Genotype by Environment Interactions of the Yield Components in Sweet Potato

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SUMMARY

A multilocal trial of sweet potato was set up in six different environments of Rwanda. Yield and its related components were observed. Genotype by environment interaction was important. There was a strong stress between number of tubers per unit area and average tuber weight. The latter trait was environmentally controlled. Under low-yielding conditions, translocation limitation seems to be more important than sink limitation. Yield related traits arise from parallel ontogenesis, though with relayed emphasis. No relation could be found between yield stability and stability of the yield components. Survival ability may shadow yield stability.

Introduction

Sweet potato growing in the Central African Highlands has to match a tremendous variability of ecological conditions. Traditional agriculture has met these variable requirements with a wealth of different local varieties. The breeder must know if breeding of new clones should be directed toward obtaining new cultivars with high environmental adaptability, and, if so, which characters are likely to contribute most to the achievement of yield stability across different environments. Among the many proposed stability parameters the "ecovalenz" parameter of Wricke (1962) is usually satisfactory. Grafius (1965), Institut des Sciences Agronomiques du Burundi (ISABU) B.P. 795, Bujumbura - Burundi pointed out that to be stable, a variety should have the longest edge of its yield parallelepiped subject to the stronger GXE interactions. GXE interactions were found to be stronger the more remote the concerned characters was in the ontogenetic sequence (Thomas et al. 1971), e.g. grain weight was more subject to GXE interaction than number of heads. Jong (1974), Lowe and Wilson (1975), Pushkaran et al (1976), Mahungu (1979), Janssens (1980), all indicated the overwhelming importance of number of tubers per unit area as yield contributor. Significant clone by environment interactions have been mentioned in sweet potato (Jong, 1974; Jong and Park, 1975; Shukla, 1976; Mahungu, 1979; Li, 1979; Saladaga, 1980; Baert, 1982). The clone by season interaction variance components for tuber yield and for average tuber size were found to be larger than the respective clone variance components (Jong, 1974).

Materials and Methods

A multilocal trial of 27 sweet potato clones was established in Rwanda (Central African Highlands). The trial was repeated across six different environments, comprising three different locations (Karama, Rubona, and Rwerere), as well as two different sites within each location, once on the hill and once in the swamp. Within each environment, the 27 clones were repeated over two randomized blocks. Plots were 4 m^2 in size in a 2 x 2 m square configuration. Each plot consisted of four 1 m^2 hills, and planting density was 8 cuttings per hill. No provision was made for guard rows, as sweet potato in the Central Highlands of Africa is grown in varietal mixtures. Hence, clones should be identified which combine a good yield potential with a strong intergenotypic competitivity (Janssens, 1980). Growing period was about six and a half months and coincided for the three hill sites with the 1981-B season (March-September), and with the 1981-C season (May-November) for the three swamp sites. The dry season spans July to September, inclusive.

In each environment, observations were made on the following traits: total number of tubers per plot (X), fresh tuber yield per plot, and fresh vine (i.e. stems + leaves) yield per plot (S). A random sample of two or three tubers was taken for each of the 27 clones, within each environment, and analyzed for dry matter content (Z). Two secondary traits were deduced: average fresh tuber weight (Y), and dry tuber yield (W). The latter trait corresponds to the yield parallelepiped according to Grafius (1965) and Mahungu (1979). Dry matter content (X) was unweighted such that the product X.Y.Z. does not always amount to W.

Classical multi-environmental analysis of variance was performed on all traits, assuming fixed effects both for environments and genotypes.

The stress matrix was established and the standardized partial regression coefficients on yield (W) were calculated for each of the six environments according to Hamid and Grafius (1978). Environmental stability (ecovalence) was estimated for each trait and for each clone, using the V-values of Wricke (1962). Each V-value is defined as the specific contribution of a given clone to the total sums of squares for GXE interaction. The correlation matrix of the V-values among the different traits was calculated to identify which yield components contributed most to yield (W) stability.

The 27 clones are a mixture of local varieties, selections from the breeding work of Dr. Hahn at IITA (International Institute of Tropical Agriculture, Ibadan, Nigeria), accessions and selections made by the former INEAC (Institut des Sciences Agronomiques du Congo Belge) before 1960 (Lemarchand, 1956), and 15 of the author's selections. The standard variety was cv. Rusenya, a local variety originating from the border of Lake Kivu.

Results and Discussion

Environmental characterization

For each trait the environmental mean is given in Table 2. If Rubona was best for number of tubers, Karama was better for average tuber weight. Dry matter content was best in Rubona. Swamp conditions did not decrease dry matter content (28.2% vs. 27.7% on the hill), as would be expected (Ton and Hernandez, 1978). The shorter photoperiod and the drier conditions of season C are favorable for tuberization (Hahn, 1977) and have largely compensated for the moisture stress of the swamp conditions. Karama 81-C and Rubona 81-C have comparable dry weight yields although achieved through different ways. The former environment is conducive of large average tuber weight and vine yield, whereas the latter compensates its low Y by above average number of tubers (X) and dry matter content (Z)

(Table 2). In the high elevation of Rwerere (Table 1), three components are below average: X, Y and to a lesser degree, S (vine yield).

Table 1. Location characteristics.

		Karama	Rubona	Rwerere
Elevation (m)		1,347	1,650	2,060
Aver. Yearly Temp.(°C)		21.3	19.9	14.3
Aver. Yearly Max. Temp.		28.4	25.1	22.6
Aver. Yearly Min. Temp.		14.3	14.6	5.9
Aver. Yearly Precip. (mm)		899	1,171	1,096
Aver. Nr. of Sun Hours/Year		22,869	21,817	17,852
Aver. Yearly Evaporation (mm)		1,440	1,380	836
Polar Coordinates		30°17'E;02°16'S	29°46'E;02°29'S	29°53'E;01°30'S
Soil	81-B	Xero-Kaolisoil	Humic Kaolisoil	Kaolisoil
Type	81-C	Hygro-Xero Kaolisoils	Grey Hydromorphic Soils	Grey Hydromorphic Soils

Table 2. Environmental performances.

Trait	Karama 1981-B	Karama 1981-C	Rubona 1981-B	Rubona 1981-C	Rwerere 1981-B	Rwerere 1981-C	Global Analysis
Number of tubers/m^2	7.7	13.0	21.9	18.9	6.7	6.8	12.5
Average tuber weight(g)	73.7	145.0	60.9	62.4	47.1	31.1	70.0
Fresh weight yield (g/m^2)	353.2	1701.0	1346.7	1161.0	346.0	215.0	854.0
Dry matter content (%)	25.9	26.3	30.1	34.1	27.2	24.1	27.9
Dry weight yield (g/m^2)	92.2	441.0	391.0	398.0	94.7	52.7	245.0
Fresh vine yield (g/m^2)	745.7	2520.2	1179.0	1015.2	904.7	420.2	1131.0

Sequence and genetic importance of the respective components

From the analysis of variance it appears that Y (average tuber weight) was not under significant genetic control, but mainly under environmental control, suggesting that sink limitation (Hahn, 1977) is less important, if not absent, under low yielding situations, and that component compensation (Adams, 1967) will alleviate, if necessary, insufficient sink size. The X and Y yield components had GXE interaction variance components which were larger than the respective genotype variance components viz. 22.4% vs. 13.1% and 11.1% vs. 2.0% in accordance with Jong (1974). Dry matter content (Z) and fresh vine yield (S) had their respective

GXE and genotype variance components of similar size, 32.6% vs. 31.9% and 20.7% vs. 23.1%. Dry tuber yield (W) had intermediate variance components, respectively 11.2% and 7.1%.

Genetic control decreased along the following component sequence: Z (31.9%), S (23.1%), X (13.1%), and Y (2.0%). According to Grafius and Thomas (1971), and Hamid and Grafius (1978), genetic determination of the yield components is the stronger when ontogenetically closer in the sequence development of the components. Grafius (1978) stated that "plasticity is inversely proportional to ontogenetic proximity." In sweet potato, however, the corresponding decreasing Z, S, X, and Y sequence is questionable from a morphogenetic and physiological point of view. Dry matter content of the tubers (Z) is built up only after tuber initiation. Even if the dry matter content of the other plant parts is high previous to tuber initiation, it does not imply that translocation to the tubers will be efficient. Moreover, all four components tend to vary during the growing process. Z and Y will increase gradually during growing process, S will peak at about 4 months, and X will plateau at about 3 months. One could speak of parallel ontogenesis with relayed emphasis for each of the components along the following sequence: S, X, Y, Z. The fact that the last component in the sequence, Z, is under strong genetic control can be explained by a smaller number of genes governing this trait.

The yield parallelipiped

For each of the 27 clones, the X, Y, Z components necessary to construct the yield parallelipiped (W) according to Grafius (1965), as well as the S component, are given in Table 3. The best yielder, cv. Rusenya (W = 1.61), is characterized by a below avergage tuber weight (Y = .93), all other components being above average viz.; X = 1.35, Z = 1.10, and S = 1.66. However, it was outyielded in four out of six environments. It is concluded that in low-input agriculture, selection should aim at identifying environment specific genotypes, rather than attempting to breed for widely adapted genotypes.

The stress matrix

Simple, partial, and multiple correlations were calculated among the different traits, using the overall genotype means (Table 4). Only number of tubers (X) was significantly correlated with dry tuber yield ($r = .45^{+}$). However, most partial correlations were highly significant. Components X, Y, Z, and S, all contributed signficantly to the final dry tuber yield viz. $.73^{++}$, $.72^{++}$, $.57^{++}$, and $.42^{+}$ (Table 4). The multiple determination coefficient of W was very high ($R^2 = .88$). All yield components (X, Y, Z, and S) were negatively related among themselves giving further evidence to the stress theory of Grafius (1970). Stress (or competition) was strongest between X and Y ($r = -.65^{++}$), supporting the view that "number and size tend to have an inverse relationship" (Grafius, 1978). Determination was average for Z ($R^2 = .59$), and least for vine yield ($R^2 = .40$). The latter lack of determination may be attributable to an uncompleted growing cyclus at 6.5 months under Central African Highland conditions, and/or to a possible limitation of the translocation process for most clones.

Relative importance of the yield components in different environments

It has been suggested that stress is more important in higher yielding locations as well as within higher yielding varieties (Adams, 1967; Thomas et al, 1971; Hamid, 1980). The multiple determination coefficient of W as a function of

X, Y, Z, and S gives an immediate estimate of overall stress. Two low yielding environments, Rwerere 81-B and Rwerere 81-C (Table 2), had nevertheless strong stress conditions (R^2 = .88 and .94, respectively). Hence, high yield per se does not seem the prime cause of stress, but rather the competition between the components to tap the available environmental resources. In Rwerere, the average yearly temperature is 14.3°C, and the average yearly minimum temperatura is only 5.9°C (Table 1). Below 15°C, tuberization process is strongly inhibited (Hahn, 1977). Hence, the strong competition between the yield components may result from strong cold stress imposed simultaneously on all components. Henceforth, it can be deduced that low yielding environments will generate a small stress factor (R^2) in so far at least one of the components is not subject to environmental stress.

Table 3. Number of tubers/m^2 (X), average tuber weight (Y), dry matter content (Z) dry tuber yield (W), and fresh vine yield (S) expressed as a fraction of the respective overall mean.

	Genotype	Number of tubers X	Average tuber weight Y	Dry matter content Z*	Dry tuber yield W	Fresh vine yield S
1	Gahungezi 1435	.74	1.51	1.12	1.10	.66
2	RUB 204	1.08	1.12	.97	1.24	.97
3	CL 1663	.79	.94	1.21	1.01	.59
4	TIS 2498	.98	1.06	.98	1.19	.43
5	No. 1142	.74	1.24	.85	.71	.40
6	RUB 205	.99	1.03	1.13	1.42	1.11
7	RJ 1609	.81	1.17	1.00	.98	.79
8	CL 1658	1.25	.85	1.14	1.09	1.28
9	Nyirak. 1636	.74	.89	1.04	.73	.60
10	RUB 202	.81	.94	1.09	.85	1.13
11	Mugenda 1603	.88	.63	.90	.60	1.59
12	Rusenya	1.35	.93	1.10	1.61	1.66
13	Nyiranjyojyo	.96	.83	1.19	1.05	.93
14	RJ 1612	1.46	.70	1.07	.89	.64
15	TIS 2534	1.28	.91	.76	.96	.76
16	2 - 4 - 2	1.16	.97	.69	.86	.62
17	Anne-Marie	1.20	1.16	1.07	1.33	1.84
18	Nyiramujuna 352	1.02	.87	1.06	.94	1.03
19	Bukarasa 1581	.73	1.11	1.04	.67	.73
20	TIS 2544	1.16	1.26	.88	1.20	.82
21	RUB 201	.87	1.11	.75	.77	.59
22	Bukarasa	.96	.95	1.09	1.09	1.26
23	Nkondoyigisabo	.83	.87	.97	.64	1.57
24	Caroline Lee	1.11	1.29	.97	1.37	1.05
25	RUB 203	1.60	.82	.98	1.02	1.04
26	RUB 203	.86	.84	.99	.74	.98
27	Cordes Rouges	.62	1.01	.95	.96	1.93
(6	Mean environments)	12.5/m^2	70.0 g	27.9% *	245 g/m^2	1.131 g/m^2

*unweighted mean

Table 4. Matrix of simple (lower triangle) and partial (upper triangle) correlations between yield and related components.

Simple Corr. \ Partial Corr.	Number of tubers X	Average tuber weight Y	Dry matter content Z	Dry tuber yield W	Fresh vine yield S	R^2	R
NR of tubers (X)		-.65**	-.48*	.73**	-.29	.81	.90**
Average tuber weight (Y)	-.27		-.46*	.72**	-.44*	.83	.91**
Dry matter content (Z)	-.07	-.11		.57**	-.10	.59	.77**
Dry tuber yield (W)	.45*	.34	.34		.42	.88	.94**
Fresh vine yield (S)	.09	-.25	.21	.25		.40	.63*

*, ** = respectively significant at p = .05 and p = .01.

R^2 = multiple determination coefficient.

R = multiple correlation coefficient.

For each environment, the relative importance of each component is given by the standardized partial regression coefficients (Table 5). Within each environment, number of tubers is generally the best yield contributor and average tuber weight, second best, although both traits contribute equally in the global analysis (Table 5). Dry matter content is the third best yield contributor in the global analysis, but has only significant contributions in the three highest yielding environments, Karama 81-C, Rubona 81-B, and Rubona 81-C (Table 5). This supports the view that Z is ontogenetically the last trait in the component sequence. Its contribution will only be of significant importance there where environmental resources will be large enough (Grafius and Thomas, 1971) to support further dry matter buildup. Vine yield is an overall poor yield contributor (b = .27+), and becomes negligible within each environment except in Rwerere 81-B. This is an apparent contradiction, as the breeder does know that good top growth is essential to ensure good yield. The four best yielders (Rub 205, Rusenya, Anne-Marie, and Caroline Lee) all happen to have above-average top growth (Table 4). Hence, high top growth should be combined with good translocation of the photosyntates to the tuber sink. Henceforth, translocation limitation seems to be more important than sink limitation under the low yielding conditions of the Central African Highlands.

Relative contribution of the yield components to environmental yield stability

The V-values (Wricke, 1962) of the different traits were calculated for each clone. As expected, there was a positive correlation between V-values and corresponding trait performances for dry tuber yield (r = .48++), vine yield (r = .54++) and number of tubers (r = .37), in accordance with Thomas et al, (1971).

Unexpectedly, no significant simple or partial correlation among V-values of different traits could be found. Hence, dry tuber yield stability cannot be explained by the stability of any of the components.

Yield stability of cv. Rub 204 (V = .103) corresponds with environmental stability for all yield components, whereas cv. Anne-Marie achieves yield stability (V = .271) in spite of high V-values, i.e. low ecovalence, for its components.

The shortest side of the yield parallelipiped of cv. Anne-Marie is dry matter content (Table 4) and yet it has a high V-value for dry matter (V = 79), which in turn should result in a low yield stability according to Grafius (1965). Component complementation does not explain yield stability of each of the genotypes, nor does the shortest edge of the yield parallelepiped. This leads to the suggestion that each of the four components has separate and specific physiological adaptation mechanisms towards changing environments. The interrelation of these mechanisms is survival oriented, rather than yield oriented. Hence, survival stability is shadowing stability of yield and its components, especially under low yield conditions. Each trait possesses several defense mechanisms against stress stimuli, more or less pronounced according to the particular genotype. For instance, drought adaptation can initiate either leaf drop or stomatal closure.

Table 5. Standardized partial regression coefficients of the four components w.r.t. dry tuber yield (W) in each environment, and respective multiple determination coeficients of W.

	Karama		Rubona		Rwerere		Global
	1981-B	1981-C	1981-B	1981-C	1981-B	1981-C	Analysis
Number of tubers (X)	.38	.95**	.97**	.78**	.60**	.59**	.62**
Average tuber weight (Y)	.45*	.79**	.99**	.67**	.34**	.56**	.62**
Dry matter content (Z)	.36	.50**	.70**	.42**	.12	.13	.39**
Fresh vine yield (S)	.11	.09	-.13	.15	.22*	.08	.27*
R^2	.44	.94	1.00	.98	.88	.94	.88

*, ** = respectively, significant at p = .05 and p = .01.

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