improvement of such complex trait could be handled through indirect selection, i.e., selection for a component trait or traits involved in the pathway leading to the formation of the complex trait.

Path-coefficient analyses have been deemed more informative and useful than simple correlation coefficients (Kang, 1994; Gravois and McNew, 1993). A path coefficient is a standardised partial regression coefficient, which measures the direct influence of one trait upon another trait and permits the separation of correlation coefficients into components of direct and indirect effects (Li, 1977). A path-coefficient analysis simultaneously captures the effects of intricate relationships among various traits under study. Useful information obtained from simple correlation coefficients can be enhanced by partitioning them into direct and indirect effects for a set of a priori cause-effects interrelationship, as has been demonstrated in various crops (Kang *et al.*, 1983; Gravois and Helmes, 1992; Gravois and McNew, 1993; Board *et al.*, 1997). Once a plausible diagram indicating relationship between cause and effect is obtained, then path coefficient becomes an effective statistical tool to describe direct and indirect effects of yield components.

The objective of this study was to investigate the relationship among storage root yield components.

MATERIAL AND METHODS

Field experiments were conducted at Bulisa, low-altitude (02° 02' N latitude, 31° 25' E longitude, 650 m a.s.l), Namulonge, mid-altitude (0° 32' N latitude, 32° 53' E longitude, 1250 m a.s.l) and at Kapchorwa, high-altitude (01° 24' N latitude, 34° 27' E longitude, 1750 m a.s.l.) in Uganda during 1997/98 and 1998/99 growing seasons.

Ten cassava genotypes were used, two originating from each source viz. East Africa lowland (Nyarukuhi and Nyarubekane), mid-altitude (Migyera and SS4), and high altitude (Eala 07 and Serere) and West Africa lowland (TMS 81/01365 and TMS I 91/0057) and midland altitude (TMS I 91/0067 and TMS I 92/0397). No fertiliser was applied and only manual weeding was done, whenever necessary. A complete randomised block design with plot size of 5 m x 16 m and a spacing of 1 m x 1 m replicated three times was used at each location. Stem cuttings, each 25 cm long with at least four nodes, were planted horizontally.

Data were collected three times at three, six and nine months after planting from a destructive sampling plot 3 m wide by 2 m long. The data collected included plant height, height at first branching, stem diameter at 15 cm above ground, average internode length of the first five nodes on the main stem, storage root number, storage root girth, fresh weight of leaves, fresh weight of stems, storage fresh yield, storage root dry matter, and sugar and starch content. Dry yield was estimated by multiplying fresh storage root yield by dry matter content (Kawano *et al.*, 1987). Simple phenotypic correlation analysis was performed to study any linear relationship between the different plant traits. Multiple regression analysis was performed for each location and a combined regression analysis over locations was done to determine which variables adequately and consistently explained the observed variation for cassava storage root yield. Two statistical criteria were used to choose the best regression equation; the coefficient of determination (R^2 adjusted) and Mallow's statistic, C(p) (SAS, 1988). R^2, gives an indication of how the variation of yield was explained by the linear function of the independent variables (Gomez and Gomez, 1984) and the second $C_{(P)}$, permits comparison of the different prediction models and the one with the smallest numerical value is the fitted model.

Only one-year results were used for the path analysis since genotype x year interaction was indicated (Steel *et al.*, 1980). Callis model analysis (SAS, 1988) was used to investigate the causal effects of the storage root yield and five variables were used to prepare a path analysis.

Based on the diagram of causation (Fig. 1) simultaneous equations (n-1) for calculating direct effects of each of four traits (1 to 4) on the trait number 5 were developed

$$\begin{aligned} P_{15} + r12\,P_{25} + r_{13}P_{35} + r_{14}\,P_{45} &= r_{15} \\ r_{12}P_{15} + P_{25} + r_{23}P_{35} + r_{24}\,P_{45} &= r_{25} \\ r_{13}P_{15} + r_{23}\,P_{25} + P_{35} + r_{34}\,P_{45} &= r_{35} \\ r_{14}P_{15} + r_{24}\,P_{25} + r_{34}P_{35} + P_{45} &= r_{45} \end{aligned}$$

where r_{ij} represent correlation coefficient between ith and jth traits (i= 1 to 4, and j=2 to 5) and Pi_5 represents direct effect of ith trait on trait number 5.

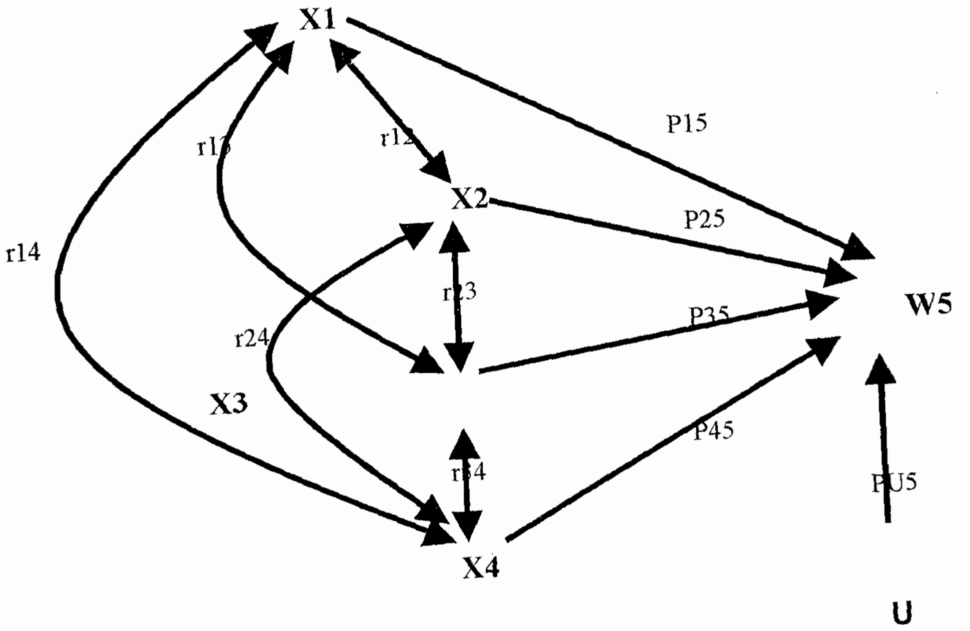

Figure 1. Causation diagram indicating relationships between storage root yield and yield traits.
X(1) is storage root number; X(2) is storage root weight; X(3) is storage root girth; X(4) is total leaf area; W (5) is storage root yield and U is the residual.

RESULTS AND DISCUSSION

Storage root dry yield was positively correlated (P<0.01) with storage root number (r=0.53), storage root weight (r=0.37), storage root girth (r=0.54), stem girth (r=0.38), weight of leaves (r=0.38) and weight of stems (r= 0.58) (Table 1) suggesting that these traits contributed to dry yield. Sugar content was positively (r=0.20, P <0.05) correlated with leaf area and negatively correlated with dry matter content (r=0.28, P <0.01). Starch content was only significantly positive correlated (r=0.32, P<0.001) with dry matter content. CIAT (1975) and Kawano *et al.*, (1987) reported similar results on the relationship between starch and dry matter content. However, dry matter content was significantly negatively correlated (P<0.01) with storage root weight (r=-0.25), suggesting that when the storage root weight is big the dry matter content tend to be low. Mahungu *et al.* (1994a) reported that dry matter of storage root exhibits least merit in comparison with other plant traits evaluated in yield variation. The high correlation coefficients obtained for storage root number and girth suggested that they were the most important traits contributing to storage root dry yield components. Kasele (1983) reported that storage root number was more closely correlated with root dry weight than individual weight of storage roots and that consequently yield increase was mainly due to the increase in both numbers of storage roots and individual storage roots weight. However, the results of the simple correlation analysis found none of the storage root traits to be related to cyanogenic potential. Mahungu *et al.* (1994a) reported similar findings and a low broad-sense heritability (0.35-0.32) for this trait. They concluded that cyanogenic potential does not confer a useful survival or protective mechanism on the plant. Tai (1990) suggested, however, that physiological process might have a direct or indirect influence on the final yield that is obtained.

The results of multiple regression analysis for each location and for the combined data over locations are presented in Table 2. They indicated that the fresh storage yield variation varied from one location to another, indicating location effect. However, two independent variables, storage root number and storage root weight were found to be

TABLE 1. Phenotypic correlation coefficients among quantitative morphological characteristics measured at three locations in Uganda during two years for 10 cassava genotypes

	ptht	La	ptiol	rtn	rt wt	rtdia	stmdi	wtlvs	wtstm	dmc	sugar	starch	cnp
Dryld	0.49***	0.15	0.15	0.53***	0.37***	0.54***	0.38***	0.38***	0.58***	0.09	0.06	0.02	0.11
Ptht	-	-0.31***	0.15	0.26**	0.21**	0.48***	0.44***	0.26***	0.56***	0.20*	-0.10	0.05	0.03
La		-	-.31***	0.49***	0.26**	0.21*	0.48***	0.44***	0.26**	0.56***	0.20*	-0.19	0.08
Ptiol			-	0.17*	-0.04	-0.01	0.06	0.46***	0.34***	-0.01	0.12	-0.19	0.09
Rtn				-	-0.23**	0.30***	0.30***	0.40***	0.42***	0.01	-0.14	0.06	0.02
Rtsize					-	0.41***	0.23**	0.05	0.31***	-0.25**	-0.02	0.06	0.01
Rtdia						-	0.69***	0.13	0.36***	-0.08	-0.09	0.16	0.08
Stmdi							-	0.34***	0.44***	0.01	-0.12	-0.02	0.10
wtlvs								-	0.78***	0.15	-0.01	-0.32	0.12
wtstm									-	0.12	-0.10	-0.21	0.07
dmc										-	-0.28***	0.32***	0.03
sugar											-	-0.01	0.05
starch													
cnp													-

Where: ptht=plant height; La= leaf area; dryld= dry yield; ptiol=petiole length; rtn=storage root number; rt wt = storage root weight ; rtdia=storage root girth; stmdi=stem girth; wtlvs=weight of leaves; wtstm=weight of stems; dmc=dry matter conten; cnp: cyanogenic potential

*, **, and ***: Significant at 5%, 1% and 0.1% respectively

common to best-fit models at all locations, suggesting that the two are very important in storage root determination. The storage root girth was retained in the model at low and mid-altitude and in the combined model but not at high altitude.

The best model for mid-altitude (R^2=0.92, $C_{(P)}$ =2.7) gave a fitting equation with the following indicators: plant height, leaf area, storage root number, storage root weight, and storage root girth. At low altitude, the equation included leaf area, petiole length, storage root number, and weight of stems of the plant (R^2=0.78, $C_{(P)}$ =5.7) while only height at first branching, storage root number and storage root weight were responsible for the variation in storage root yield at high altitude (R^2=0.78, $C_{(P)}$ =1.7). The combined model had the following parameters: leaf area, petiole length, storage root number, storage root weight, storage root girth, weight of stem, and starch content of the storage root (R^2=0.70, $C_{(P)}$ =5.6). All variables retained in the linear models contributed significantly ($P<0.05$) to the variation for storage root yield. The coefficient of determination was highest at mid-altitude (R^2=0.98) with low and high altitudes having R^2=0.78. The variables that were consistently

TABLE 2. Regression equations for determining storage root yield with several cassava plant traits

Altitude	Location	Variable	Parameter estimated	SE	Probability
Low	Bulisa	Intercept	0.123	0.693	0.860
		Leaf area	-0.041	0.012	<0.003
		Petiole length	0.141	0.032	<0.001
		Storage root number	0.202	0.052	<0.001
		Storage root weight	1.846	0.519	<0.001
		Storage root girth	0.049	0.009	<0.001
		Weight of stem	-0.170	0.087	<0.05
		R^2 (adjusted)	0.78		
		C(p)	5.7		
Medium	Namulonge	Intercept	-0.772	0.725	0.299
		Plant height	0.009	0.003	<0.001
		Leaf area	-0.032	0.009	<0.001
		Storage root number	0.418	0.052	<0.001
		Storage root weight	12.626	1.201	<0.001
		Storage root girth	-0.029	0.014	<0.05
		R^2 (adjusted)	0.92		
		C(p)	2.7		
High	Kapchorwa	Intercept	-0.238	0.505	0.643
		Height of 1st branching	-0.283	0.008	<0.05
		Storage root number	0.283	0.051	<0.001
		Storage root weight	6.263	0.854	<0.001
		R^2 (adjusted)	0.78		
		C(p)	1.7		
	Combined	Intercept	0.369	0.607	0.545
		Leaf area	-0.024	0.009	<0.01
		Petiole length	0.104	0.028	<0.001
		Storage root number	0.280	0.040	<0.001
		Storage root weight	2.488	0.404	<0.001
		Stiorage root girth	0.045	0.007	<0.001
		Weight of stem	-0.221	0.058	<0.001
		Starch content	-0.015	0.006	<0.05
		R^2 (adjusted)	0.70		
			C(p)	5.6	

SE: Standard error for estimates
C(p): Mallow's statistic
R^2 adjuste): Adjusted coefficient of determination

important were storage root number, storage root weight, and storage root girth. Williams (1972) reported similar results that storage root diameter was a major component in yield whereas Varma and Mathura (1993) suggested that storage root weight and girth could constitute effective indirect selection for yield. The results indicated that storage root yield was relatively well predicted at mid-altitude.

The variation of storage root yield at high altitude and low altitude was not accounted for by the same independent variables as at mid-altitude. The results also showed that variables from the combined data explained only 70% of the total storage yield variation. The unaccounted variation was most likely due to the interdependency of variables, to G x E as previously indicated and to random factors that constitute the noise. It suggests also that we do not know or have not included in this study all the underlying causes which contribute to variation in yield (Sokal and Rohlf, 1995).

Causal-effects and interrelationship for storage root yield. Based on the results of simple correlation and regression analysis, only five variables were found to be more related to storage root yield and were used in path analyses. Indirect path analysis was used to determine the magnitude and directions of multiple effects on storage root yield. Assuming a linear relationship between storage roots yield and plant attributes which explains variation in the former, path diagrams were developed with CALIS procedure (SAS, 1988) to investigate the causal effects of storage root yield using a modified form of the model proposed by Tai (1975). According to Gravois and Helmes (1992) a cause–effect diagram for the development showing the relationship between storage root and other plant trait was obtained and is presented in Figure 1. Leaf area was, however, included in the diagram although it affects the storage root yield negatively, implying competition between the two. Based on the schematic diagram indicating relationship between cause and effect, the path coefficient analysis was used as the statistical tool to describe direct and indirect effects of yield components.

Storage root yield has four main components: leaf area (N1), the number of storage root per unit area (X2), the storage root girth (Y3), and the storage root weight (Z4). These yield components are initiated at different stages in the ontogeny of the plant and are differentially affected by the environmental factors, U.

The calculation of direct and indirect path coefficients (the standard partial regression coefficient) that estimate the strength of the relationship between the cause (N1, X2, Y3 and Z4) and effect W5 (Sokal and Rohlf, 1995) is presented in Table 3. The direct and indirect effects of four variables (storage root number, storage root weight, storage root girth, and total leaf area) were found to explain 72% of the variation for storage yield. The direct effect of storage root number on yield (P=0.53) was equal to the correlation coefficient (r=0.53), suggesting that selection through this trait could be effective in identifying a genotype with high storage root yield. The direct effect of storage weight on yield was high and positive (P=0.45) while its indirect effect through storage root number was negative (P= -0.12) leading to a low value of correlation coefficient vis a vis the direct path coefficient. Negligible direct and indirect effects of dry matter content on yield were observed, confirming results obtained from simple correlation analysis (Table 1). Dry matter content was then discarded from the main yield components. Tai (1975) reported, however, that dry matter content was one of the storage roots yield components whereas results from the Democratic Republic of Congo (DRC) and Nigeria (Ibadan), reported that dry matter was not strongly associated with storage root yield (Mahungu 1983; Mahungu *et al.*, 1994a,b; Ntawuruhunga, 1992). Kawano *et al.* (1998) also reported that selection for dry matter content could be conducted without serious effects on other yield components. The storage root girth had a high correlation coefficient (r=0.57), but its direct effect (P=0.217) was relatively low because its indirect effects through storage root number and storage root weight were important. This confirms the report (Williams, 1972) that storage root girth is an important component of the storage root weight. The leaf area negatively affected the storage root yield implying a competition between the two characters. Cock *et al.* (1979) and Hunt

TABLE 3. Estimates of direct and indirect effects path coefficients for storage root dry yield of cassava grown at three sites in Uganda during 1997/98

Leaf area vs. dry yield	
Direct effect of leaf area on yield	-0.244
Indirect effect of leaf area on yield via storage root number	0.021
Indirect effect of leaf area on yield via root weight	-0.062
Indirect effect of leaf area on yield via root girth	-0.013
Total indirect effects	-0.05
Total (Direct + Indirect) effect	-0.297
Storage root s number vs. dry yield	
Direct effect of storage root number on yield	0.530
Indirect effect of storage root number on yield via leaf area	-0.010
Indirect effect of storage root number on yield via root weight	-0.106
Indirect effect of storage root number on yield via root girth	0.064
Total indirect effects	
Total (Direct + Indirect) effect	-0.058
Storage roots weight vs. dry yield	
Direct effect of root weight on yield	0.454
Indirect effect of root weight on yield via leaf area	0.033
Indirect effect of root weight on yield via storage root number	-0.124
Indirect effect of root weight on yield via root girth	0.090
Total indirect effects	-0.004
Total (Direct + Indirect) effect	0.454
Storage root girth vs. dry yield	
Direct effect of root girth on yield	0.217
Indirect effect of root girth on yield via leaf area	0.015
Indirect effect of root girth on yield via storage root number	0.157
Indirect effect of root girth on yield via root weight	0.189
Total indirect effects	-0.05
Total (Direct + Indirect) effect	0.575
R^2	0.72
Residual (U)	0.590

U: unknown source of variation

(1994) considered leaf area as an important parameter in cassava storage root yield in their cassava growth models.

The residual effect (R^{2}) determines how best the causal factors account for the variability of the dependant factor, the storage root yield. Its estimate (0.59) means that only 41% of the total variation in storage roots yield were explained. The level of determination is low. Some other factors (59%) that have not been considered here need to be included in this analysis to account more appropriately for the total variation of the storage root yield. Our results were based on phenotypic correlation among traits, further investigation would take into consideration genetic correlation which are more intrinsically useful than phenotypic correlation in deciding on selection strategies (Kang, 1994). In conclusion, storage roots number, storage root weight, and storage root girth were found to be important yield components.

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