Cultivar variation in wound healing efficiency of sweetpotato and the effect on shelf-life

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ABSTRACT

The short shelf-life of the sweetpotato storage roots under tropical marketing conditions is a major limitation in many developing countries. Wound healing ability was found to be a major factor in determining the shelf-life of sweetpotato cultivars. The ability of cultivars to lignify wounds was expressed as a lignin index measured with phloroglucinol staining. Lignin indices correlated negatively with susceptibility to weight loss, water loss and microbial attack. There were significant differences in the lignin indices between cultivars. A high dry matter content generally coincided with a low lignin index. This relationship was consistent for 37 cultivars from East Africa and the United States of America. Dry matter content is therefore an important factor in determining the shelf-life of sweetpotatoes.

Introduction

In the tropics, sweetpotatoes (*Ipomoea batatas* L) tend to have a relatively short shelf-life, which is a constraint for marketing and availability of the crop in urban areas. In a study conducted in East Africa, it was found that the main limiting factor for storability of sweetpotatoes under marketing conditions is weight loss which is primarily (~ 90%) due to water loss (Van Oirschot, 2000). Weight loss results in

shriveling and it has been shown that high rates of water loss at one week after harvest also coincide with susceptibility to rotting (Rees *et al.* 1998). One of the most prevalent micro-organisms causing soft rot of sweetpotato is the fungus *Rhizopus* (Snowdon 1991).

Most of the moisture loss occurs due to damage of the protective periderm, and such damage forms an avenue for micro-organism attack. It is, however, impossible to avoid damage during harvesting. In temperate areas, it is common practice to cure roots (i.e. promote wound-healing) before storage. The process of curing of sweetpotatoes is well known and described in the literature. Wounds in sweetpotatoes cure best when the roots are exposed to temperatures of 28-30°C and a RH > 85% (Kushman and Wright 1969). During curing the following processes occur chronologically: first, the outer cell layers desiccate, then, after 2 to 3 days the cells below the surface start to show lignification. After approximately 6 days, a new periderm-like layer, the wound periderm, is formed underneath the lignified layer (Walter and Schadel 1982). After curing treatments, sweetpotato roots can be stored for over one year where temperature control is possible (Picha 1986).

In many tropical locations, curing is not actively practised but it is often assumed that the conditions are such that it takes place naturally (Collins and Walter 1985; Woolfe 1992). However, the high rates of weight loss and the short shelf life, put this into doubt, and it is possible that although the temperature is high enough, the levels of humidity are too low for effective curing. Considering the situation in East Africa, very little is known about the curing characteristics of African germplasm, which could differ from temperate varieties.

Several methods have been developed to measure the progress of wound healing during curing. The lignification of cell walls can be followed relatively easily using phloroglucinol staining and the number of lignified cell layers (Walter and Schadel 1983). Another technique, developed by Lulai and Orr (1995) involved measurement of the rate of water loss directly through the wound surface using a modified leaf porometer. By following the rate of water loss during the healing process, the level of

wound healing could be estimated. Nielsen and Johnson (1974) used the susceptibility to surface rot (*Fusarium oxysporum*) to investigate wound healing efficiency.

In this paper, different aspects of wound healing under the environmental conditions previaling in East Africa are reported. A range of sweetpotato cultivars was assessed and compared with two Irish potato (*Solanum tuberosum*) cultivars. The efficiency of wound healing was measured in three ways: by rate of water loss; susceptibility to microbial invasion; and as a lignification index using the level of lignification under a wound.

Materials and Methods

Plant material

This study considered 37 sweetpotato cultivars and two potato cultivars. Of the sweetpotatoes, 16 cultivars were grown at the International Potato Center (CIP) in Nairobi, Kenya, three cultivars were grown by The National Root and Tuber Crops Programme at Ukiriguru, Tanzania, and 18 cultivars were grown by USDA-ARS in the USA. The potato tubers were bought from a local market in Nairobi, Kenya.

Wounding

The roots and tubers were artificially wounded by cutting a shallow wound with a potato peeler. The size of the wounds was approximately 2 x 5 cm and 1.7 mm deep.

Storage conditions

The experiments were conducted at the National Agricultural Research Laboratories (NARL), Nairobi, Kenya and at the Natural Resources Institute (NRI), Chatham, UK. At NARL, the roots were kept in crates under ambient conditions. The crates were lined with plastic for the first two days to increase humidity. At NRI, roots were maintained at controlled temperature and levels of humidity as specified. The humidity and temperature of the storage environment were recorded using either Squirrel data loggers (Grant Instruments, UK) equipped with Vaisala probes or Tinytalk miniature dataloggers (Gemini, Chichester, UK).

Rate of water loss

The rate of water loss through the wound surface and intact periderm was measured using a modified PP-Systems porometer (PP-Systems, Hitchin, UK). Measurements were taken on the day of wounding (0) and at 3, 6, 8, 10 and 13 days thereafter upon 5 to 10 wounded roots per storage time.

Microbial invasion

Wounds that were allowed to cure for 3 and 6 days were assessed for their susceptibility to *Rhizopus oryzae*. Mycelial discs (9 mm) were cut from the border of a 2-day-old PDA (Potato Dextrose Agar) culture of *R. oryzae* and placed on the wound with the mycelial side facing down. The roots were incubated for 2 days in transparent polyethylene bags (40 cm x 50 cm) that were each punctured with 16 holes for ventilation. Each bag contained one root of every cultivar; nine roots were used per cultivar for the assessment after 3 days, and 7 roots per cultivar for the assessment after 6 days. The relative humidity and the temperature in the bags were recorded with electronic data loggers (Onset Computer Corp. 1998) and were found to be 94.2 to 97.5% and 21.7– 24.0°C, respectively.

In order to assess the extent of tissue degradation by the inoculated pathogens, the roots/tubers were then cut longitudinally through the point of inoculation (Duarte and Clark 1993). The wounds were further assessed for lignification as described below.

Lignification

Wounds were cut out of the roots or tubers, and four thin cross sections (approx 0.5 mm thick) per wound were cut with a razorblade. The sections were stained with phloroglucinol (1% in 95% ethanol) for 2 min and transferred to concentrated HCl for 30 s, then rinsed in water for 30 s. Each wound was given a score between 0 and 1 based on the continuity of lignification seen in 3-4 sections across the wound. (See Table 1 for examples). The average lignification score for 3-4 sections was called the 'lignification index'.

Microscopy

In some cases, tissue blocks of 7 x 7 x 7 mm, including both wound surface and native periderm, were cut and fixed in a Formalin Acetic Acid solution (Ethanol 70%,

Formalin 5%, Acetic Acid 5%). The tissue blocks were than dehyrdated in toluene (99%) and embedded in paraffin wax (Paraplast Plus, Sigma). Sections of 15 μm thickness were cut using a microtome. Before staining, the embedded sections were dehydrated in a series of toluene (2x 100%) and ethanol (2x 100%, 1x 90% (last)). Sections were stained for lignin with Phloroglucinol and HCl as described above. For Sudan III staining, the sections were stained overnight in a saturated solution of Sudan III (Sigma) in 70% ethanol. The sections were covered with Aquamount (BDH) while still moist.

The morphology of the lignified layer was assessed at 100x enlargement using a microscope (Leitz, UK) equipped with a graticule. Micrographs were taken using a Minolta X-700 camera mounted on the microscope.

Dry matter contents

The dry matter contents were assessed using approximately 20 g of diced or sliced tissue which was then dried in an oven at 80°C for 48 hours.

Statistical analysis

All analyses were carried out in Genstat (Rothamsted, UK). Analysis of variance was used to assess differences among the cultivars. The association between lignification and weight loss, transpiration rate and susceptibility to *R. oryzae* was determined using contingency tables for which significance was tested using the Pearson Chi Square tests. Categories were created for the level of weight loss and transpiration based on their distribution. For susceptibility to rotting the two categories constituted no rotting and rotting. The relationships between rate of water loss and storage time, and between the lignin index and DM content were assessed using linear regression. For this, the mean values of each cultivar were taken.

Results and Discussion

Water loss and wound healing efficiency

Immediately after wounding, the rate of water loss from the wounds measured with a porometer ranged between 200 and 400 $mmol \cdot m^{-2} \cdot s^{-1}$. This is many times higher than the rate of water loss through undamaged periderm which ranges between 12 and 18 $mmol \cdot m^{-2} \cdot s^{-1}$ (Van Oirschot 2000). At this stage, there were no differences observed among the cultivars tested. Figure 1 presents the profiles of water loss through the wound surface during healing for ten sweetpotato and two potato cultivars.

The water loss profiles of potato were significantly different from those of sweetpotato. The transpiration rate through potato wounds decreased rapidly after wounding, confirming the findings of Lulai *et al.* (1996), while for sweetpotato the transpiration rates decreased more slowly. Thus the barrier under a potato wound forms more rapidly, or has a more effective sealing capacity than in sweetpotato. The barrier formed in potato stains positive with Sudan III but not with phloroglucinol/HCl, and is therefore assumed to consist mainly of suberin (Lulai and Morgan 1992). The barrier in sweetpotato on the other hand stains bright red with phloroglucinol/HCl and only lightly with Sudan III (Van Oirschot 2000) and is believed to be a ligno-suberin-like substance with more lignin character (McClure 1960).

Among the sweetpotato cultivars, however, there were also some significant differences (Figure 1). The transpiration rates through wounds in Zapallo and Yan Shu 1 were always lower than for Kemb 10, KSP 20 and SPK 004. At all time points, the differences among cultivars were significant.

Lignification under the wound surface

Plates 1 to 4 present micrographs of sections cut through sweetpotato wounds. The micrographs presented here illustrate the trends that were seen in lignification. Lignification started generally at the periphery of the wounds under the periderm, and subsequently developed towards the centre of the wound (Plate 1). When roots were kept at high humidity, the lignified layers were closer to the surface than at lower humidity (Plate 2). At low humidity, some of the cultivars did not produce a

continuous lignin layer, but the layer would be patchy (Plate 3), or even absent (Plate 4). In roots with patchy lignification, lignin is generally present near the periderm (Plate 2) but discontinuous at the centre of the wound.

In order to compare cultivars for wound healing efficiency, the thickness of the lignified layer was initially used as in St Amand and Randle (1991). However, it seemed more appropriate to investigate the continuity of a lignified layer. The physiological relevance of this was confirmed by the data obtained as described below.

Lignification corresponds to reduced water loss

The same wounds that had been assessed for water loss using the porometer were also assessed for lignification, and it was found that the two were related. The level of water loss was significantly related to the presence of lignin under the wound surface. Table 2 presents a contingency table using the paired data on lignin and water loss of individual roots, irrespective of the cultivar. For simplicity, the data for transpiration rate were divided into three categories (low, intermediate and high) and the data for lignification into two categories (complete lignification, and incomplete/absence of lignification). Using Pearsons tests, significant associations ($P<0.05$) were found at 6, 8, 10 and 13 days after wounding. Thus complete lignification under the wound is important for reducing the evaporation of water through the wound surface. Only at day 3, when wound healing had not proceded very far, was there no association. Whether a continuous lignin layer itself prevents water loss or whether its formation immediately precedes that of a wound periderm (St Amand and Randle, 1991), which is the effective layer, is unclear. It should be noted that unlignified wounds also exhibited a decrease in their transpiration rate. This is probably the result of drying out of the upper cells which forms a physical barrier for water loss.

Lignification prevents microbial infection

Wounds were also assessed for their susceptibility to microbial infection. Table 3 presents a contingency table of paired data of sweetpotato roots that illustrates that susceptibility to rotting is more often found for wounds that have not lignified than in lignified wounds. The table presents data analysed in two ways, discriminating the completeness of the lignified layer versus the presence of lignin. In the former case,

two categories considered were presence of lignin (patchy or continuous) and absence of lignin, while in the latter case the two categories were complete lignification as opposed to absence or patchyness of lignification. Completeness was significantly related while the presence of lignin did not relate. This association was more significant at day 6 than at day 3 ($\chi^2 = 6.71$; $P = 0.010$; $\chi^2 = 25.33$; $P < 0.001$). There was no association between absence as opposed to presence of lignin. It may be concluded that lignification plays an important role in preventing microbial attack, but as in the case of water loss it is vital that the lignification is continuous to function as an effective barrier.

The lignification index

Two major conclusions can be drawn from previous sections. Firstly, lignification is (or is associated with) a crucial step in the wound healing process. Continuous lignification is directly associated with reduced water loss and reduced microbial infection. Secondly, not all wounds lignify under the conditions tested. It should be noted that the conditions tested are not optimal for curing as the relative humidity is not high enough. Other scientists have described lignification under curing conditions (Walter and Schadel 1983; St Amand and Randle 1991), and in these cases the lack or failure of lignification was not described. To describe the extent of lignification more accurately a lignification index was used, for which the continuity of the lignin layer as seen by phloroglucinool/HCl staining was expressed on a scale from 0 to 1.

A wide range in efficiency of wound healing at moderate humidity was observed among cultivars (Table 4). The results presented here are mean results of several trials. Most cultivars were consistent in their wound healing efficiency. The standard deviations indicated that for the cultivars with intermediate overall efficiency, the performance of individual roots could vary considerably. Some of the well-known US cultivars, e.g. Regal and Beaux, give results suggesting low efficiency. This might be due to the fact that screening was delayed for 3 months after the harvest. Further trials will be conducted to check this.

The effect of relative humidity on wound healing

Figure 2 presents the lignification indices of 13 sweetpotato cultivars obtained at different relative humidities: high - 97%, intermediate - 65% and low - 58%. At high RH, all cultivars had a lignin index close to 1.0. This is in agreement with findings from Strider and McCombs (1958) who reported that under optimal curing conditions there was no difference in the rate of wound phellem formation between a range of cultivars. However at the lower humidities there was a very significant difference between the cultivars in ability to lignify wounds, with high dry matter cultivars healing less efficiently (indicated above the figure). The regression was significant at the $p < 0.005$.

The effect of dry matter content on wound healing

Examination of the physiological characteristics of the cultivars indicated a relationship between the dry matter content and lignification index at lower humidities (indicated above the Figure). Among the 37 cultivars tested there was also a strong negative correlation between DM content and efficiency of wound healing expressed as a lignification index (Figure 3, correlation coefficient = -0.987, significant at $p < 0.001$). According to the regression model the probability that wounds heal (lignin index) decreases with increasing dry matter content, and, on average, if the dry matter content increases by 1%, the lignin index decreases by approximately 0.034. According to the model wound healing ability is explained for 27.6%.

The mechanism by which the DM content affects wound healing is not understood. It is possible that wound healing ability is directly related to the rate of desiccation of the tissue. Porometer readings indicate that tissue with a high DM content initially loses water at the same rate as tissue with a low DM content, and might therefore reach a critical level of moisture content more rapidly than tissue with a low DM content. The hypothesis would be that below a critical level of moisture content the tissue is too stressed, resulting in failure to form the protective lignified layer under the wound.

Desiccation of several outer cell layers of the wound occurs normally prior to lignification. Observations upon the thickness of the desiccated cell layer correspond with the above hypothesis (Van Oirschot, 2000). The desiccated tissue at the wound surface was thicker for roots with high DM content , and also in cases where wounded roots were stored at low relative humidity (58-65%). Tissue of unhealed wounds stained with safranin, which indicated the presence of phenolics. This might indicate that the healing mechanism was initiated by the synthesis of lignin precursors but was not completed.

The rate of desiccation may not, however, be the only factor affecting the wound healing ability since there were some consistent outlying cultivars. The cultivar KSP 20 consistently healed less well than predicted from the DM/lignin index relationship, while Caplina and Yarada consistently healed better than expected.

Conclusions

Although wound healing involves many processes in addition to lignification, the results presented in this communication confirm that lignification correlates with effective wound healing that protects the underlying tissue against microbial invasion and water loss. Thus significant associations were found between lignification and susceptibility to *Rhizopus oryzae* and lignification was also associated with reduced transpiration rates through wounds and weight loss.

The findings here illustrate that there are significant differences between the behaviour of sweetpotato roots and potatoes. In all cases, potato showed a much slower rate of water loss than sweetpotato. The differences probably lie in the fact that potato is a stem tuber while sweetpotato is a storage root and thus originate from different parts of the plant.

Under tropical marketing conditions lignification of wounds does not always occur. A lignification index can be used as quick and simple method to estimate the extent that wound healing occurs. High lignification indices were obtained for the cultivars Yan Shu 1 and Zapallo, while the cultivars SPK 004 and Kemb 10 showed a consistently low lignification index.

A high dry matter content in cultivars correlated with a low lignification index. This relationship was consistent for 37 cultivars tested. There were however some outliers (e.g. KSP 20) which indicates that other factors are likely to be involved in the lignin index.

Acknowledgements

This publication is an output from a research project funded by the United Kingdom Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID *[R6507: Crop Post-Harvest Research Programme]*. The authors would like to thank all collaborators: International Potato Center (CIP), National Agricultural Research Laboratories at KARI, Nairobi, Kenya. The Tanzanian National Root and Tuber Crops Programme, Ukiriguru, Tanzania, USDA-ARS, USA. The authors are grateful to DFID for funding the project.

References

Collins, W.W. and W.M. Walter. 1985. Fresh roots for human consumption. Pp. 153-173 in Sweet potato products: a natural resource for the tropics (J.C.Bouwkamp, ed). CRC Press Inc, Boca Raton, Florida.

Duarte, V. and C.A. Clark. 1993. Interaction of *Erwinia chrysanthemi* and *Fusarium solani* on sweet potato. Plant Disease 77: 733–735.

Kushman L.J. and F.S. Wright. 1969. Sweet potato storage. USDA Agriculture Handbook no. 358.

Lulai E.C., M.T. Glynn and P.H. Orr. 1996. Cellular changes and physiological responses to tuber pressure bruising. American Potato Journal 73: 197-209.

Lulai E.C. and W.C. Morgan. 1992. Histochemical probing of potato periderm with neutral red: a sensitive cytofluorochrome for hydrophobic domain of suberin. Biotechnic and Histochemistry 67: 185-195.

Lulai E.C. and P.H. Orr. 1995. Porometer measurements indicate wound severity and tuber maturity affect the early stages of wound-healing. American Potato Journal 72: 225-241.

McClure T.T. 1960. Chlorogenic acid accumulation and wound healing in sweet potato roots. American Journal of Botany 47: 277-280.

Nielsen L.W. and J.T. Johnson. 1974. Postharvest temperature effects on wound healing and surface rot in sweetpotato. Phytopathology 64: 967-970.

Picha D.H. 1986. Weight loss in sweet potatoes during curing and storage: contribution of transpiration and respiration. Journal of the American Society for Horticultural Science 11: 889-892.

Rees D., R. Kapinga, E. Rwiza, R. Mohammed, Q van Oirschot, E. Carey and A. Westby. 1998. The potential for extending shelf-life of sweet potato in East Africa through cultivar selection. Tropical Agriculture (Trinidad) 75; 208-211.

St Amand, P.C. and W.M. Randle. 1991. Ethylene production as a possible indicator of wound healing in roots of several sweet potato cultivars. Euphytica 53: 97-102.

Snowdon, A.L. 1991. Sweetpotatoes. a *colour atlas of post-harvest diseases of fruits and vegetables, Vol. 2: Vegetables.* Pp. 364-381, Wolfe Scientific Ltd, London, England.

Strider D.L. and C.L. McCombs. 1958. Rate of wound phellem formation in the sweet potato. American Society for Horticultural Science 72: 435-442.

Van Oirschot, Q.E.A. 2000. Storability of sweet potatoes under tropical conditions; physiological and sensory aspects. PhD Thesis, Cranfield University, UK.

Walter W.M. and W.E. Schadel. 1982. A rapid method for evaluating curing progress in sweet potatoes. Journal of the American Society for Horticultural Science 107: 1129-1133.

Woolfe, J.A. 1992. Sweet potato. An untapped food resource. Cambridge University Press, Cambridge.

Table 1. Scores for lignification of sweet potato wound sections

	Score	Completeness of the lignin layer		
	Lignification score	Presence of lignin	Completeness of lignification	Distribution of lignin in wound = lignin
Complete lignification	1	1	1	
Patchy lignification	0.5	1	0	
No lignification at all	0	0	0	

Table 2. Association between lignification and the rate of water loss through wounds at 3, 6, 8, 10 and 13 days after wounding.

				No. of roots			
Time after Wounding	**Transpiration (T) (mmol/s/m²)**			**No lignin or Patchy lignin**	**Continuous Lignin layer**	**χ^2-Value**	**P value**
3 days	Low	76	> T	5	9	3.26	= 0.196
	Intermediate	76	< T < 89	7	4		
	High		T > 89	10	5		
6 days	Low	43	> T	0	12	11.80	= 0.003
	Intermediate	43	< T < 58	8	4		
	High		T > 58	5	8		
8 days	Low	37	> T	3	9	17.20	< 0.001
	Intermediate	37	< T < 64	1	10		
	High		T > 64	10	1		
10 days	Low	30	> T	1	9	8.36	= 0.015
	Intermediate	30	< T < 69	3	8		
	High		T > 69	7	3		
13 days	Low	14	> T	2	9	8.71	= 0.013
	Intermediate	14	< T < 19	0	12		
	High		T > 19	6	6		

Table 3. Contingency table using the incidences of roots rotting and/or lignification. In (A) patchy lignified roots were grouped with complete lignified roots, and in (B) patchy lignification was grouped with 'no lignin'.

Time after wounding	Rotting	(A) Presence of lignin		(B) Completeness of lignified layer	
		No Lignin	Patchy lignin Complete lignification	- No lignin – Patchy lignin	Complete lignification
Day 3	No Rotting	11	26	14	23
	Rotting	18	31	28	21
		Pearson Chi Square = 0.46 P = 0.496 Fisher's exact test: P = 0.6455		**Pearson Chi Square = 6.71 P = 0.010 Fisher's exact test: P = 0.01544**	
Day 6	No Rotting	5	28	5	28
	Rotting	15	19	26	8
		Pearson Chi Square = 3.14 P = 0.076 Fisher's exact test: P = 0.0861		**Pearson Chi Square = 25.33 P < 0.001 Fisher's exact test: P < 0.001**	

Table 4. The lignification index for 37 different sweetpotato cultivars after artificial wounding. All the roots were exposed to a relative humidity of approximately 65% and a temperature of 25°C. (CT = Controlled Temperature room at NRI (UK), NC = under natural conditions at NARL (Kenya))

Cultivar	Country grown	Experimental Conditions	Lignin Index
Zapallo	Kenya	CT	1.00
Yarada	Kenya	CT	0.98
BP1-SP-2	Kenya	CT	0.95
W-308	USA	CT	0.93
Yan Shu 1	Kenya	CT	0.92
W-325	USA	CT	0.82
SP/93/3	Tanzania	CT	0.78
Julian	Kenya	CT	0.76
Sinia B	Tanzania	CT	0.76
W-287	USA	CT	0.71
PI595856	USA	CT	0.70
PI595873	USA	CT	0.70
Salyboro	Kenya	CT	0.70
SPN/0	Tanzania	CT	0.68
Sumor	USA	CT	0.68
Tinian	USA	CT	0.68
Santa Amaro	Kenya	NC	0.60
W-317	USA	CT	0.59
W-345	USA	CT	0.58
KSP 20	Kenya	CT	0.58
Beaux	USA	CT	0.55
W-341	USA	CT	0.54
Mugande	Kenya	NC	0.32
SC1149-19	USA	CT	0.31
SPK013	Kenya	NC	0.30
Caplina	Kenya	CT	0.28
Kemb 10	Kenya	CT	0.27
Regal	USA	CT	0.27
97K-11	USA	CT	0.27
NIS/94/320	Kenya	NC	0.25
Tanzania	USA	CT	0.25
White Regal	USA	CT	0.19
PI538354	USA	CT	0.18
Picadito	USA	CT	0.17
Sowola	Kenya	NC	0.13
SPK 004	Kenya	CT	0.12
KSP20	Kenya	NC	0.09
Naveto	Kenya	NC	0.06

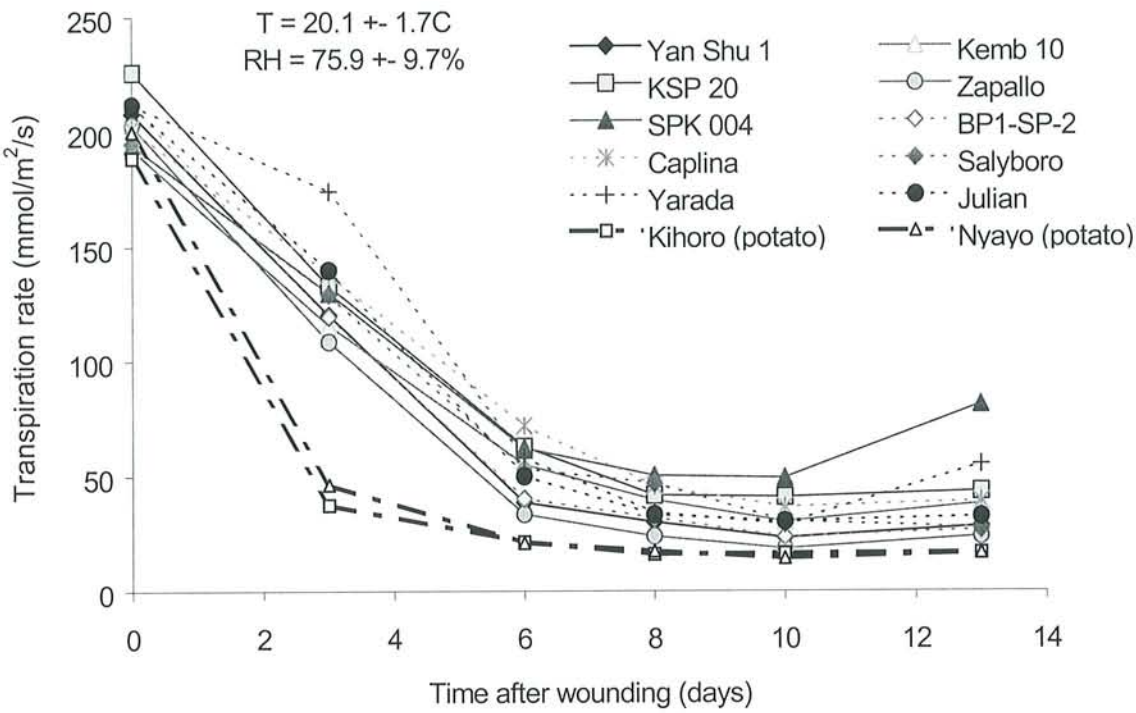

Figure 1. Transpiration rate across artificially inflicted wounds on ten sweetpotato and two potato cultivars during. Each value is the mean of measurements on ten roots. Sweetpotatoes were grown by CIP Nairobi and potatoes purchased in Nairobi.

Plate 1 to 4 Micrographs of sweetpotato wound sections showing the lignified layer and desiccated layer.

1. Lignification in Zapallo at high relative humidity (x 100)
2. Lignification in Kemb 10 at intermediate relative humidity (x 40)
3. Patchy lignification in KSP 20 at intermediate relative humidity (x 40)
4. No lignification in SPK 004 at intermediate relative humidity (x 40)

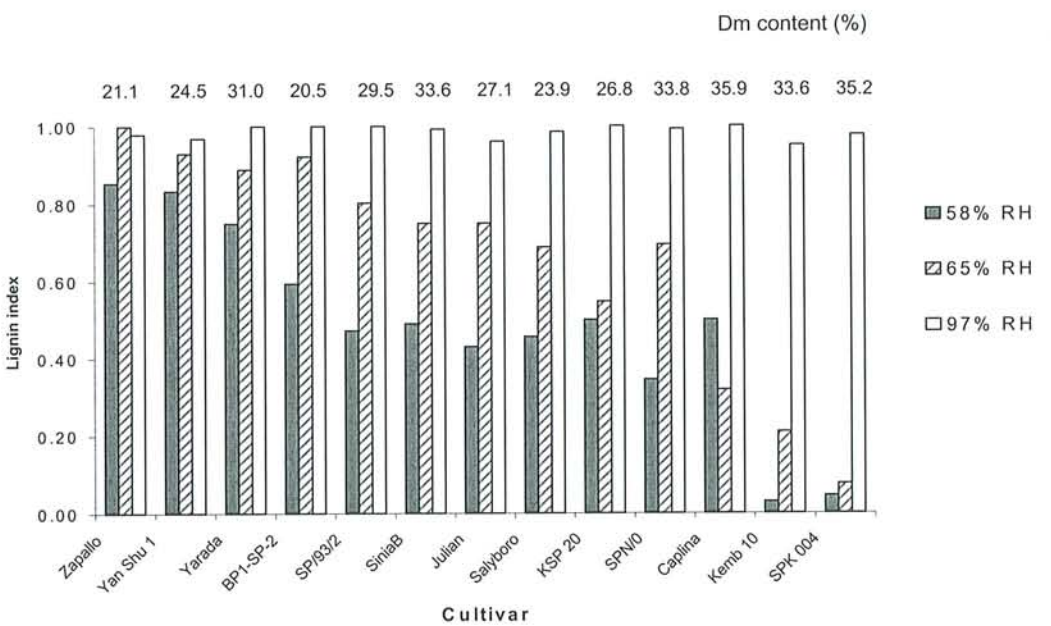

Figure 2. The lignification index of 13 sweetpotato cultivars as stored under three different relative humidities.

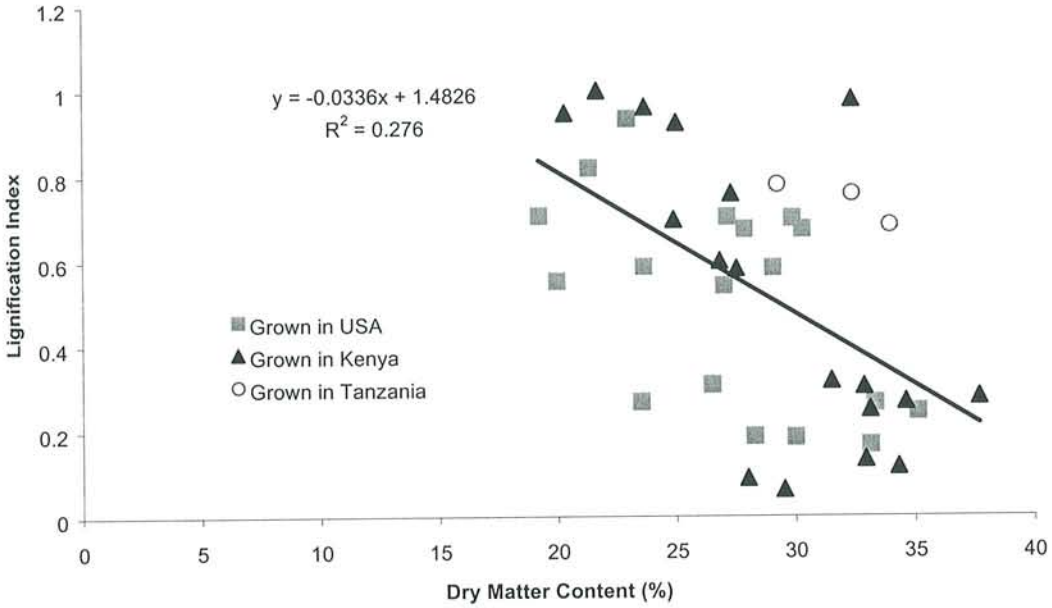

Figure 3. The relationship between cultivar DM content and the lignification index. Lignification was measured at 4 or 5 days after wounding. Each point presents the data of one cultivar grown in Kenya, Tanzania or the United States.