Session III

Crop improvement for sustainable intensification of root and tuber crops

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Heritability estimates for an Accelerated Breeding Scheme (ABS) in clonally propagated crops - using sweetpotato as a model

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Abstract

Breeding of clonally propagated crops usually requires five or more years to produce outputs. An accelerated breeding scheme (ABS) can be designed in clonally propagated crops provided that the genotype by year interaction is low for the considered crop. The objectives of this study were to describe an ABS for clonally propagated crops and to investigate the efficiency of this breeding scheme on the basis of variance components, heritability estimations and model calculations for sweetpotato. In total 4243 clones from a seed nursery were planted nearly simultaneously at three locations in 1m row plots. The observed traits were storage root yield, upper biomass, dry matter, total carotenoids, iron and zinc contents of storage roots. Model calculations were carried out with a test capacity 12000 and 8000 field plots and a laboratory capacity of 8000 and 4000 samples. The ABS proposed reduces the time needed for one recurrent selection cycle in population improvement of sweetpotato form four to two years (the time needed for variety development is reduced from 7 to 4 years). The heritability estimates in the proposed ABS were within the range of 0.5 and 0.6 for storage root yield and upper biomass, 0.6 to 0.7 for iron and zinc and > 0.8 for dry matter and total carotenoids. For storage root yield the optimum resource allocation of 4000 and 12000 field plots was to plant 2000 or 4000 genotypes, at two and three locations, respectively. For low laboratory capacity the best allocation was to evaluate all genotypes at one location. For high laboratory capacity the best allocation was to use one or two locations. We conclude that our proposed ABS might be a very attractive breeding scheme for sweetpotato and other clonally propagated crops.

Keywords: Breeding scheme – clonally propagated crops - allocation of breeding resources – *Ipomoea batatas* – G x E interactions – variance components – heritability.

Introduction

Most breeding programs of clonally propagated crops follow a breeding scheme starting with population development until variety release that takes on average of 7-8 years in root and tuber crops. The long duration of this process often frustrates breeders and their clients. The definition of a clonally propagated crop is that the material to cultivate and maintain a variety is obtained by asexual reproduction. Usually the materials to propagate the crop are tubers, roots, stem cuttings or corms. It should be noted that clonally propagated crops are comprising also many forage crops, nearly all types of fruit and wooden ornamentals, many cut flowers and pot plants, as well as forest trees. Owing to the long crop duration of many fruits, wooden ornamentals and forest trees the time factor in breeding these plants becomes much more important compared to root and tuber crops. Apart from the crop duration the time needed to develop a better genotype is determined by the breeding scheme and high through put screening methods – both together determine the breeding efficiency. High through put screening methods are presented elsewhere at this symposium.

The essential components of a breeding scheme are: (1) definition of breeding objectives (we need to know what is needed), (2) generation of genetic variation for breeding objectives (we need a population in which its merits to select individuals), and (3) selection of individuals within the population, which match or are more close to our objectives compared to others. The breeding objectives can be grouped into yield, quality, and stress resistances. Usually several traits have to be considered by the breeder and the value of a genotype is determined by a good performance overall traits. Here we will consider yield as the most relevant trait together with several nutritional quality traits. Resistances to stresses are not considered, although this group of traits

often exhibit lowest acceptable values at which genotypes become useless. The generation of genetic variation is one of the most difficult components of a breeding scheme, because the genetic gain by selection depends not only on the genetic variation of a population. The population mean and its improvement from generation cycle to generation cycle (recurrent selection cycles) are at least as important as the variation of a population. Especially this component of breeding schemes for clonally propagated crops might be much more difficult to manage compared to other crops. The reason is that clonally propagated crops are highly heterozygotes hybrids and usually autopolyploid. This makes it easy to generate populations with a large genetic variation (provided the clonally propagated crop can be crossed), but it makes it very difficult to improve the population mean. Here we want to leave the first and second component a breeding scheme to focus on the third component: "selection of individuals within the population".

The third component in a breeding scheme – the selection of individuals within a population - bears in clonally propagated crops easily achievable improvements of the breeding efficiency. The basis is that each genotype in a population of clonally propagated crops is fixed. No genetic changes among genotypes occur after the generation of a population until genotypes are recombined for the next recurrent selection cycle. Hence a clone variety can be identified as soon as possible within a population provided that the heritability is not low.

The heritability for fixed genotypes (also called the broad sense heritability) is defined as:

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GxL}^2}{l} + \frac{\sigma_{GxY}^2}{y} + \frac{\sigma_{GxLxY}^2}{ly} + \frac{\sigma_\varepsilon^2}{lyr}},$$

where: σ_G^2, σ_{GxL}^2, σ_{GxY}^2, σ_{GxLxY}^2, and σ_ε^2, are the variance components due to the effect of genotype, genotype by location interaction, genotype by year interaction, genotype by location by year interaction, and plot error, respectively; and where: l, y, and r, are number of locations, years and plot replications, respectively. Obviously the heritability is not set into concrete even if the magnitude of σ_G^2 is constant. The heritability depends largely on σ_{GxL}^2, σ_{GxY}^2, σ_{GxLxY}^2, and σ_ε^2 as well as the test precision determined by l, y, and r (Patterson 1997). Even in the case where the σ_G^2 is very small the breeder can gradually increase the heritability very close to 1, provided he could make huge amounts of investments in numbers of locations, years and replications. From the above formula it can also easily been seen that in the case of no or very small σ_{GxY}^2, the breeder can gradually increase the heritability close to 1 by making no investments into years (in other word by using only one year) and allocate all resources into locations. Furthermore, it can be seen that the number locations are much more important than replications for increasing the heritability. Above it was mentioned that this is the definition of the so called broad sense heritability. The narrow sense heritability takes into account that not all the genetic variation can be used in improving the population mean (see above the 2nd component of a breeding scheme). The narrow sense heritability is not relevant for the third component of a breeding scheme in clonally propagated crops (Wricke and Weber 1986).

There were three objectives in this study. First to present an accelerated breeding scheme (ABS) for clonally propagated crops in which temporal variation of test environments is spatial variation of test environments in early stages of a breeding program. The second objective was to estimate variance components and heritabilities for the proposed ABS in early breeding stages by using sweetpotato as a model to provide information which traits merits selection in ABS. Sweetpotato is a quite suitable crop for such a study because it has a high propagation coefficient (30 and more cuttings of a genotype in a seedling nursery can be easily obtained within 4 months). The third objective was to allocate for sweetpotato the optimum of the resource allocation in ABS.

Material and methods

Accelerated Breeding Scheme (ABS)

The ABS is building out on the general principle of breeding clonally propagated crops. This principle is to break normal clonal propagation by introducing a crossing step which culminates in sexual seed production. After the genetic recombination, all subsequent propagation steps are asexual in nature, i.e. clonal propagation. The population developed from seeds consists of very different and heterozygous genotypes, which do not exchange genetic material. Each of these seed plants grown in the so-called seedling nursery can be considered a potential new variety. This is the base population for selection. This selection in breeding clonally propagated crops is described most often in plant breeding textbooks as a process conducted in several steps and years (Figure 1).

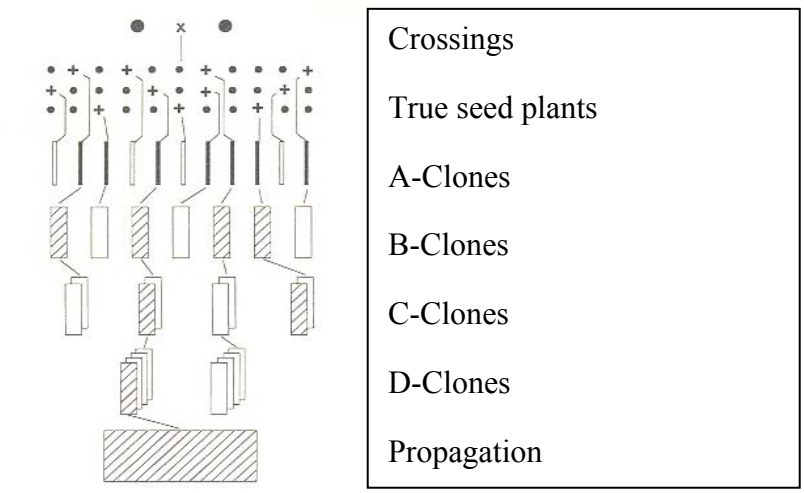

Figure 1. General scheme of breeding clonally propagated crops (Becker 1993)

The breeding scheme illustrated in Figure 1 is straightforward and is most often interpreted as requiring selection sequentially in several steps over several years. The diagram implies that there are two parents crossed, followed by 5 subsequent selection steps in time. This is very misleading. First, parental selection is a very difficult task and the breeder must work with many parents (the correlation between parental performance and offspring performance can be very weak in clonally propagated crops). Second, there is no further genetic development as one moves between selection steps. In other word, the selected D-clone in figure 1 is absolutely genetically identical with the true seed plant the selected D-clone is tracing back to. Theoretically, the breeding scheme illustrated in figure 1 could be rotated and all selection work done in one year. To which this can be done practically depends on the crop duration, the propagation rate and the genotype by year interaction (no or small σ^2_{GxY}) and the result is the ABS. The principle of the ABS for clonally propagated crops is to do as much as possible simultaneously, what is done in the general breeding scheme in Figure 1 sequentially in several steps over several years..

In the ABS all genotypes developed from seeds are planted simultaneously in several environments in small plots (in our experimental study 3 plants per row) without replications. It should be noted that development of new genotypes (crossings) raising seed plants and multiplication of planting material for multi-location field trials requires in sweetpotato not more than 1 year. The first multi-location field trials in ABS for sweetpotato starts at the beginning of year 2 and this first series of trials are completed within 4 to 5 months. The ABS applied for sweetpotato requires 1 year for crossings and multiplication of planting material. In the second year, a very large number of clones are planted in at least two environments (this can be managed by 1 assistant, 3 technicians and casual laborers). A visual agronomic evaluation (sufficient storage root formation, acceptable storage root size shape and form) can be conducted (at least at one environment preferable at a stress environment for example drought) to allocate work to genotypes which merit data recording – this can be linked to a farmer participatory breeding approach (Grüneberg et al. in press). All genotypes (or all selected

clones on basis of the agronomic evaluation) are measure across environments for storage root yield, upper biomass yields and storage root quality traits. In the case all clones are evaluated across environments this is a one stage selection process (traits can be aggregated into an index). In case only selected clones on basis of the visual agronomic evaluation are measured across environments the ABS becomes two stage selection process (further modifications to a three stage selection process to measure virus diseases are straight forward). This accelerated breeding scheme can be visualized as a rotated general breeding scheme for clonally propagated crosses and is illustrated in figure 2.

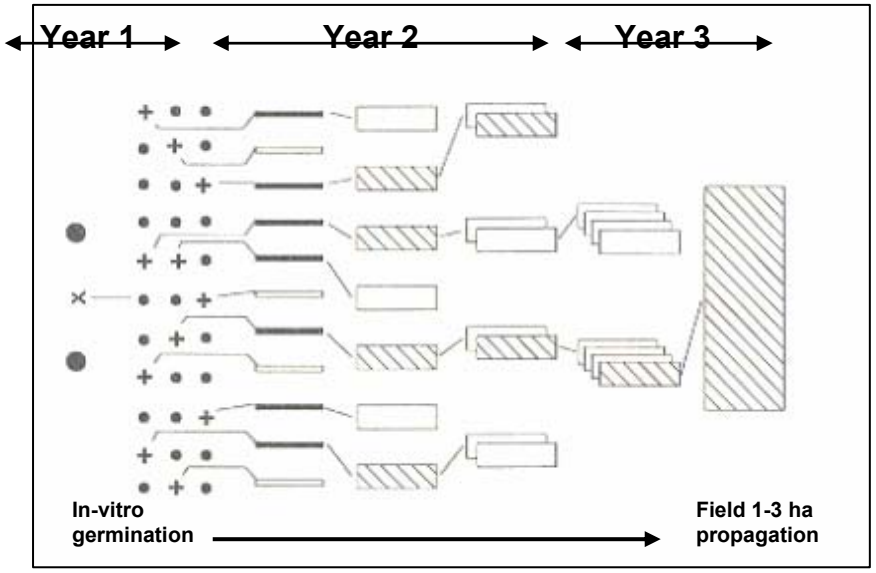

Figure 2. Accelerated breeding scheme (ABS) for clonally propagated crops, illustrated here with an in-vitro germination to keep clones virus free.

Planting material and field experiments

In total 4243 sweetpotato genotypes were planted at three environments, namely La Molina (LM), San Ramon (SR), San Ramon without fertilizer treatment [SRWF (an area at the station without fertilizer application)] in 1 m row plots (comprising 3 plants, 0.25m distance between plants and 0.25m distance to the next plot) and 0.9 m distance between rows (total size of the experiment at each environment about 0.45 hectares). The planting date at LM, SR, and SRWF was 13.01.2006, 20.01.2006, and 21.01.2006, respectively. The harvest date at LM, SR, and SRWF was 30.05.2006, 06.06.2006, and 08.06.2006, respectively. The breeding population was tracing back to a polycross with 128 clones (comprising CIP-Numbers: YM89., SR90., and SR93.) aiming at the development of an orange fleshed breeding population at CIP. This population was designated as "Jewel".

Data analysis

Storage root yield (RYLD in kg/m^2), upper biomass yield (FYLD in kg/m^2), agronomic score (AGRO from 1 to 5), storage root dry matter (DM in %), total carotene (TcDM in ppm), iron (FeDM in ppm) and zinc (ZnDM in ppm) concentrations of storage roots were recorded. TcDM, FeDM, and ZnDM were recorded on storage root dry matter basis using Near Infrared Spectroscopy calibrations (Zum Felde et al. at this symposium). All traits were recorded at LM and SR; however, at SRWF only RYLD and AGRO (1 – 5) were recorded. The analysis of variance was carried out using SAS6.12 (SAS Institute Inc. 1988, SAS Institute Inc. 1997) specially using the procedure MIXED and the method REML (Patterson 1997). The variance components σ_G^2, σ_E^2 and σ_{GxE}^2 were estimated, where: σ_G^2, σ_E^2, and σ_{GxE}^2 are the variance components due to the effect of genotype, location and genotype by environment interaction, respectively. The corresponding model in the analysis is $y = \mu + g + e + gxe$. The

heritability was calculated by $h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GxE}^2}{l}}$, where: l the number of environments. The correlation between RYLD and AGRO was determined by Spearman rank correlation for each environment using the SAS procedure CORR.

The estimated variance components ratios $\sigma_G^2 : \sigma_{GxE}^2$ and a total test capacity of 12000 and 4000 plots for RYLD were used to calculate the optimal allocation of resources for the response to selection (Wricke and Weber 1986) for the 300 best clones (selection of 300 clones to be tested in advanced and elite trials). The same was done for quality traits (storage root dry matter, total carotenoids, iron and zinc) with a laboratory capacity of 8000 and 4000 samples. The response to selection R was given in standardized units $R_s = \frac{R}{\sqrt{\sigma_G^2}}$. Self written programs, in SAS IML programming language were used.

Results

The RYLD across genotypes in the breeding population Jewel were clearly differed among environments and ranged from 1.1 kg/m^2 to 2.1 kg/m^2 (Table 1). SRWF appeared to be a low yielding selection environment in which more clones obtained lower AGO scores values compared to LM and SR. At environments LM and SR two and six observations, respectively, appeared to have unrealistic RYLD and FYLD values. This resulted in maximum RYLD values of 14.9 kg/m^2 in LM and SR and maximum FYLD values of 14.9 kg/m^2 and 20.0 kg/m^2, respectively. For LM a lower DM mean value was observed compared to SR. For the remaining quality traits, namely TcDM, FeDM and ZnDM, a higher mean at LM was observed compared to SR. Quality traits appeared to be within the range reported in the literature (Woolfe 1992). Correlations between RYLD and AGRO scores were 0.558, 0.452 and 0.593 for LM, SR and SRWF, respectively (results not presented).

Table 1. Mean, minimum and maximum of observed traits and number of evaluated genotypes (N) for each environment

Trait	N Genotypes	Mean	Min.	Max.
	La Molina (LM)			
RYLD (kg/m^2)	3986	1.8	0	14.9
FYLD (kg/m^2)	3985	3.9	0.1	20.0
Agro (score)	3905	2.2	1	5
DM (%)	1946	27.7	13.6	51.1
TcDM (ppm)	1940	184	0	3313
FeDM (ppm)	1940	24.0	3.6	47.7
ZnDM (ppm)	1941	13.3	6.7	31.6
	San Ramon (SR)			
RYLD (kg/m^2)	4080	2.1	0	14.9
FYLD (kg/m^2)	4081	2.8	0.1	16.0
AGRO (score)	3978	2.3	1	5
DM (%)	1929	32.0	18.2	54.0
TcDM (ppm)	1925	93	0	593
FeDM (ppm)	1931	20.5	10.5	33.1
ZnDM (ppm)	1931	10.1	4.7	18.8
	San Ramon without fertilization (SRWF)			
RYLD (kg/m^2)	4027	1.1	0	8.6
Agro (score)	4243	1.8	1	5

For all traits σ^2_G was clearly different from zero (Table 2). High σ^2_G estimates were observed for RYLD, FYLD and DM. Low to medium σ^2_G estimates were observed for FeDM and ZnDM. An extreme large σ^2_G was of observed for TcDM. The σ^2_{GxE} / σ^2_G ratio was clearly >1 for RYLD and FYLD, about 1 for FeDM and ZnDM, whereas for DM and TcDM the σ^2_{GxE} / σ^2_G ratio is clearly <1. The observed h^2 estimates were between 0.5 and 0.6 for RYLD and FYLD, between 0.5 and 0.7 for FeDM and ZnDM, and > 0.8 for DM and TcDM. A striking observation was that by discarding all data records with AGO scores < 3 the estimates and the σ^2_{GxE} / σ^2_G do not change much for FYLD, DM, TcDM, FeDM, and ZnDM, except RYLD. Obviously there was still remaining genetic variation for RYLD after a selection for AGRO and h^2 for RYLD was not low. However, by discarding all data records with AGO scores < 3 the number of observations was considerably lower.

Table 2. Variance component and heritability estimates for observed traits (ratio $\sigma^2_G : \sigma^2_{GxE}$ in brackets) for two groups of clones divided on basis of agronomical scores

Traits	σ^2_G	σ^2_E	σ^2_{GxE}	N Obs	N Loc	h^2
	Observations with Agronomic Scores 1 to 5					
RYLD (t^2/ha^2)	47.7 (1)	23.2	98.0 (2.05)	12093	3	0.59
FYLD (t^2/ha^2)	237.0 (1)	52.1	349.0 (1.47)	8066	2	0.58
DM ($\%^2$)	13.94 (1)	8.18	6.22 (0.45)	3875	2	0.82
TcDM (ppm^2)	33651 (1)	3453	9539 (0.28)	3865	2	0.88
FeDM (ppm^2)	7.41 (1)	5.79	7.61 (1.03)	3874	2	0.66
ZnDM (ppm^2)	3.10 (1)	4.63	2.92 (0.95)	3872	2	0.68
	Observations with Agronomic Scores larger or equal 3					
RYLD (t^2/ha^2)	36.2 (1)	23.0	110.4 (3.05)	3655	3	0.50
FYLD (t^2/ha^2)	202.0 (1)	16.6	265.2 (1.31)	2718	2	0.60
DM ($\%^2$)	14.13 (1)	11.28	5.01 (0.36)	2040	2	0.85
TcDM (ppm^2)	31518 (1)	5593	11896 (0.38)	2038	2	0.84
FeDM (ppm^2)	7.39 (1)	7.45	7.60 (1.03)	2038	2	0.66
ZnDM (ppm^2)	3.07	5.28	2.88 (0.94)	2038	2	0.68

For RYLD the highest R_s was reach with a value 1.46 for the allocation 6000 or 4000 genotypes (12000 plots) planted at 2 or 3 locations, respectively, assuming a σ^2_{GxE} / σ^2_G = 2 (Table 3). In case σ^2_{GxE} / σ^2_G = 3 the optimum allocation of 12000 plots is moving to 4000 genotypes and 3 locations. However, if the test capacity is considerably lower (4000 plots) the optimum allocation is 2000 genotypes planted at 2 locations for a σ^2_{GxE} /

σ_G^2 of 2 or 3. However, with a test capacity of 4000 plots the response to selection is about 25% to 33% lower, compared to a test capacity of 12000 plots. For quality traits there is the general trend to find the optimum allocation if the laboratory capacity is completely used for one location. Only for a laboratory capacity of 8000 samples and a $\sigma_{GxE}^2 / \sigma_G^2 = 1$ the optimum was allocated at 8000 or 4000 genotypes at 1 or 2 locations. The differences between using one and two locations appeared not to be large as long as the laboratory capacity is large. However, if the laboratory capacity is small it appears that this capacity should completely allocated to genotypes without using different locations. The determined optimum resource allocation is close to the experimental design used in this study for the variance component estimations [for RYLD: about 12000 plots, 4000 genotypes, 3 locations; for quality traits: about 4000 quality samples, 2 locations (Table 1)]. For DM and TcDM the resource allocation in the experimental part of this study corresponds to 10% less R_s (2000 genotypes, 2 locations) compared to the optimum R_s (4000 genotypes, 1 locations). For FeDM and ZnDM this was only 5% less R_s. It should be noted that the genetic variance for DM and TcDM was extreme (Table 2), so that some reductions of R_s for TcDM and DM can be tolerated due to the high R (not standardized response to selection). The R for FeDM and ZnDM is considerable lower compared to the R of DM and TcDM. Note R values can be easily determined by $R = R_s\sqrt{\sigma_G^2}$ (results not presented).

Discussion

The long duration of a breeding process often frustrates breeders and their clients. Donors are also reluctant to invest in breeding when concrete outputs (varieties) take so long to produce. Since all genotypes in clonally propagated crops are fixed (potentially varieties) it is strait forward to design an accelerated breeding scheme (ABS) for clonally propagated crops. Our proposed ABS is consequently replacing temporal variation of test environments (years) by spatial variation of test environments (locations and treatments at locations). In other word everything what can be done simultaneously is made simultaneously, but with incooperation of sequential selection steps within the same year to reduce work (i.e. the AGRO evaluation in this study). The visual agronomic evaluation in our experimental study clearly showed that this procedure is useful to discards low yielding genotypes, which do not merit further evaluations (correlations between RYLD and AGRO within the range of 0.452 and 0.593 were observed).

Our proposed ABS requires only that the clonally propagated crop can be crossed and that it can be cloned rapidly. To managed thousands of genotypes at several environments the clones are planted in small plots. The ABS reduces the selection process in early breeding stages form 4 years to 2 years. However, this is followed by yield trials in later breeding in large plots. It is important to note that this concept makes it also possible to conduct very short recurrent selection cycles. In our ABS for sweetpotato 300 clones are selected within 2 years to be used for recombination tests for the next recurrent selection cycle as well as for the yield trials in later breeding stages. Since we work with two populations in each year one population is undergoing recombination and multiplication, while the other population is in the fields (each year field and crossing capacity is fully used). It should be noted that short recurrent selection cycles is one of the two keys to improve the population mean (the second key is efficient selection of parents for their recombination ability). Moreover, the advantage of ABS is that it allows to estimate variance components and genetic correlations, which is quite important in case of negative genetic correlations for population improvement and recurrent selection.

Table 3. Response to selection in standardized units (R_s) of the 300 best genotypes for storage root yield (RYLD) and storage root quality in an ABS

Trait	$\sigma_G^2 : \sigma_{GxE}^2$	Plot capacity	N Genotypes	N Locations	R_s	Rel. R_s
RYLD	1:2	12000	12000	1	1.35	92
			6000	**2**	**1.46**	**100**
			4000	**3**	**1.46**	**100**
			3000	4	1.43	98
	1:3		12000	1	1.17	80
			6000	2	1.31	90
			4000	**3**	**1.34**	**92**
			3000	4	1.32	90
	1:2	4000	4000	1	1.09	75
			2000	**2**	**1.10**	**75**
			1333	3	1.03	71
			1000	4	0.95	65
	1:3		4000	1	0.94	64
			2000	**2**	**0.98**	**67**
			1333	3	0.94	64
			1000	4	0.88	60
Quality traits	1:1	8000	**8000**	**1**	**1.54**	**106**
(i.e. iron & zinc)			**4000**	**2**	**1.54**	**106**
			2667	3	1.47	101
			2000	4	1.39	95
	1:1	4000	**4000**	**1**	**1.33**	**91**
			2000	2	1.27	87
			1333	3	1.15	79
			1000	4	1.04	71
Quality traits	1 : 0.5	8000	**8000**	**1**	**1.78**	**123**
(i.e. dry matter & carotenoids)			4000	2	1.69	116
			2667	3	1.57	108
			2000	4	1.46	100
	1:0.5	4000	**4000**	**1**	**1.54**	**106**
			2000	2	1.39	95
			1333	3	1.23	84
			1000	4	1.09	75

There is no information if it is possible to select and to obtain genetic gains in an ABS in early breeding stages for sweetpotato and to our knowledge there is no information for such a system in clonally propagated crops at all. We expected that it is possible to obtain genetic gains for quality traits in an ABS for sweetpotato. It should be noted that the untapped nutritional food quality of sweetpotato is under exploitation in many breeding programs in the world. Our results show that it is nearly certain to select and obtain significant responses to selection for quality traits in an ABS for sweetpotato. A genetic variation of about $\sigma_G^2 \approx 14\ \%^2$, $\sigma_G^2 \approx 33000\ ppm^2$, $\sigma_G^2 \approx 7.5\ ppm^2$, $\sigma_G^2 \approx 3.0\ ppm^2$, were observed for storage root dry matter, total carotenoids, iron and zinc concentrations of storage roots, respectively. It was not expected to observe considerable amounts of genetic variation for storage root yield and upper biomass yield in ABS. However, variance components of $\sigma_G^2 = 47.7\ t^{2/}/ha^2$ and $\sigma_G^2 = 237\ t^{2/}/ha^2$ for storage root yield and biomass yield, respectively, are clearly not small. We assume that it is also is possible to select and to obtain genetic gains for yield in an ABS. Moreover, it was unexpected that a visual agronomic screening (AGRO) was not reducing σ_G^2 across all observed traits, except storage root yield. Considerable amount of work can be saved by including such a visual agronomic selection step in an ABS (measuring and sampling only those genotypes with AGRO >= 3 in our study). It appears that with such an agronomic evaluation some traits are becoming more pronounced and get lower genotype environment interactions (i.e. FYLD, DM and TcDM).

A clear advantage of the ABS is that it considers the genotype by environment interaction already from the beginning of a breeding program. In the general breeding scheme for clonally propagated crops (Fig.1) the genotype by environment interaction is not considered in early breeding stages. The result is an extreme inflation and over estimation of σ_G^2 in early selection stages. Those who have ever conducted heritability estimations for yield at one location with two replications know how unrealistic large these estimates are. In other word in the general breeding scheme the genotypes in the selected fraction are over estimated, especially for yield, and often do not keep their "promise" in later breeding stages. However, this leads to a still weak aspect in our study on the ABS: the magnitude of σ_{GxY}^2. Also in our study the σ_G^2 might be overestimated depending on the genotype by year interaction. We assumed here that σ_{GxY}^2 is zero or low and then it can be neglected for an ABS study. We do not know if this is true. However, the magnitude of σ_{GxY}^2 depends extremely on regions and sub-regions. In example in Europe - with its very different soils and different weather conditions each year - the σ_{GxY}^2 is very small across crops, whereas in the great plains of the USA and Canada - with very homogenous soil conditions and differences in rainfall each year - the σ_{GxY}^2 is not small across crops. Estimates of σ_{GxY}^2 are not available for sweetpotato. However, in East Africa we estimated instead of σ_{GxY}^2 the σ_{GxS}^2 (variance component due to genotype by season interactions). For storage root yield the observed ratio $\sigma_G^2 : \sigma_{GxL}^2 : \sigma_{GxS}^2 : \sigma_{GxLxS}^2 : \sigma_\varepsilon^2$ was 1 : 1.46 : **0.96** : 1.83 : 2.62. For storage root dry matter the observed ratio $\sigma_G^2 : \sigma_{GxL}^2 : \sigma_{GxS}^2 : \sigma_{GxLxS}^2 : \sigma_\varepsilon^2$ was 1 : 0.04 : **0.0** : 0.15 : 0.63 (Grüneberg et al. 2004). This study was based on field trials comprising few genotypes and many environments, which represent later breeding stages. We expect a small σ_{GxY}^2 interaction in early breeding stages in which trials are carried out with many genotypes and few locations, but this needs to be confirmed. Currently we investigate such trial with breeding material from early breeding stages at two locations and years.

In conclusion our proposed ABS clearly reduce the time needed for breeding and it is nearly certain that it will lead to significant breeding progress for quality traits in sweetpotato and other clonally propagated crops. It might also be a very attractive breeding scheme for yields at least in sweetpotato. The allocation of resources into three environments for yield selection in ABS might be optimal or very close to the optimum. The allocation of laboratory capacity in more than two environments can not be recommended.

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Inheritance of plant and tuber traits in diploid potatoes

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Abstract

Inheritances of morphologic plant and tuber traits were studied at the greenhouse and field in Peru. The traits considered were: Presence of albino seedlings, stem wing shape, flower color, tuber flesh color and depth of eyes.

Thirteen native diploid Peruvian potato cultivars (eight of *Solanum stenotomum* and five of *S. goniocalix*) showing contrasting differences for the traits studied. These clones, from the potato collection of the National Agrarian University, were used as progenitors to obtain 26 hybrid progenies (10 crosses and their reciprocals and six additional one way crosses).

Albinism was controlled by a single *locus* with dominant allele ***A*** responsible for green color and ***a*** in homozygous condition, albinism. For the depth of eyes, deep controlled by the allele ***Eyd*** appeared dominant over shallow, ***eyd***. In the remaining traits various types of gene interactions were found. Stem wing shape would be controlled by a two *loci* producing double dominant epistasis. A two *loci* simple recessive epistasis would control flower corolla color. A more complex three *loci* epistasis appeared to control primary tuber flesh color. For secondary color purple, red and yellow colors would be controlled by three *loci,* purple (allele **P**) and red (allele **R**) dominant over yellow (**pprr**) but **P** was epistatic over **R**. No reciprocal effects were found in any of the studied traits.

Keywords: Diploid potatoes, Disomic inheritance, Genetics.

Introduction

Studies of inheritance of various plant and tuber traits traced back to 1910. Often, the few existing reports do not clearly define hereditary patterns and results on some characters are contradictory. In several reports conclusions were based on insufficient number of individuals per progeny, insufficient number of crosses or there was not enough contrast in the traits showed by the parents crossed. Environmental influence on stem, flower, tuber skin and flesh colors were not been reported.

Albinism due to chlorophyll absence preventing photosynthesis is a lethal trait observed in many plant species. Potato albino seedlings of a white or light pink color have an 8 to 12 day short life surviving on endosperm stored reserves.

The objectives of the present study was to determine the inheritances of several morphologic plant and tuber traits studied in a single season at the greenhouse and later at the field at La Molina, Peru. The traits considered were: Presence of albino seedlings, stem wing shape, flower color, tuber flesh color and depth of eyes.

Literature review

Lam and Erickson (1971) found that albinism on *S. chacoense* was controlled by the recessive allele **a**, and normal green color by **A** being the *locus* on chromosome 12. Estrada (1960), studying albinism on diploid and tetraploid species had similar conclusions.

For Howard (1970) pigment distribution on tuber skin and stem was controlled by *locus* **I.** The *locus* **E** controlled red color on the periderm, stem and flower color. Authors cited by Bradshaw and Mackay, 1994, proposed that *locus* **I** controlled pigment distribution on tuber skin and stem (Kelly, 1924 and Howard, 1962). Lunden, 1937 postulated a *locus* **E** responsible of red color in the periderm, tuber eyes, stem and flowers.

Taylor (1978), cited by Bradshaw and Mackay (1994) found that stem wing type was controlled by one gene with crenulated (C-) dominant to straight (cc).

Reports on flower color show some agreement. Hermsen (1978), found two complementary dominant genes controlling flower color. Taylor (1978) also cited by Bradshaw and Mackay, (1994) reached similar conclusions but both loci segregating on a random chromatid model.

Salaman (1926) Fruwirth (1912) cited by Howard (1970) and Howard (1978) found that primary tuber flesh color depended on a single *locus*. The dominant allele controlled yellow and its recessive, white. Other genes may be responsible of various yellow tones observed.

Literature reports about inheritance of depth of eyes are contradictory. East (1910) suggested that shallow eyes were dominant over deep. Salaman ((1911) and Nilsson (1913) both cited by Li *et al*. (2005) found that this trait was controlled by one *locus* but deep eyes were dominant over shallow. Huber (1930) cited by Li *et al*. (2005) also agreed that deep eyes were dominant but two complementary genes were responsible for shallow eyes. Finally, Li *et al*. (2005) found that inheritance of this trait was no clear but suggested a one locus control being deep dominant over shallow eyes.

Materials and methods

Crosses among 13 native diploid cultivars with contrasting traits (eight *S. stenotomum* and five *S. goniocalix*) produced 26 progenies (10 crosses and reciprocals and six one way crosses). Albinism was evaluated on seedlings at the greenhouse 10 days after germination. Flower color was evaluated in the field using CIP´s pigmentation scale and tuber traits evaluated at harvest. Data were analyzed with the Chi-Square Test for each progeny followed by Chi-Square homogeneity Test. For space reasons, results on the tables only show contrasting segregation ratios found among all progenies considered in the study.

Results and discussion

Inheritance of Albinism

Hypothesis: One *locus* control with allele **A** controlling green color and **aa**, albino. Segregation of four progenies agreed with the hypothesis with ^{2} values inferior to the critical value $\chi^2_{(1\ df;\ \alpha = 0.05)} = 3.84$. Results agreed with Estrada (1960) and Lam and Erickson (1971).

Table 1. Four progeny segregation for green to albino seedlings 10 days after germination

Progenitors		Possible		N° observed seedlings				
Female	Male	Female	Male	Green	Albino	Total	Ratio	^{2}
Pitiquiña	Kulliriñón	Aa	Aa	104	27	131	3/4 : 1/4	**1.35**
Kulliriñón	Pitiquiña	Aa	Aa	96	31	127	3/4 : 1/4	**0.02**
Llipiñawi	Kulliriñón	Aa	Aa	118	30	148	3/4 : 1/4	**1.77**
Llipiñawi	Pitiquiña	Aa	Aa	98	37	135	3/4 : 1/4	**0.42**

Inheritance of stem wing type

Hypothesis: Two *loci* double dominant epistasis with alleles **C+D** and **C** and **D** = wavy wings **(W)** and **ccdd =** straight wings **(R)**. The segregation of the 20 progenies agreed with the hypothesis with χ^2 values inferior to the critical value $\chi^2_{(1\ df;\ \alpha = 0.05)} = 3.84$.

Table 2. Observed stem wing segregation ratios observed on 20 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Wavy	Straight	Total		
Ccdd (W)	ccdd (S)	3	118	128	246	1/2 : 1/2	**2.30ns**
Ccdd (W)	Ccdd (W)	6	296	126	422	3/4 : 1/4	**2.96ns**
CcDd (W)	Ccdd (W)	3	205	24	229	7/8 : 1/8	**0.42ns**
CCDd (W) (W)	CcDd (W)	8	653	0	653	All : 0	**0.00ns**

Results disagreed with those of a single *locus* control proposed by Choudhury (1944) and Taylor (1987) cited by Bradshaw and Mackay (1994).

Inheritance of flower corolla color

Hypothesis: Two *loci* showing simple recessive epistasis would control this trait. In the first *locus*, dominant allele **C =** Pigment synthesis and **cc** = no synthesis (white) and in the second, **M** = purple tones and **mm** = red tones. Recessive **cc** epistatic over **M** and **m** alleles. All 17 calculated χ^2 values were inferior to the critical $\chi^2_{(2\ df;\ \alpha = 0.05)} = 5.99$, showing the agreement of the experimental results with the proposed hypothesis.

Table 3. Observed flower color segregation ratios on 17 progenies

Suggested genotypes		N° of crosses	N° plants observed				Expected ratio	Homogeneity ^{2} test
Female	Male		Purple	Red	White	Total		
CcMm (P)	CcMm (P)	6	256	71	107	434	9 : 3 : 4	**7.98ns**
ccmm (W)	CcMm (P)	2	25	30	53	108	1 : 1 : 2	**0.23ns**
ccmm (W)	Ccmm (R)	3	0	86	79	165	0 : 1 : 1	**4.34ns**
CcMm (P)	CCMM (P)	2	133	0	0	133	All : 0 : 0	**0.00**
CcMm (P)	Ccmm (R)	4	96	96	61	253	3 : 3 : 2	**4.07ns**

The results agreed with Hermsen (1978) and Taylor (1978), both cited by Bradshaw and Mackay (1994) who proposed two complementary dominant genes controlling this trait. We also observed that environmental factors, particularly temperature and light intensity, influence the expression of color intensity.

Inheritance of primary tuber flesh color

Hypothesis: Results suggested that this trait would be controlled by three *loci*. The **C** allele controls Xanthophyll synthesis and **cc** = No Xanthophyll synthesis (white). In the other two *loci*, **A + B** = yellow, **A** and **B** alone = cream and **aabb =** white. Due to difficulty to distinguish yellow and cream, data of these two colors were consolidated to differentiate from white. All 22 χ^2 values were inferior to the critical $\chi^2_{(1\ df;\ \alpha = 0.05)} = 3.84$.

Table 4. Observed primary tuber flesh color segregation ratios observed on 22 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Y + C	White	Total		
CcAaBb (Y)	CCAabb (C)	9	684	87	771	7/8 :1/8	**10.00ns**
CcAaBb (Y)	ccAaBb (W)	2	87	92	179	15/32: 17/32	**0.46ns**
ccAaBb (W)	ccAabb (W)	2	0	174	174	0 : All	**0.00**
CCAaBb (Y)	CcAaBb (Y)	4	334	13	347	31/32: 1/32	**6.68ns**
CCAabb (C)	ccAabb (W)	5	289	103	392	3/4 : 1/4	**3.88ns**

These results disagreed with Salaman (1926) and Fruwirth (1912) cited by Howard (1970) and Howard (1978) who considered that primary flesh color depended on a single *locus* with a dominant allele controlling yellow and its recessive, white. On the other hand, results agreed with their suggestion that other genes may be involved on the various yellow tones observed.

Inheritance of secondary tuber flesh color

Hypothesis: Results suggested that purple, red and yellow would be controlled by three epistatic *loci* with complete dominance. . In the first, **A** = Anthocyanin synthesis induction and **aa** = no induction (yellow), in the second, allele **P** = purple and **pp** = no color and in the third, **R** = red and **rr** = no color and **P** epistatic over **R**. All 20 calculated individual χ^2 values were inferior to the critical one $\chi^2_{(1\ df;\ \alpha = 0.05)} = 3.84$.

Table 5. Observed primary tuber flesh color segregation ratios observed on 20 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Purple	Red	Total		
AAppRR (R)	Aapprr (Y)	8	0	32	32	0 : All	**0.00**
AAPpRR (P)	Aapprr (Y)	7	21	21	42	1/2 : 1/2	**0.00**
aaPprr (Y)	AAPpRR (P)	3	32	7	39	3/4 : 1/4	**1.03**

Inheritance of depth of eyes

Hypothesis: Because of difficulty to clearly distinguish semi deep and deep phenotypes, both classes were consolidated as **SD + D** and only shallow, **S** were kept independent. Results of 18 progenies for depth of eyes strongly suggested that in diploid potatoes this trait was controlled by three independent *loci* S, T and U each showing complete dominance of deep and semi – deep over shallow eyes. All 18 calculated individual χ^2 values were inferior to the critical one $\chi^2_{(1\ df;\ \alpha\ 0.05)} = 3.84$.

Table 6. Observed Depth of eyes segregation ratios observed on 18 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		SD + D	Shallow	Total		
SsTtuu (SD)	SsTtUu (D)	4	347	4	351	32/31 : 1/32	**0.78** ns
Ssttuu (SD)	SsTtUu (D)	9	751	37	788	15/16 : 1/16	**10.68** ns
Ssttuu (SD)	SsTtuu (SD)	5	374	50	424	7/8 : 1/8	**1.28** ns

These results agreed with previous results about dominance of deep over shallow eyes but strongly disagree with a single *locus* control of the trait Segregation data on 18 crosses clearly show a three loci control. Also, contrary to other author's suggestions about strong environmental influence over this trait, we believe that depth of eyes is one of the most constant potato traits and that environmental effects are not significant.

Conclusions

1. Albinism would be controlled by one *locus* with two alleles **A** = green and **a** = albino**.**
2. Stem wing type would be controlled by 2 *loci* showing a double dominant epistasis where **C + D** together and**, C** and **D** individually = wavy wings and **ccdd** = straight wings.
3. Two epistatic *loci* would control flower color. In the first *locus*, allele **C =** presence of pigment and **cc** = absence of pigment (white) and the second, **M** = purple tones and **mm** = red tones, being the recessive **cc** epistatic over the **M** and **m** alleles.

4. Primary flesh color would be controlled by 3 *loci* where **C** = Xanthophyll synthesis and **cc** = no synthesis (white). In the 2nd and 3rd *loci*, dominant **A** and **B** alleles control cream color and both together **(A + B)** produce yellow while the recessive genotype **aabb**, controls white.
5. Secondary flesh color would be controlled by three alleles. In first *locus*, **A** = anthocyanin synthesis and **aa** = no synthesis (yellow). In the 2nd and 3rd *loci*, alleles **P** = purple and **R** = red and **pprr** doesn't show secondary flesh color. At the same time **P** is epistatic over **R.**
6. Depth of eyes appears controlled by three *loci* showing complete dominance. Allele **S**, **T** and **U** would produce deep and semi deep eyes while the recessive **ssttuu** would be the only with shallow eye phenotype.
7. Heterozygosis of most of the progenitors used in this research is evident as indicated for the wide segregation in al studied traits.
8. In spite of the significant number of reciprocal crosses were studied, no maternal effects are evident in any of the studied traits.

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Plant and tuber trait inheritance in autotetraploid potatoes (4x)

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Abstract

Inheritance of various morphologic plant and tuber traits in 4x potatoes was studied at the greenhouse and the field at La Molina, Peru. Traits considered were: Seedling and adult plant stem pigmentation stem wing type, tuber primary flesh color, eye depth and knobbiness.

A group of 32 progenies from crossing and selfing 12 native Peruvian cultivars (*Solanum tuberosum* L. ssp. *andigena*) of the National Agrarian University's potato germplasm and four commercial hybrids of the ssps. *andigena* x *tuberosum* of *S. tuberosum* L.were studied.

Seedling and adult plant stem color was controlled by a single *locus* with allele **P** (pigmented) dominant over **p** (green). However, in adult plant color distribution the same **P** allele showed dosage effects: **PPPP** with solid pigmentation while **pppp** green. **PPPp, PPpp** and **Pppp** with mixed proportions of pigmented to green areas based on the number of **P** alleles.

Stem wing shape was controlled by two *loci* showing double dominant epistasis. Tuber knobbiness and presence of eyebrows were controlled by single *loci* showing complete dominance. The inheritance of the other listed traits would be controlled by two or three *loci* showing different types of epistasis.

Primary tuber flesh color appears under control of two *loci* showing complete dominance. Alleles **A + B =** Yellow, **A** and **B** individually = Cream and **aaaabbbb =** White flesh. Tuber eye depth would depend on one *locus* with allele **S** = Semi deep and deep and **s** = shallow. Finally, tuber knobbiness might be controlled by one *locus* where allele **K** = normal tuber shape and the recessive *nulliplex* genotype, **kkkk**, would produce knobby tubers.

Keywords: Genetics, Tetrasomic inheritance, Autotetraploid potatoes.

Introduction

Despite of morphologic trait genetic research on tetraploid potatoes started in 1910, existing information on inheritance of some traits is limited, unclear and some times contradictory. Several reports did not include either sufficient number of observed individuals per progeny or sufficient contrasting characters in the progenitors used in these studies.

Importance of environment effects has not been reported neither its influence on traits such as stem pigmentation and flower, tuber skin and tuber flesh colors.

Literature Review

Kumikura (1967), in Bradshaw y Mackay (1994) suggest that stem pigmentation might be due to a single dominant gene while Howard (1970) suggested that stem color may depend on four *loci* but without showing experimental evidence.

Kelly, (1924) and Howard, (1962) (in Bradshaw and Mackay, 1994) proposed one *locus* **I** that controlled the distribution of the pigments in the tuber skin and stem. Also, Lunden (1937) postulated a *locus* **E** responsible of red color in the periderm, tuber eyes, stem and flowers.

Taylor (1978) in Bradshaw and Mackay (1994) found that wing stem type was controlled by one gene with crenulated (C-) dominant to straight (cc).

Salaman (1926) and Fruwirth (1912) cited by Howard (1970) and Howard (1978) considered that primary flesh color depended on a single *locus* with a dominant allele controlling yellow and its recessive, white.

Extensive literature review by Bradshaw y Mackay (1994) indicates that deep tuber eyes are dominant over shallow and that dosage effects might be responsible of deepness.

Materials and methods

A group of 34 progenies from selfings and crosses of 12 native Peruvian 4x cultivars (*Solanum tuberosum* L. ssp. *andigena*) of the National Agrarian University's potato collection and four commercial hybrids of ssps. *andigena* x *tuberosum* of *S. tuberosum*) were studied. Stem color was evaluated at flowering using CIP´s pigmentation scale. Tuber skin and flesh color, shape eye depth were evaluated at harvest. Data on all traits for individual progenies were analyzed with the χ^2 test followed by a homogeneity test for individual χ^2 values.

Results and discussion

Inheritance of seedling stem color

Hypothesis: Results on 10 tetraploid progenies suggested that stem pigmentation (pigmented *vs* green) was controlled by a single *locus* with dominant allele **P** = pigmented while recessive **p** = green.

Table 1. Observed seedling stem color segregation ratios on 10 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Purple	Green	Total		
pppp	Pppp	3	365	337	702	1/2 : 1/2	**2.65ns**
Pppp	Pppp	1	170	50	220	3/4 : 1/4	**0.61ns**
pppp	PPpp	2	383	96	479	5/6 : 1/6	**0.03ns**
Pppp	PPpp	2	421	41	462	11/12 : 1/12	**2.87ns**
PPpp	PPpp	2	453	17	470	35/36 : 1/36	**0.00ns**

Tetrasomic inheritance segregation ratios modified the phenotypic frequencies obtained with disomic inheritance. Results of the present research agreed with those of Kumikura (1967) but strongly disagreed with Howard (1970) who postulated a three gene control of this trait.

Inheritance of Adult Plant Stem Color

Hypothesis: Results on segregation for adult plant stem color of 28 progenies suggested a single *locus* control with the dominant allele **P** = pigmented and the recessive **p** = green.

Table 2. Observed adult plant stem color segregation ratios on 28 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Purple	Green	Total		
pppp	Pppp	3	235	229	464	1/2 : 1/2	**0.88ns**
Pppp	Pppp	4	349	125	474	3/4 : 1/4	**1.79ns**
pppp	PPpp	6	564	78	642	5/6 : 1/6	**3.84ns**
Pppp	PPpp	8	822	56	878	11/12 : 1/12	**6.12ns**
PPpp	PPpp	7	727	19	746	35/36 : 1/36	**3.18ns**

Data on Tables 1 and 2 show marked genotypic differences at that *locus* among parents. In addition, stem color showed two additional components, **(a).**Distribution, and **(b).** Intensity.

Differences in stem pigment distribution suggest dosage effects. The expected genotypic array upon selfing a *duplex* is **1/36 PPPP: 8/36 PPPp: 18/36 PPpp: 8/36 Pppp: 1/36 pppp** with a phenotypic array: **35/36 P_ _ _ (pigmented): 1/36 pppp (green)**. However, among the 35/36 pigmented there were distinct levels in the variables **(a).** and **(b).** mentioned before.

(a). Color distribution would depend on number of **P** alleles per genotype. A q*uadruplex* (PPPP) was fully pigmented, and a *duplex* (PPpp) has more pigment distribution than a *simplex* (Pppp). **(b).** Stem pigment intensity could have a variable expressivity of the P allele related to the environment, mainly light intensity and temperature. Under greenhouse conditions, Llama Senqa and Ayllu Papa stems were near to black while in the field's lower light intensity and temperature, stems still were black but showed greens areas throughout.

Inheritance of stem wing type

Hypothesis: Results on 14 progenies suggested that this trait is controlled by two *loci* showing double dominant epistasis with alleles **C + D** and **C** and **D** individually = Wavy while alleles **ccccddd =** Straight Wings.

Table 3. Observed stem wing type segregation ratios on 14 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Purple	Green	Total		
ccccdddd	Ccccdddd	1	34	28	62	1/2 : 1/2	**0.58ns**
ccccdddd	CcccDddd	6	527	141	668	3/4 : 1/4	**5.77ns**
CcccDddd	Ccccdddd	2	141	26	167	7/8 : 1/8	**0.06ns**
CcccDddd	CcccDddd	5	615	41	656	15/16 : 1/16	**3.28ns**

Results disagreed with those of Taylor (1978), in Bradshaw y Mackay (1994) who found that this trait was controlled by a single *locus* with wavy (W) dominant over straight (S).

Inheritance of primary tuber flesh color

Hypothesis: Results on 34 progenies suggested that this trait is controlled by two *loci* showing complete dominance with alleles **A + B =** Yellow and A and B individually = Cream while alleles **aaaabbbb =** White. Due to difficulty to distinguish yellow and cream, data of these two colors were consolidated to differentiate from white. All 34 χ^2 values were inferior to the critical $\chi^2_{(1\ df;\ \alpha = 0.05)}$ **= 3.84.**

Table 4. Observed primary tuber flesh color segregation ratios on 34 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		Y + C	White	Total		
aaaabbbb (W)	aaaabbbb (W)	2	0	241	241	0 : All	**0.00**
aaaabbbb (W)	Aaaabbbb (C)	1	93	72	165	1/2 : 1/2	**2.67ns**
aaaabbbb (W)	AaaaBbbb (C)	3	390	115	505	3/4 : 1/4	**2.37ns**
AAaabbbb (C)	aaaabbbb (W)	4	532	113	645	5/6 : 1/6	**1.00ns**
AaaaBbbb (C)	Aaaabbbb (C)	3	408	66	474	7/8 : 1/8	**1.66ns**
AAaabbbb (C)	Aaaabbbb (C)	4	523	43	566	11/12 : 1/12	**1.36ns**
AaaaBbbb (C)	AaaaBbbb (C)	5	794	46	840	15/16 : 1/16	**3.43ns**
AAaaBBbb(Y)	Aaaabbbb (C)	10	1597	27	1624	71/72 : 1/72	**15.12ns**
AAaaBBbb(Y)	AAaaBBbb(Y)	2	294	0	294	++	**0.23ns**

[++]**1295/1296 : 1/1296**

These results disagreed with Salaman (1926) and Fruwirth (1912) cited by Howard (1970) and Howard (1978) who considered that primary flesh color depended on a single *locus* with a dominant allele controlling yellow and its recessive, white.

Inheritance of depth of eyes

Hypothesis: Because of difficulty to clearly distinguish semi deep and deep phenotypes, both classes were consolidated as **SD + D** and only shallow, **S** was kept independent. Results of 19 progenies for depth of eyes suggested that in 4x potatoes this trait was controlled by one *locus* with dominant allele **S** = Semi deep and Deep eyes while **s** be responsible for shallow eyes. All 19 calculated individual χ^2 values were inferior to the critical one $\chi^2_{(1\ df;\ \alpha\ 0.05)} = 3.84$.

Table 5. Observed primary tuber flesh color segregation ratios on 34 progenies

Suggested genotypes		N° of crosses	N° plants observed			Expected ratio	Homogeneity ^{2} test
Female	Male		SD + D	S	Total		
ssss (S)	ssss (S)	1	0	147	147	0 : All	**0.00**
Ssss (SD)	ssss (S)	3	229	218	447	1/2 : 1/2	**1.75ns**
Ssss (SD)	Ssss (SD)	8	930	313	1243	3/4 : 1/4	**11.44ns**
SSss (D)	Ssss (SD)	2	270	19	289	11/12 : 1/12	**0.89ns**
SSss (D)	SSss (D)	1	169	8	177	35/36 : 1/36	**1.99ns**
SSss (D)	SSSs (D)	4	642	6	648	All : 0	**0.15ns**

Results on segregation of 19 progenies agreed with previous reports about dominance of deep over shallow eyes on 4x potatoes. However, in a few progenies observed results did not fit with the expected according to the hypothesis which might be due to difficulty to separate semi deep and deep phenotypes. Also, data suggest a possible dosage effect of the **S** allele in the expression of eye depth as suggested in literature.

Inheritance of tuber knobbiness

Hypothesis: Tuber knobbiness is a rare trait observed in the cultivar Allkachokllo, among the progenitors utilized. Segregation of four progenies from crossing normal shaped cultivars (Amarilis, Canchan, Yungay and Ccompis) to Allkachokllo suggested that this trait depends on a single *locus* with dominant allele K = Normal shape and the recessive k = Knobby tuber**.**

Table 6. Observed tuber knobbiness segregation ratios on four progenies

Pedigree		Possible genotype		N° observed plants			Ratio	^{2}
Female	Male	Female	Male	Normal	Knobby	Total		
Amarilis	Allkachokllo	KKkk	kkkk	147	34	181	5/6 : 1/6	0.58ns
Canchan	Allkachokllo	Kkkk	kkkk	92	76	168	1/2 : 1/2	1.52ns
Yungay	Allkachokllo	Kkkk	kkkk	104	81	185	1/2 : 1/2	2.86ns
Ccompis	Allkachokllo	Kkkk	kkkk	54	57	111	1/2: 1/2	0.08ns

Conclusions

9. Seedling and adult plant stem pigmentation appears controlled by one *locus* with alleles **P** = pigmented and **p** = green. In adult plants, stem pigment distribution would involve dosage effects of P allele with complete cover in *quadruplex* genotypes (PPPP) with gradual decrease on *triplex* (PPPp), *duplex* (PPpp), and *simplex* (Pppp).
10. In adult plant stems**,** pigmentation intensity appears to be influenced by environment factors mainly light intensity and temperature.
11. Stem wing type might be controlled by two *loci* with double dominant epistasis. **C + D** together and **C** and **D** individually = wavy wings and **ccdd** = straight wings.
12. Primary tuber flesh color appears under control of two *loci* showing complete dominance. Alleles **A + B =** Yellow, **A** and **B** individually = Cream and **aaaabbbb =** White flesh**.**
13. Eye depth might depend on one *locus* with allele **S** = Semi deep and deep and **s** = shallow.
14. The tuber knobbiness might be controlled by one *locus* where allele **K** = normal tuber shape and the recessive *nulliplex* genotype, **kkkk**, would produce knobby tubers.

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Breeding for heat tolerance and disease resistance for the warming potato growing environments

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Abstract

The potato is normally adapted to grow under cool to mild temperature regimes. However, in the recent years the climate of many potato producing areas is warming up and rainfall distribution is becoming erratic and scarce. These trends may continue in the foreseeable future, as a result of the global weather change.

Breeding potatoes for heat tolerance, earliness and disease resistance started at the International Potato Center (CIP) in 1974 aiming to extend the potato crop to warmer; humid and arid areas of the developing world. At present, the importance of these potatoes has been boosted by the gradual global weather warming that has started to affect its production areas. CIP evaluated large populations genetically diverse and selected clones in two arid and warm and two humid and hot locations in Peru with further testing in African an Asian countries.

Within *Solanum tuberosum* L. ssps *tuberosum* and *andigena* adapted to grow under long days (Neo-*tuberosum*) and to a lesser extent in the diploid *S. phureja – S. stenotomum* populations, some heat tolerant and early maturing genotypes (80 to 90 days growing period) were selected. Intercrossing them produced a rapid increase of heat tolerance and early maturity. Next step was introducing resistances particularly to virus diseases. As a result CIP developed clones that could maintain the crop where warming climate may limit potato production.

Keywords: Earliness, Heat tolerance, Disease resistance, Combining ability.

Introduction

An important part of potatoes produced in developing countries concentrate in rainy hilly areas of variable altitude with cool to mild temperature. Under the global warming these areas are being affected and the expected increase of 4 to 5°C would alter tuberization, extend the growing period and enhance susceptibility to pests and diseases. Erratic rainfall patterns already observed are causing water stresses. In such a scenario, probably many of the presently grown varieties may suffer significant yield reduction and will need to be replaced.

Since 1974 the International Potato Center (CIP) headquartered in Peru, started a breeding program to improve potato adaptation and increase food production in the humid warm tropics as well as in semi arid areas of the tropics and subtropics of the developing world which are densely populated by people of scarce resources and great need of food.

This paper reports the work developed at CIP for adaptation to these environments emphasizing its genetic aspects and resources, its breeding philosophy and strategy and its outputs as new varieties released in Peru and other countries.

Genetic aspects of potato adaptation to hot environments

Daylength and temperature responses are basic factors for adaptation to changing environments. Research results showed that long day reaction for tuberization was recessive to short day reaction (Mendoza and Haynes, 1977). Also, it was suggested that adaptation to hot and warm conditions would be recessive to that to cool environments. The critical daylength concept established that each genotype has its own value, *i.e.*, 13 hours, above which tuberization stops and below which it takes place normally (Mendoza and Haynes, 1976). Likewise,

each genotype would have a critical temperature, *i.e.*, 16C°, above which tuberization stops and below it takes place normally. Daylength and temperature responses appeared correlated as long days and high temperatures act in the same direction as did response to short days and low temperatures. For instance, under a mean temperature of 24°C and a 13 hour photoperiod, a clone with a critical day length of 15 hours, would tuberize better than other with a critical day length of 12 hours. Recessiveness of heat tolerance was confirmed as intercrossing selected heat tolerant genotypes produced a steady increase in the frequency of clones showing that attribute (Mendoza, 1976, Mendoza and Estrada, 1979).

Genetic resources for the breeding work

The initial material for evaluation and selection under short day hot environments was formed by a large number of US and European *S. tuberosum* ssp. *tuberosum* varieties and breeding lines, *S. tuberosum* ssp. *andigena* (neo-tuberosum) adapted to long days and warmer temperatures than those of the Andean region and with immunity to PVX and PVY and late blight minor gene resistance (Plaisted, 1980) and a diploid S. *stenotomum* – S. *phureja* population adapted to long days (Mendoza and Haynes, 1977). Also, diploid hybrids of the wild species *S. sparsipilum*, *S.chacoense*, *S. bulbocastanum* and *S. berthaultii* were included as sources of disease resistance (Mendoza and Estrada, 1979).

Breeding philosophy

Mendoza and Haynes, 1974; proposed that heterosis for tuber yield would be maximized by increasing allelic diversity, provided that parental materials besides a wide genetic background would have a proper level of environmental adaptation. This was demonstrated by further experimental research results (Amoros and Mendoza, 1979; Mendoza, 1980).

Mendoza and Estrada, 1979; proposed that the yield of a genotype (**X**) may be expressed as the function **X = f(A + Y + R)** where **A**, are genes controlling adaptation to temperature and daylength, mayor factors in potato growth and development; **Y**, are the genes controlling yield *per se* related to the plant's capacity and efficiency to use light energy and transform it into chemical energy in the form of plant material, including tubers and **R**, are the genes controlling resistance or tolerance to diseases, pests and environmental stresses.

At present, many developing countries still grow cultivars selected under temperate and favorable conditions that may not adapt and perform under warm or hot environments. Therefore, breeding potatoes for developing countries where growing conditions might have more severe environmental constraints and more damaging pest and diseases, required selecting robust cultivars with the **A**, **Y** and particularly **R** genes to ensure an increased and stable yield to provide a greater food security.

Stepwise breeding strategy

First step: Evaluation of a large number of genetically diverse clones to select for heat tolerance in Peru in two semi arid and warm sites, La Molina and later Tacna, and two humid and hot, San Ramon and Yurimaguas.

Second step: Intercrossing selected clones to build a base population to apply recurrent selection for general combining ability for heat tolerance, earliness and agronomic attributes. These materials were later evaluated in hot and humid African an Asian countries

Third step: After progressing in heat tolerance, resistances to viruses X, Y and PLRV, bacterial wilt and early blight were introduced using resistant and adapted progenitors,

Fourth step: Increase testing and selection in warm environments of African and Asian countries to identify potential new varieties.

Fifth step: Use heat tolerant and high yielding clones to improve earliness of materials of other CIP programs as late blight resistance and use of true seed for commercial production.

Breeding results

Heat tolerance

Progress in heat tolerance had a slow starting but speeded up as early maturing heat tolerant clones were identified and intercrossed to produce new populations for the recurrent selection with progeny testing scheme. Results confirmed that heat tolerance was a recessive character.

This early work lead to selection of a few clones such as: DTO-33, DTO-28, DTO-2, LT-1, LT-2, LT-3, LT-4, LT-5, LT-6, LT-7, Maria Tropical, and others that showing heat tolerance. Selected clones were tested for general combining ability and a few like LT-1. LT-7, DTO-2, Maria Tropical among others proved to be excellent progenitors transmitting their attributes to a large number of progenies. The testing process continued identifying new heat tolerant progenitors like B71.240.2, Serrana, Katahdin, Atlantic, AVRDC-1287.19, TS-2, TS-4, 866.1, WRF-1923.1, 377888.8, 378015.3, 378015.13, 7XY.1, R128.6 etc., were used to combine their attributes with resistance to viruses and other diseases. **LT-5** resistant to late blight became the variety **MEVA** in Madagascar and **LT-8** released as **COSTANERA** in Peru.

Combining heat tolerance and virus resistance

With improved adaptation, the next step was to introduce resistances to the most common pathogens of the hot environments, the viruses PVX, PVY, and PLRV. LT-1 was a parent of the two first heat tolerant PVX and PVY immune clones: LT-8 and LT-9 that besides their good attributes were excellent progenitors. These two progenitors became the foundation of CIP's virus resistance breeding program leading to selection of excellent PVX and PVY immune progenitors as XY.4, XY.8, XY.13, XY.16, XY.20, etc Later these were used to breed *multiplex* XY immune and combine PVX and PVY immunities with PLRV resistance.

Combining heat tolerance and Phytophthora infestans late blight resistance

Several heat tolerant clones derived from *S. tuberosum* ssp. *andigena* adapted to long days (*neo-tuberosum*) were minor gene resistant to late blight. Several late blight resistant clones released in developing countries had as male progenitor a mixture of pollen from heat tolerant material (bulk early) or the clones 7XY.1, R128.6, 377888.8 and N551.12 (Table N° 1)

Combining heat tolerance and Alternaria solani early blight resistance

Since early blight could be a serious problem in several warm environments screening for resistance were carried out in Peru (San Ramon) and Brazil (Brasilia) finding several resistant clones such as Maine-28, Maine-47, NDD-277.2 and Atlantic. Crosses of these to heat tolerant material were evaluated in Brazil and 30 clones were selected as resistant and listed as CNPH/CIP. Numbers 001 and 006 [(377888.7 (N-565.2 x DTO-28) x NDD-277.2], 002. 004 and 005 (Serrana x NDD277.2), 014, 015, 016, and 017 (Atlantic x 378015.16), 018, 019, 020, 021 (Maine 28 x 378015.16), 022 and 023 (Y84.011 x LT-7), 024 (AVRDC-1287.19 x Y011), 025 (C83.633 x EB Bulk), 026, 027 and 028 (378015.16 x Y84.011), 029 (CFS-69.1 x Y84.011) and 031 (Y84.004 x WNC-521.22). Research on inheritance of resistance to early blight permitted to obtain heritability estimates of $h^2 = 0.7$ and $h^2 = 0.8$ that explains the fast transfer of resistance to heat tolerant clones (Mendoza *et al*, 1987)

Combining heat tolerance and Ralstonia solanacearum, bacterial wilt resistance

This resistance is complex due to existence of races 1 and 3 that interact with the environment and complicated by latent tuber infection. Moreover, heritability of resistance is low, $h^2 = 0.19$ determining that response to selection is slow (Anguiz and Mendoza, 1997). Resistance in cultivated materials is rare but despite of this, CIP identified some resistant clones: Cruza-148, BR-63.65, BR-63.74, BR-63.76, MS-35.22 and MS-1C.2. These were crossed to heat tolerant material and the following clones were selected in Peru and Philippines.

Several heat tolerant and bacterial wilt resistant clones were identified in Peru: BW-1 (BR-63.65 x Katahdin), BW-2 and BW-3 (BR-63.65 x Atlantic), BW-10 (BR-63.74 x DTO-28) BW-11 and BW-12 (BR-65.74 x WRF-1923.1). **BW-11** released as **KINGA** in Madagascar.

Later, in Philippines the resistant clones FBA-1 [(377835.11 (BR-63-65 x Atlantic) x BW Bk.], FBA-2 {381064.3 [(BR-63.74 x WRF-1923.1) x AVRDC-1287.19] x BW Bk., FBA-3 {[379673.17 (377847.4 x Maria Tropical)] x BW Bk.} and the full sibs FBA-15, FBA-16 and FBA-17 {381064.10 [(BR-63.74 x WRF-1923.1) x AVRDC-1287.19] x 7XY.1}

Table 1. Diseases resistant new varieties derived from heat tolerant progenitors developed from CIP's breed material released in Asia, Africa and Latin America

Variety	Country	Female	Male	L. blight	B. wilt	Viruses
DHeera	Bangladesh	Maine-53	377888.8	MR	---	---
Heera	Bangladesh	377831.1	M. Tropical	MR	---	---
Chamak	Bangladesh	Serrana	LT-7	MR		Imm.PVY
Ingabire	Burundi	378493.915	Early Bk.	R	---	---
Muruta	Burundi	CFK-69.1	14XY.1	MR	R	---
Muziranzara	Burundi	65-ZA.5	DTO-28	R	---	---
Ruzinko	Burundi	378493.915	Early Bk.	R	---	---
Babungo	Cameroon	379703.3	7XY.1	MR	---	---
IRA- 92	Cameroon	Renska	7XY.1	MR	---	Imm.PVY
Cipira	Cameroon	378493.915	Early Bk.	R	---	---
Baseko	Congo	Serrana	Atzimba	R	---	---
Enfula	Congo	65-ZA.5	CFK-69.1	MR	---	---
Floresta	Costa Rica	I-959 x XY Bk.	866.1 x P_2C_6.25	R		
Cooperation	China	Serrana	XY.4	MR	MR	Imm. X+Y
Kinga	Madagascar	BR-63.74	WRF-1923.1	MR	R	---
Meva	Madagascar	Snow Flake	N551.12	R	---	---
Amarilis	Peru	376724.1	Early Bk.	R	---	---
Raniag	Philippines	Y84.025	378015.16	R	---	---
Kinigi	Rwanda	65-ZA.5	YY.1	MR	---	Imm.PVY
Mabondo	Rwanda	Murca	378676.6	R	R	---
Mizero	Rwanda	BL-2.9	R128.8	R	---	---
Yayla Kizi	Turkey	Serrana	15XY.4	MR	---	Imm.PVY
Victoria	Uganda	378493.915	Early Bk.	R	---	---
Kisoro	Uganda	378493.915	Early Bk.	R	---	---

MR = Moderate resistant, **R** = Resistant, **Imm.** = Immune

Selection of high general combining ability progenitors derived from heat tolerant material for use in potato production from true seed (TPS)

The progenitors DTO-28, LT-7, LT-8, R-128.6, 378015.3, 378015.16, the TS clones numbered from 1 to 15, and the varieties Serrana and Atlantic were either breed or identified within the heat tolerance breeding work.

Conclusions

All the materials described provide an excellent genetic foundation to face the weather warming that will accentuate in the forthcoming years that will particularly affect food production in the developing world.

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Potato multiple virus resistant potatoes in Peru

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Abstract

The potato is highly susceptible to virus diseases that may drastically reduce tuber yield and quality being PVX, PVY and PLRV the primary causal agents of the **"crop degeneration"** that gradually reduces yield. Farmers of developed countries use certified seed to avoid virus damage even planting susceptible cultivars. In the developing world where quality seed is expensive, scarce or unavailable, virus resistance is the only way to control virus damage.

Immunities to PVX and PVY are simply inherited at independent *loci* with dominant immunity alleles. PLRV infection resistance despite of its polygenic control has a sizable additive gene action and medium-high heritability that ensures a good response to selection.

Breeding multiple virus resistant potatoes started at the International Potato Center (CIP) in the 1980´s. As a result *triplex* progenitors, XXXxYYYy, were assembled being important for transmitting immunity to both viruses to 96.4% of its progenies when crossed to any susceptible *multiplex* genotype, xxxxyyyy.

High yielding PVX and PVY immune progenitors crossed with PLRV resistant sources produced multiple virus resistant materials from which early maturing, high yielding and good tuber quality new cultivars are grown in Peru and African and Asian countries.

Keywords: Potatoes, Breeding and genetics, Virus resistance, Combining ability.

Introduction

The potato, *Solanum tuberosum* L. has many enemies: 23 viruses, 38 fungi, 6 bacteria and 1 viroid. From these, the most damaging are *Phytophthora infestans* causing late blight and leaf roll (PLRV), Y (PVY) and X (PVX) viruses, main agents of "potato degeneration" causing a gradual weakening of plants and reducing tuber yield and quality as infection rate increases with time. Vegetative propagation enhances virus spread in time and space as infected seed tubers carry disease from one season to the next and from one field to another.

Farmers of developed countries avoid virus disease damage using certified seed tubers that frequently renewed permits planting susceptible cultivars. However, in most developing countries certified seed could be too expensive, scarce or unavailable forcing farmers to often use infected seed. In this scenario, the only effective control of "degeneration" is the use of virus resistant cultivars. Otherwise, reduction of tuber yield and quality might be significant.

This paper reports the virus resistance breeding developed at CIP from 1982 to 1997 emphasizing its genetic aspects, philosophy and pragmatic strategy, genetic resources utilized and its outputs as new varieties released in Peru and other countries (Mendoza *et al.* 1989).

Genetic aspects of virus resistance

PVX and PVY immunities are controlled by single *loci* with complete dominance. At the PVY *locus* the allele **Y** controls immunity and **y**, susceptibility and segregate under a random chromatid model, $\alpha = 1/7$ (Mendoza *et al.*, 1996). At the PVX *locus* **X** controls immunity and **x**, susceptibility, under a random chromosome model, $\alpha = 0$ (Mendoza *et al.*, 2008a).

In addition, at an autotetraploid single *locus* several genotypes are possible, *i. e., quadruplex* (YYYY), *triplex* (YYYy), *duplex* (XXxx), *simplex* (Yyyy) and *nulliplex* (yyyy). Since PVY and PVX immunities are dominant, the presence of a single Y and X alleles will confer immunity to both viruses. However, their parental value is significantly different when crossed to any susceptible clone, xxxxyyyy. . A *simplex* XxxxYyyy produces 25% of progenies immune to PVX and PVY, a *duplex* XXxxYYyy, 69% of immunity and a *triplex* XXXxYYYy, 96.4% of immunity. Therefore, the superiority of *multiplex* progenitors is evident as they practically solve the problem of both PVX and PVY infections.

Inheritance of resistance to PLRV is complex and not as well known as that of PVX and PVY. Several mechanisms have been described as resistances to infection, multiplication, translocation, insect vectors, etc. The most studied resistance to infection would be polygenic and inherited with a sizable additive gene action reflected by its medium - high narrow sense heritability, $h^2 = 0.69$, that ensures an important response to selection (Salas, 2007).

Breeding philosophy

Potato production in most areas of the developing world is based on foreign cultivars often susceptible to virus diseases. Farmers of the countries where the seed originate avoid virus damage planting healthy seed. However, a primer cause of low potato productivity in most developing countries is the use of infected seed-tubers, due to high cost, scarcity or lack of certified seed. Since PLRV, PVY and PVX are mayor agents of "crop degeneration" reducing tuber yield and quality, selection of resistant varieties and assembly of superior progenitors for their breeding programs is the only economic solution (Mendoza, 1989a).

Sequential breeding strategy

To accomplish the objective of selecting high performing multiple virus resistant cultivars, a pragmatic strategy with modifications to traditional breeding methods was designed.

(1). Testing and selecting a large number of clones under diverse environments to search for wide adaptation to day length and higher temperature,

(2). Progeny testing clones selected in **(1)** for general combining ability (GCA) to identify those transmitting their traits to a high proportion of progenies (Mendoza, 1980)

(3). Growing seedlings in the greenhouse under 16 hours of day length to improve adaptation to medium and long days followed by testing under warm environments,

(4). Since the genetic control of PVX and PVY immunities was simple while that of PLRV was more complex, the work was split in two phases applied sequentially at different times:

(a). Start combining PVX + PVY immunities to bred *multiplex* selected progenitors and

(b). Crossing PVX+PVY immune with the PLRV resistant progenitors, selected by progeny testing, to develop high yielding multiple virus resistant varieties (Mendoza *et al*, 1989b).

Genetic resources for the breeding work

Immunities to PVX and PVY came from *S. tuberosum* L. ssp. *andigena* native cultivars (Huaman, 1980, Gálvez *et al*., 1992) and long day adapted *andigena* (*Neo tuberosum*) developed at USA (Plaisted, 1980). An additional input of *neo-tuberosum* was the late blight resistance and higher temperature adaptation besides virus resistance. Additional PVX immunity came from a few US and European cultivars derived from *S. acaule* and PVY immunity from a few clones bred in Europe derived from *S. stoloniferum* (Mendoza, 1989).

Resistance to PLRV infection had a wider genetic origin with an important contribution of wild species, particularly *S. demissum*. Commercial resistant varieties and breeding clones imported from Argentina, Chile, UK, Germany, Scotland, Netherlands, Poland, etc., were included.

Breeding results

Stepwise assembly of multiplex PVY and PVX+PVY immune progenitors

(i). Why *multiplex* progenitors? Crossing *triplex* (XXXxYYYy) to a susceptible (xxxxyyyy) clone produce 96.4% of immunity to both viruses. Therefore, using *triplex* progenitors avoids an expensive and time consuming screening as near all progenies are immune and provides a total genetic control of these viruses and facilitates combining with resistance to important diseases as leaf roll, late blight, etc. (Mendoza, 1993).

(ii). Initial crosses of (PVX imm.) x (PVY imm.) clones: (Xxxxyyyy) x (xxxxYyyy) ⇒ **¼ XxxxYyyy** : ¼ Xxxxyyyy : ¼ xxxxYyyy : ¼ xxxxyyyy. Seedlings were inoculated with a mix of both viruses. The *simplex* PVX + PVY immune did not show symptoms and were field evaluated and selected for agronomic traits and their immunity was verified by grafting and ELISA testing...

(iii). Crossing high yielding, early maturing, heat tolerant to *simplex* PVX + PVY progenitors: (xxxxyyyy) x (XxxxYyyy) ⇒ 1/4 Immune to both X and Y : 3/4 susceptible to either X or Y or both. Immune clones were tested for yield, tuber quality, and earliness, and the selected rechecked by grafting and then progeny tested to determine their parental value. The outcome was selecting outstanding progenitors: XY.4, XY.9, XY.13, XY.16, XY.20, LT-8, LT-9, 7XY.1, etc.

(iv). Crossing *simplex* (XxxxYyyy) x (XxxxYyyy) ⇒ 9/16 imm. : 7/16 susc. Of the 9/16 immune only 1/9 was *duplex* and identified back crossing to a susceptible tester. Field testing, rechecking for immunity and assessing parental value followed.

(v). The most complex phase was intercrossing *duplex* to select *triplex* and *quadruplex.* (XXxxYYyy) x (XXxxYYyy) ⇒ 1225/1296 imm.: 71/1296 susc. Out of the 1225/1296 immune it was expected only 6.25 *triplex* or *quadruplex*. The clones identified were *triplex* at both *loci*. Outcomes: Highly selected PVX + PVY triplex: TXY.2, TXY.3, TXY.4, TXY.8 and TXY.11 are now available for breeders use.

Combining PVX + PVY immunities with PLRV resistance

General Combining ability field testing conducted at CIP, for PLRV resistance of several clones and cultivars permitted identifying excellent progenitors transmitting resistance to a high proportion of their progenies: Serrana and Pentland Crown (Brandolini *et al*, 1992), the CIP progenitors product of the strategy discussed are: LR93.156, [(G7445 x YY.1) x Y84.004], LR93.160 (Mariella x XY.13), and full sibs C93.154 and C93.156 [(Monalisa x YY.5) x Y84.004)] (Salas, 2007) and Sedafin, Pirola, Bzura and Mex-32 (Mendoza, 2008),

As outputs of this breeding strategy that developed triplex immune PVY and PVX + PVY immune progenitors were crossed to previously identified PLRV resistant parents, several new varieties were released in Peru and other countries.

Virus resistant cultivars released in other countries: **IPORÁ** (Serrana x 7XY.1) in Uruguay, **CHAMAK** (Serrana x LT-7) in Bangladesh, **IRA-92** (Renska x 7XY.1) in Cameroon, **KINIGI** (65.ZA.5 x YY.1) in Rwanda, **MURUTA** (CFK-69.1 x 14XY.4) in Burundi, etc.

Table 1. High yielding, early maturing and virus resistant varieties released in Peru in the last 15 years

Variety	Progenitors	
	Female	Male
Costanera	LT-1 (Katahdin x Aquila)	(PVY + PVX Bulk)
Tacna	Serrana (Argentina)	XY.4
Maria Bonita	378015.18	PVY Bulk
Basadre	Sedafin (Chile)	388809.2 (Y84.007 x Y84.020)
Primavera	B-71-74-49.12 (Argentina)	385280.1 (LT-8 x 575049)
Única	387521.3 (AVRDC-1287.19 x 7XY.1)	Aphrodite (Netherlands)
Reiche	MEX-32 (Mexico)	XY.9

An important outcome of the strategy is the variety **TACNA** selected for earliness, yield, agronomic characters and PVX and PVY immunities and PLRV resistance in San Ramón and La Molina and later in Tacna, a southern semi arid testing site in Peru, where it showed moderate tolerance to salinity and drought. It was renamed as **COOPERATION-88** in China and planted in 120,000 ha in 2007 becoming the largest adopted CIP-breed variety worldwide (CIP Newsletter, 2009). Recognition should be given to the late Dr. Rene Chavez (University of Tacna) who collaborated with the author in its evaluation. Tacna's progenitors are (Serrana x XY.4). XY.4 is an important progenitor developed in CIP with parents: LT-8 [LT-1(Aquila x Katahdin) x PVX+PVY Bk.] x TS-4 [377887.17(N567.8 x R-704.19) x LT-7]. Progenitors LT-1, LT-7, LT-8 and TS-4 were breed in Peru within this strategy.

Additionally, CIP has bred several clones immune to PVX and PVY and resistant to other diseases derived from the triplex, i.e., TXY.8 x 387170.9 (bacterial wilt), TXY.3 x India-1039, (highly resistant to late blight), TXY.2 x 104.12LB (bacterial wilt), etc.

At present, within a special project, a population developed crossing triplex TXY.3, TXY.6 and TXY.11 to late blight resistant progenitors is under field evaluation. Selection is being carried out for agronomic and tuber traits and blight resistance with no need to screen for PVX and PVY as the great majority of clones should be immune to both viruses.

Conclusions

(1). Development of a breeding philosophy and a pragmatic breeding strategy using some arguments different to those of traditional potato breeding to select varieties for the developing world. Early maturity, tuber yield and quality, adaptation to stressing environments and disease resistances were mayor objectives pursued.

(2). Developing highly selected *simplex*, *duplex* and *triplex* PVY and PVX+PVY immune progenitors. The last group transmits their joint immunity to 96.4% of progenies when crossed to any susceptible genotypes, simplifying breeding for multiple resistances to important diseases.

(3). From advanced clones developed at CIP as a result of **(1)** and **(2)**, release by national programs in Peru and other countries several new commercial varieties of early maturity, high yield and tuber quality, PVX+PVY immunity and some also resistant to PLRV.

(4). It is hoped that CIP continues selecting new *triplex* progenitors and enhances their use to select the highly needed multiple resistant varieties for the developing countries, such as the long time due Late blight+PLRV+PVY+PVX.

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Development of processing potato cultivars by conventional and biotechnological approaches for the Indian subtropics

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The bulk of potato produced in India is utilized for table consumption. However, with the liberalization of economy, demand for processed potato products started increasing since 1990. At present, nearly 4-5% of the total produce is being processed and the processing sector is witnessing continuous growth. This created a demand for processing variety that can be grown under short-day condition with a growing period of 90-100 days. Therefore, an ambitious project on developing processing varieties suitable for growing under short-day winter months in subtropical plains was initiated that revolutionized the potato processing sector in India. The institute has so far developed four varieties suitable for processing into chips and one variety for French fries. These varieties are suitable for growing during winter months and give higher processing grade yield than any exotic variety within 90-100 days of growing period. Cold storage is an integral requirement of post-harvest handling of potato in India. Unfortunately, potato accumulates high amount of reducing sugars during cold-storage that makes it unfit for processing. This poses a serious impediment to otherwise fast emerging potato processing industry. It is not possible to develop cold-chipping potato cultivars through conventional breeding due to lack of suitable germplasm. Two different biotechnological approaches through metabolic engineering have been adopted to block the step leading to conversion of sucrose to reducing sugars either by inhibiting the vacuolar invertase activity, the enzyme responsible for synthesis of reducing sugars, or silencing of gene encoding potato vacuolar invertase (*INV*) at post transcriptional level.

Keywords: Indian processing varieties, Tuber characters, Potato products, Cold sweetening.

Potato is mainly consumed as a vegetable and forms an indispensable ingredient of Indian diet. However, with the liberalization of economy demand for processed potato products started increasing since early nineties, and several multinational companies (MNC) entered the field of potato processing. Since indigenous varieties were not suitable for producing quality processed products, the MNCs imported bulk of potato varieties from Europe and America. However, in view of quarantine problems related to bulk import involving risk of entry of new pests and diseases in the country, the Indian government allowed import of limited quantity of seed of a few processing varieties like 'Atlantic' and 'Frito-Lay' hybrids. These varieties when grown under Indian conditions produced low yields and were also susceptible to late blight, the most devastating disease of potato (Pandey *et al.,* 2008a).

The European and American potato varieties are developed for long-day (about 14-16 hr photoperiod) and long crop durations of 120-180 days. But in India, the potatoes are grown mainly in sub-tropical plains in winter under short-day condition, very different from that prevalent during the potato crop season in temperate countries. Also, unlike temperate countries, where the potato harvest is followed by severe winter, the harvest in the plains of India is followed by hot summer, making post-harvest operations difficult (Table 1). Thus the variety and technological requirement of potato cultivation in India are totally different from those of temperate world (Marwaha *et al.,* 2005). Obviously, these important aspects were overlooked by the industry while importing exotic varieties.

Among exotic processing varieties introduced by processing industry, only 'Atlantic' showed some promise. Despite its low yield and susceptibility to late blight, it was introduced in some selected regions. But the variety suffered high post-harvest losses due to 'hollow heart', a physiological disorder. These factors deterred wide scale adoption of 'Atlantic'. Due to non-availability of suitable raw material, the potato processing industries had no option but to use Indian table varieties even for processing into chips. The varieties like Kufri Jyoti and Kufri Lauvkar, procured mainly from warmer climate of Malwa region in Madhya Pradesh, (Ujjain, Indore), formed the main stay of the industry. The bulky and perishable raw material from these regions used to be transported at high cost over long distances to the industries located in north-western plains, which resulted in increase in the cost of production of products (Pandey *et al.,* 2005). Besides, these varieties contained low dry matter (<20%) and high reducing sugars (>0.1% on fresh wt basis), and produced chips of inferior quality.

Table 1. Potato growing conditions in sub-tropical and temperate regions

Parameter	Sub-tropical	Temperate
Day/night temperatures	25-30 °C / 2-15 °C	15-25 °C / 15 °C
Photoperiod	9-11 hr/day	14-16 hr/day
Frosting	Common	Absent
Crop duration	90-100 days	140-180 days
Post-harvest conditions	Harvesting followed by hot summer and rains	Harvesting followed by severe winter
Result	Low yields, low dry matter, high reducing sugars, short dormancy and poor keeping quality	High yields, high dry matter, low sugars, long dormancy and good keeping quality

Thus, availability of processing quality potatoes became a major bottleneck for growth of potato processing industry in India, which posed a challenge to the Central Potato Research Institute, Shimla. The institute accepted the challenge and initiated an ambitious project for development of indigenous processing varieties in 1990. The breeding strategy involved - (a) identification of parents with high tuber dry matter and good general combining ability for yield; (b) hybridization in the hills at Kufri during summers and raising of the segregating progenies in the plains, the same year to save time; (c) assessment of segregating populations for as many easily identifiable characters (viz. tuber colour, shape, eye depth, specific gravity, late blight resistance, etc.) as possible in the initial stages to eliminate undesirable genotypes; (d) extensive evaluation of selected genotypes in subsequent generations for tuber dry matter, reducing sugars, chip colour and yield; and (e) final evaluation of selected hybrids under industrial processing conditions.

With consistent efforts of eight years and after sifting through several hundred thousand genotypes, India's first potato processing varieties christened as Kufri Chipsona-I and Kufri Chipsona-2 were released in 1998 (Gaur *et al.,* 1998, 1999). Both the varieties have high tuber dry matter, produce light colour chips, possess resistance to late blight and give good tuber yield. Of the two Indian processing varieties, Kufri Chipsona-1 became very popular with the farmers and industry. This variety is capable of producing high quality processing potatoes in all parts of the country besides giving high yields similar to popular table varieties of the region.

Release of two indigenous high yielding disease resistant processing varieties provided the much needed relief to processing industry. After cultivation of these varieties for 3-4 years, it has been realized that Kufri Chipsona-1 produces low proportion of processing grade potatoes at some place in India and Kufri Chipsona-2 has poor storability. Keeping above problems in view, another processing variety, Kufri Chipsona-3, was developed in year 2005 (Pandey *et al.,* 2006). This variety produces about 11-15 per cent more total and processing grade tuber yield than the best control variety Kufri Chipsona-1 by virtue of its larger tuber size. This variety has good storability and can be stored for longer period for use in processing (Kumar *et al.,* 2007). These attributes will enhance the profit of the farmers and give them greater freedom in selling the produce to the processor or to the ware market, depending upon the prices.

In order to provide suitable raw material to the processing industries located in the north-western plains during the crisis months of shortage from August to November, the Institute has released Kufri Himsona, the first potato chipping variety for the hills (Pandey *et al.,* 2008b), which can be grown in Kangra and Mandi districts in Himachal Pradesh and supplied to the industry.

To meet the demand of the French fry industries, an advanced hybrid MP/98-71 has been developed by the Institute, which has shown high French fry grade tuber yield, high dry matter and superior fry colour at different locations in India and has been just released as Kufri Frysona (Singh *et al.,* 2008).

Salient features of processing varieties

Kufri Chipsona-1: Kufri Chipsona-I is a selection from the progeny of the cross CP 2416 x MS/78-79 made in 1990. The plant has medium compact canopy with white flowers and the tubers are white cream, ovoid with shallow eyes and white flesh. The variety is well adapted to north-Indian plains and has a maturity period of 90-

110 days. It has resistance to late blight and gives an average yield of 30-35 t/ha and possess very good storability at ambient temperature.

Kufri Chipsona-2: Kufri Chipsona-2 is a selection from the progeny of the cross CP 2346 (F-6 from Peru) x QB/B 92-4 made in 1991. The plant has medium compact canopy with white flowers and the tubers are white cream, round with shallow eyes and creamy flesh. The variety is well adapted to north-Indian plains and has a maturity period of 90-110 days. It is resistant to late blight and gives an average yield of 30-32.5 t/ha.

Kufri Chipsona-3: Kufri Chipsona-3 is a selection from the progeny of the cross Kufri Chipsona-2 x MP/91-86 made in 1996. The plant has medium compact canopy with white flowers and the tubers are white cream, ovoid with medium-deep eyes and creamy flesh (Fig. 1). The variety is well adapted to north-Indian plains and has a maturity period of 90-110 days. It is resistant to late blight and gives an average yield of 35-40 t/ha and has good storability.

Kufri Himsona: Kufri Himsona is a selection from the progeny of the cross MP/92-35 x Kufri Chipsona-2. The plant has medium canopy with purple flowers and the tubers are white to creamy, round-oval with shallow eyes and cream pale yellow flesh. The variety is adapted to hilly regions of the country and has a maturity period of 120-140 days. It has field resistance to late blight and gives an average yield of 25 t/ha.

Kufri Frysona: Kufri Frysona is a selection from the progeny of the cross MP/92-30 x MP/90-94 made in 1998. The plant has medium compact canopy with light-red flowers with white tips and the tubers are white, oblong to long in shape with shallow eyes and white flesh (Fig. 2). The variety is well adapted to north-Indian plains and has a maturity period of 100-110 days. It is resistant to late blight and gives an average yield of 38-40 t/ha and has good storability.

Figure 1. Tubers of Kufri Chipsona-3

Figure 2. Tubers of Kufri Frysona

All the indigenous processing varieties viz., Kufri Chipsona-1, Kufri Chipsona-2, Kufri Chipsona-3 and Kufri Himsona contained 21-24% dry matter, <0.1% reducing sugars on fresh tuber weight basis, low phenols and produced high yield of light coloured chips (Marwaha *et al.,* 2008). Kufri Frysona had 23% dry matter and produced high yield of French fries having mealy texture which were of international quality (Table 2). Besides fried products, these processing varieties also produced higher yield of dehydrated products such as dehydrated chips, flour, flakes and starch (Table 3).

Table 2. Processing qualities of potato varieties and some advanced processing hybrids

Varieties/hybrids	Chips		French fries			
	Yield (%) on fresh tuber wt	Colour[1]	Yield (%) on fresh tuber wt	Colour	Texture	Overall acceptability
Kufri Chipsona-1	29.3	3.0	45.3	LC	Mealy	HA
Kufri Chipsona-2	28.7	2.5	45.0	MB	Mealy	A
Kufri Chipsona-3	28.9	3.0	46.1	LC	Mealy	HA
Kufri Himsona	29.2	2.0	46.5	LC	Mealy	HA
Kufri Frysona	30.1	4.0	46.7	LC	Crispy	HA
Kufri Surya	27.4	4.5	45.8	LY	Mealy	HA
MP/97-637	27.9	5.0	45.7	LC	Mealy	HA
MP/97-921	30.8	2.25	45.6	LC	Crispy	HA
CD (P • 0.05)	1.1	0.12	1.8	-	-	-

[1]On a 1-10 scale of increasing dark colour, chip colour score >3 was unacceptable
LC, Light cream; MB, Medium brown; LY, Light yellow; HA, Highly acceptable; A, Aacceptable

Table 3. Yield (on fresh tuber wt) and quality of dehydrated products prepared from Indian processing and table varieties

Varieties	Yield of dehydrated chips (%)	Colour of dehydrated chips	Flour yield (%)	Flakes yield (%)	Starch yield (%)
Kufri Chipsona-1	17.6	HA	18.8	17.1	10.9
Kufri Chipsona-2	17.3	HA	19.2	19.8	10.4
Kufri Chipsona-3	17.2	HA	19.9	18.2	10.1
Kufri Himsona	17.6	HA	19.5	18.7	10.3
Kufri Badshah	13.7	UA	15.3	15.2	6.7
Kufri Chandramukhi	16.7	A	17.7	16.8	8.5
Kufri Jawahar	15.7	A	17.3	16.4	6.5
Kufri Jyoti	14.1	UA	15.8	16.2	7.6
Kufri Lauvkar	15.9	A	16.7	15.8	7.7
Kufri Pukhraj	12.5	UA	14.1	13.7	7.1
CD (P • 0.05)	0.82	-	0.61	0.73	0.45

A: Acceptable, HA: Highly acceptable, UA: Unacceptable

The development of processing varieties is a land mark in efforts to diversify potato utilization and development of potato processing industry in the country. The availability of quality raw material of these varieties and standardization of storage techniques for processing potatoes at 10-12 °C with sprout suppressant CIPC [Isopropyl N-(3-chlorophenyl) carbamate] has changed the entire scenario of potato utilization in India within a short span of 10 years, from the time when the farmers were often forced to throw harvested potatoes on road to the present situation where the processors are ready to pay good premium for processing potatoes (Pandey et al., 2008a). The release of these varieties has benefited all those associated with potato production, supply and utilization chain due to unprecedented growth in processing industry.

The industrial tests conducted at the factory of M/s PepsiCo India Holding Pvt. Ltd., Channo, Sangrur (Punjab) confirmed the excellent chipping quality of Chipsona varieties grown in Punjab and western UP. The extent of unacceptable traits in chips like internal defects (ID), external defects (ED), greening (G), undesirable colour (UC) and total potato defects (TPOD) in these varieties were well within the prescribed limits (Fig. 3). All the three Chipsona varieties showed <5% undesirable colour and <15% total defects, which were the maximum acceptance limits for chips. Likewise, Kufri Frysona tested at the factory of Satnam Agri Food Products, Jalandhar, produced superior quality of French fries both at the time of harvest and after four months of storage at 10-12 °C with CIPC.

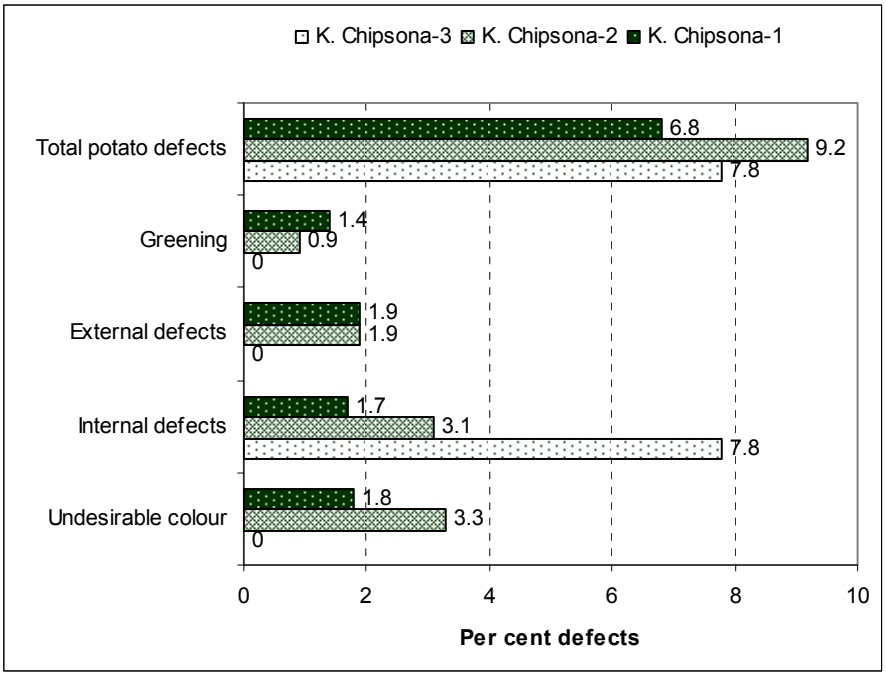

Figure 3. Per cent defects observed in potato chips prepared from Chipsona varieties during industrial testing at Channo, Sangrur (Punjab)

Industries use fresh potatoes of processing varieties from January to March. After this, they have to depend upon potatoes stored at 10-12 °C with CIPC. Due to rising food safety concerns, CIPC may have limited use in the future. Conversely, cold stored potatoes are unsuitable for processing due to high accumulation of reducing sugars yielding unacceptable dark colour and/or off-flavour in fried products. This is a very serious problem for potato processors and all the currently used Indian processing varieties are susceptible to cold sweetening. Cold-induced sweetening is a complex physiological process involving interplay of different factors. Therefore, different biotechnological approaches are being employed either to inhibit activity of two different enzymes of the cold-sweetening pathway, vacuolar acid invertase (vaINV) and UDP-glucose pyrophosphorylase (UGPase), or to silence expression of genes encoding these two enzymes. The transgenic lines are at different stages of development and expected to complement breeding efforts of the institute to circumvent the problem.

With the introduction of Chipsona varieties, consumption of potatoes by the organized potato processing industry in India has increased from 125,000 tons in year 2003 to 440,000 tons in 2007 and is growing annually at the rate of 25%, the present total processing of potatoes in the organized and unorganized sector being about 967,000 tons (Rana and Pandey, 2007). The organized and unorganized potato processing sectors presently consume about 4% of the total potato production, which was merely <1% in the year 2003. It is expected that the total utilization of potatoes in the processing sector in the year 2010 will rise to 17,40,000 metric tons or about 6% of the total production of the country. A large number of new industries manufacturing potato crisps, flakes and French fries have been installed in the organized sector in India. From just 4 or 5 companies in year 2003, the number has gone up to 30 in year 2009. This has become possible due to suitability of Indian processing varieties.

The potato processing scenario in the country has undergone a sea change in last decade. The release of indigenous processing varieties and their excellent performance in different agro-climatic zones of the country, in different crop seasons, in staggered planting in the main autumn season and during storage at 10-12 °C with CIPC has enhanced the availability of desired raw material for smooth and round the year operation of the processing industries. The national and multinationals potato processing companies in India now prefer indigenous processing varieties over exotic ones. With all these developments, India is set to have a 'crunchy revolution'.

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Adapting an instantaneous canopy photosynthesis model to simulate potato net primary productivity using remotely sensed data

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Abstract

Thornley's model uses a three-parameter non-rectangular hyperbola to describe the exponential light decay down the canopy for simulating the contribution of sun and shade leaves to the instantaneous photosynthesis of the plant. This paper summarizes a series of experiments to develop a bottom up modeling approach to convert this instantaneous plant canopy photosynthesis model into a crop model, using the potato as a prototype. Several steps were required for transforming this instantaneous model into a dynamic procedure capable of integrating the amount of carbon fixed by the plant from emergency through harvest. Model parameters were estimated using remotely sensed data, thus generating a model that could be parameterized with non-destructive and non-invasive methods. Those parameters included the light extinction coefficient, the proportion of light transmitted by the leaf, the fraction of incident diffuse photosynthetically active radiation (PAR), and the leaf area index. A spectroradiometer, a chlorophyll meter and a multispectral camera were used to derive the required parameters both within controlled and field conditions. The estimation of parameters with remotely sensed data presented R^2 ranging from 0.89 to 0.99. These parameters were integrated into a MATLAB net primary productivity model and tested with growth chamber and field data using commercial potato varieties as well as new clones. Simulated results explained above 85% of the variation in the actual yield data.

Keywords: PAR, NDVI, chlorophyll determination, autotrophic respiration.

Introduction

Remote sensing is generally defined as a group of techniques that permit the collection of data without a physical contact with the object or area under study. In our case, that object is the plant or crop canopy and the required data is the incident and reflected radiation. For agronomic applications, the region of the solar radiation spectrum that is of interests, is the range from the ultraviolet (UV) to the near infrared (NIR) and in particular the bands corresponding to the PAR, from 400 up to 700 nm.

The net primary productivity simulation model presented in this paper is based on the instantaneous canopy photosynthesis concept developed by Thornley (2002), which describes mathematically the assimilation of atmospheric carbon dioxide into plant dry matter as driven by photon flow. Thornley's model is based on four important assumptions: 1) the canopy is horizontally uniform; 2) light decays exponentially from the top to the lower strata of the foliage, with the same decay extinction coefficient regardless of the radiation source; 3) the leaf photosynthetic response can be described by a non-rectangular hyperbola model (NRH); and 4) the light dependency of an individual leaf is summarized in a single parameter of the NRH model that describes the light saturated photosynthetic rate (P_{max}), which is assumed to be proportional to the average irradiance received by the leaves.

In our adapted model, the accumulation of photosynthates per leaf area unit was calculated using a numerical integration with hourly steps. Parameters such as the leaf area index (LAI), the extinction coefficient (k), the percentage of PAR transmittance through the leaf (m) and the diffuse component of incident PAR -considered as constants in Thornley's model- were replaced with dynamic parameters that account for the temporal and spatial variability of the photosynthesis process. These parameters were approximated through remotely sensed data. Canopy photosynthesis estimates constitute the first step for the calculation of the net primary productivity, since the photosynthesis is the principal process by which plants increase their dry matter,

notwithstanding part of this chemical energy is used by the plants for processes of maintenance and growth as the autotrophic respiration that decreases the daily photosynthate accumulation.

Methodology

Thornley's model was adapted by converting it from an instantaneous canopy photosynthesis calculator into a dynamic one. The modified model calculates the gross canopy primary productivity (P_{canopy}) by way of integrating CO_2 fixed from plant emergence to harvest.

The light extinction coefficient (k) characterizes the light absorption by the canopy, and depends on the type of light, the position and the characteristics of the leaves; it varies during the day according to the solar zenithal angle. Assuming a spherical angular distribution, with leaves distributed at random within the canopy volume, the coefficient of extinction is defined as (Goudriaan, 1977, 1982):

$$K = \frac{1}{2\sin(\theta)} \tag{1}$$

The transmittance coefficient (m) is calculated by integrating the PAR energy transmitted through the leaf mesophyll. The light transmittance characterizes the physiological state of the leaf and is an indicator of its pigment concentration. The transmittance usually represents 10% of the incident energy, and it is sensitive to the chlorophyll A concentration in the leaves. The model estimates m as:

$$m = \frac{CL\_A_{\max}}{CL\_A} * 0.1 \tag{2}$$

Where:

Cl_A: Relative Chlorophyll A concentration
Cl_A_{max}: Maximum relative chlorophyll A concentration

Chlorophyll A determination

It is widely known that alterations of the PAR reflectance, in particular the corresponding to the NIR (690 - 740 nm) range, result from the sensitivity of chlorophyll A in the leaves (Knipling, 1970). In this study, the reflectance spectra were obtained using an integrating sphere - active remote sensing accessory of the spectroradiometer LI 1800- whose design presents a highly reflecting chamber in the visible and NIR regions of the spectrum and uses as source a tungsten lamp that simulates the incident solar spectrum.

The validation was conducted against chlorophyll estimates obtained from a calibrated Minolta SPAD 502 meter. This active remote sensing equipment estimates the relative chlorophyll concentration per unit of leaf area by calculating the transmittance of the leaf to specific wavelengths generated by illuminating leds.

Once the reflectance data was obtained, it was processed to calculate its first derivative w.r.t. the wavelength (DR_λ) and correlated with the relative concentrations of chlorophyll provided by the Minolta SPAD 502. The derivatives were calculated as:

$$DR_{\lambda} = \frac{R_{\lambda+1} - R_{\lambda-1}}{2} \quad (3)$$

Where:

$R_{\lambda+1}$ y $R_{\lambda-1}$: Reflectance in the wavelength $\lambda+1$ y $\lambda-1$

LAI- NDVI relationship

The LAI - ratio of total upper *leaf* surface of *vegetation* divided by the land *surface area*- is the most influential parameter in terms of the capacity for growth of a crop and its variation in time is an indicator of the growth stage (Maas, 1998a; 1998b; Guissard et al., 2005). LAI is also an indicator of the photosynthetic capacity of the crop and it is closely related to the final production. The LAI can be estimated from the Normalized Difference Vegetation Index (NDVI), which is the most used index to detect live green plant canopies in multispectral remote sensing data. The NDVI, which reflects the seasonal changes related to the vegetation instead of the quantity of vegetation, is a nonlinear transformation of the visible (red) and NIR bands of incident radiation (Rouse et al., 1974). The NDVI is calculated as follows:

$$NDVI = \left(NIR - R / NIR + R\right) \quad (4)$$

In our work the NDVI was estimated using the Dycam agricultural camera and regressed against LAI obtained from periodic destructive methods; this procedure allowed us to obtain a LAI-estimating function based on NDVI.

Diffuse PAR component

Photosynthesis simulation models commonly assume constants or consider alternating conditions of clear and overcast sky during the day, to address the difference between direct and diffuse irradiance. This approach usually generates over- or under-estimation of the diffuse component of incident radiation. Since the upper layer of the plant canopy interacts with the total PAR (direct plus indirect components) whereas the lower layers of the foliage only interact with the diffuse component of the incident PAR, it is important to calculate the diffuse component.

Following the equations of a black body defined by Planck, it has been demonstrated that the extraterrestrial PAR irradiance is a function of the temperature (equation 5).

$$I_{PAR-EXTRA}\left(Wm^{-2}\right) = \left(F\left(x_{700}\right) - F\left(x_{400}\right)\right)\sigma T^{4} \quad (5)$$

With:

$$F(x) = \frac{15}{\pi^4}\sum_{n=1}^{\infty}\frac{\exp(-nx)}{n}\left(x^3 + \frac{3x^2}{n} + \frac{6x}{n^2} + \frac{6}{n^3}\right)$$

$$x_{700} = \frac{hc}{(700)kT} \quad \wedge \quad x_{400} = \frac{hc}{(400)kT}$$

Where:

$\sigma = 5.67 * 10^{-8}$ Wm^{-2} K^{-4}. Stefan-Boltzmann's constant
$k = 1.38 * 10^{-23}$ J / K^{o}, Boltzmann's constant
$h = 6.62 * 10^{-34}$ J / s , Planck's constant
c = 3 * 10 8 m / s, Light speed in the vacuum

Spitters *et al.* (1986), calculated the quantity of global diffuse irradiance based on the incident total irradiation and the extraterrestrial global irradiation. Based on the fact that the total irradiance and the PAR at the top of the atmosphere are functions of temperature and that PAR radiation constitutes 50% of incident global radiation, (Tiba and Leal, 2004; Grossi Gallegos, 2003), Spitters' model can be modified to estimate the diffuse component of the PAR irradiance.

The results of the modified Spitters' model were validated with field measurements taken with an ASD FieldSpec VNIR (350-1075 nm) spectroradiometer and a band of black polyethylene coated with a soot sheet of 5 cm width. Measurements were taken in conditions of cleared, overcast and partially cloudy skies with the spectroradiometer shaded by the coated polyethylene throughout the data collection.

Respiration

Around 20 to 30 % of produced photosynthates are lost due to respiration (McCree, 1970). The autothrophic respiration or the respiration of photosynthetic organisms is directly proportional to the dry matter (DM) accumulation by different plant organs. Therefore, this component is determined empirically by destructive sampling throughout the growth period. The autotrophic respiration (R_a) is in turn divided into maintenance respiration (R_m) and growth respiration (R_g) (Running and Coughlan, 1988; Ryan, 1990, 1991):

$$R_a = R_m + R_g = \sum_i \left(R_{m,i} + R_{g,i} \right) \quad (6)$$

Where i denote the plant organ (leaf, stem, root, and tuber)

Finally, the net primary productivity (NPP) is calculated as the difference between the gross primary productivity (P_{Canopy}) and the autotrophic respiration (R_a):

$$NPP = P_{Canopy} - R_a \quad (7)$$

Results and discussions

Chlorophyll A determination

A high correspondence between the amplitude of the first derivative of the reflectance spectra in the region from 718 up to 726 nm and the concentrations of chlorophyll A per unit of area in three potato varieties was found (Table 1). Chlorophyll A can be adequately estimated with this remotely sensed data to parameterize the model.

Table 1. Wavelength presenting the highest determination coefficient with the chlorophyll A concentration per unit of area, for each of the three potato varieties

Variety	Wave length (nm)	Determination coefficient (R^2)
INC.-2563	725.5	99,40%
Pumamaqui	722.5	91,93%
Purranca	717.5	90,91%

LAI- NDVI relationship

The following exponential growth equation was the best predictor of LAI as a function of NDVI (R^2=0.9). This result shows the feasibility of using a multispectral camera to calibrate the LAI parameter in the model.

$$LAI = 0.2067 * \exp(2.963 * NDVI) \quad (8)$$

Diffuse PAR component

Table 2 summarizes the relationships among simulated and gauged diffuse PAR. The slopes seem to be homogeneous while the intercepts are different and estimated with greater error. Simulated data explained at least 68 % of the gauged variance. The relationships tended to be parallel but the scaling factor (Y intercept) varied with the degree of cloudiness. Although the model used is an empirical one, the results are quite good with the advantage that accessible minimum input data is required.

Table 2. Regression equations among simulated and gauged diffuse PAR radiation for clear, overcast, and cloudy skies

	Clear Sky	Overcast Sky	Cloudy Sky
Slope	0.6376 ± 0.1437	0.7507 ± 0.1405	0.5016 ± 0.1411
Intercept in Y	2.04 ± 19.21	12.71 ± 17.44	44.29 ± 15.07
Intercept in X	-3,199	-16.93	-88.30
R^2	0.7665	0.8263	0.6779
P value	<0.05	<0.05	<0.05

Net primary productivity (NPP) Simulation.

An example of the simulation results is given in Figure 1. The model explained 99 % of the variance in the measured data, and the residuals were randomly distributed around zero. In order to obtain this level of accuracy, experimental data on maximum light-saturated photosynthesis (P_{max0}) and photosynthetic efficiency (α) is needed. When the required lab equipment to produce the data is not available, reference literature values can be verified through iterations with the model, testing them against experimental calibration data under the environmental conditions to be modeled. The example presented was conducted using the following initial values: $P_{max0} = 0.2_{*}10^{-6}$ $kgCO_2m^{-2}s^{-1}$and $\alpha = 10^{-8}$ $kgCO_2$ $(JPAR)^{-1}$

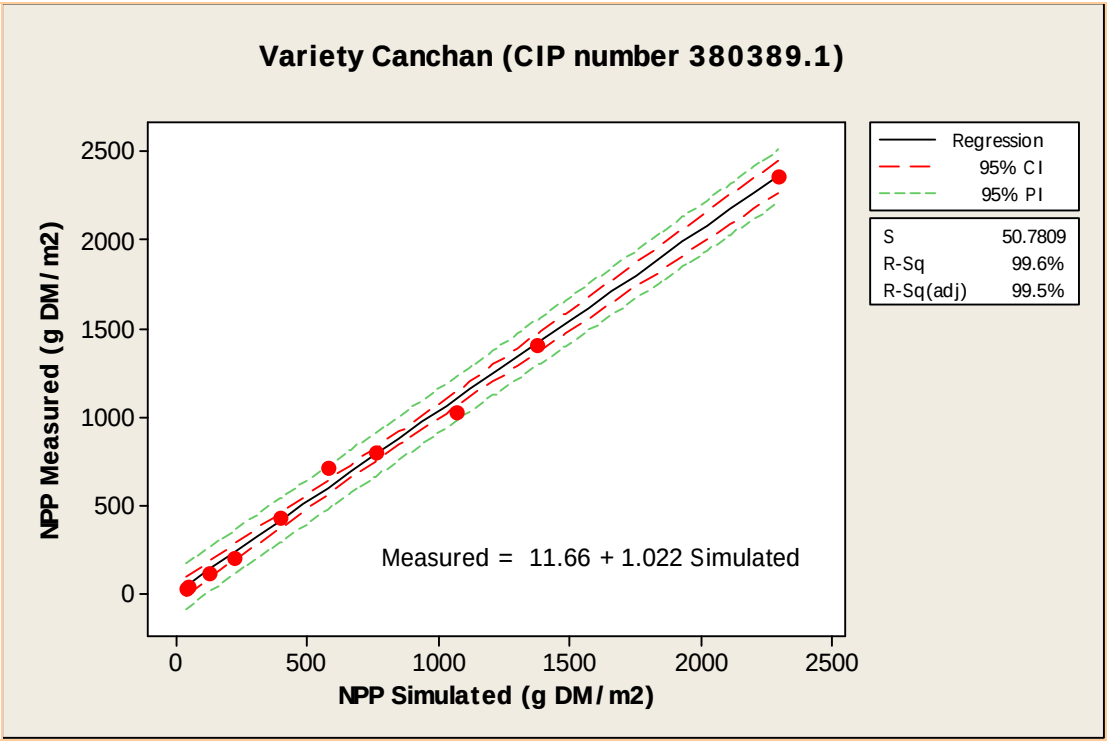

Figure 1. Net primary productivity simulation (grams of dry matter /m^2), for potato plants, variety Canchan.

Running an hourly periodicity of assimilation of photosynthates allows for a more realistic simulation of the photosynthetic process. It accounts for the nonlinear changes in solar radiation throughout the day, which are better mimicked, and events such as the stomatal closure when radiation is above the saturation threshold thus providing more accurate DM accumulation estimates. Models with daily steps, using average light conditions or pool energy levels, tend to overestimate DM production.

There are other sources of errors in this model, which are embedded in Thornley's assumptions. Assuming a horizontal uniform canopy tends to simplify the different levels of illumination received by leaves. This simplification overestimates the light interception, since leaves located in different positions in the canopy volume can have different levels of illumination. Moreover, assuming an exponential decay of the light within the canopy can underestimate the amount of light actually intercepted by the leaves located within it.

Models based on photon conversion into photosynthates do not take into account the stomatal saturation or closing by effects of temperature or other abiotic agents, thus overestimating the results. Biochemical models based on the kinetics of the enzyme Rubisco, such as the model described by Farquhar *et al.* (1980), explain with greater precision the photosynthesis process. Nonetheless, this type of models requires more input parameters and specialized equipments to estimate them, which makes them less accessible for most plant researchers. Therefore, dynamic models such as the one presented in this paper, based on light absorption, constitute a good alternative for predicting net primary productivity of C_3 plants.

Conclusions

The dynamic model presented here provides an efficient method for calculating the potential NPP of C_3 plants such as the potato. The model includes analytical solutions to substitute for initial parameters difficult to estimate without specialized equipments thus this model provides a practical analytical tool that does not demand large computational resources. Moreover, the possibility of estimating some of the key biophysical parameters e.g. the concentrations of chlorophyll A, the LAI and the diffuse component of PAR by means of non-destructive remotely sensed data, makes this model a good and reliable alternative to conventional techniques.

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Adaptability and storability of CIP potato clones under long-day conditions of Central Asia

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Abstract

After the breakdown of the USSR, potato seed and production systems collapsed in all central Asian republics resulting in a loss of valuable Russian and local varieties and consequent import of poorly adapted cultivars. In an effort to assist NARS of Central Asia, CIP supplied advanced potato clones for evaluation of their varietal potential under long day conditions as a means to support local farm-based and formal seed systems, among them some germplasm materials from the Lowland Tropic Virus Resistant (LTVR) population. In Uzbekistan, the most promising clones identified in three years' multilocation trials were as follows: 390478.9, early bulking, 388676.1, 397073.16, 391180.6, mid-early and 397077.16, medium maturing, with multilocation adaptability, while 388615.22 was early bulking and 392797.22 (UNICA) was mid-early maturing. The latter two clones showed the best performance in the lowlands during the first and second growing season, respectively. Storability was assessed under traditional and controlled atmospheric conditions and clones classified according to their dormancy period. Clone 397073.16 had the most noticeable apical dominance and the longest sprout length in both storage methods. A positive correlation existed between weight loss and the length of the longest sprout for all the clones, under the traditional storage method. The highest weight losses were reported for clone 397069.11 (8.84%) under controlled storage conditions and 397073.16 (8.03%) under traditional store conditions at 53 and 45 days from dormancy release, respectively. The study indicated that under traditional storage conditions, varieties with longer dormancy period and slower rate of sprout growth have limited weight loss during storage and, therefore, better keeping quality.

Keywords: Potato, Seed systems, Dormancy, Apical dominance, Weight loss.

Introduction

Uzbekistan was part of the USSR until it became independent in 1991. It is located approximately between 37-45° N and 55-72° E. The country has a total area of 44.8 million hectares with only 4.5 million hectares arable, out of which 4 million are irrigated (FAOSTAT, 2007). A vast area is covered by deserts, mountains and steppes. Climate is strongly continental and subject to extremes of temperature during winter and summer with abrupt changes even during the day; factors that limit cropping options. Rainfall is variable and uncertain, with periodic droughts. Most rains come during the spring, but these are generally scarce with less than 40 mm per month. After wheat and rice, potato is the most important food crop in Uzbekistan, cultivated on an area of about 52 000 ha. It is estimated that the double-cropping system of the lowlands covers about seventy percent of the total potato area with the second growing season (mid-July to October) prevailing as far as cultivated area is concerned. The remaining potato area is cultivated in the single-cropping season of the highlands, with planting in May and harvest in September-October. This cropping pattern is spread all over central Asian countries. Before independence, the Uzbek population consumed potatoes partially produced locally and partially imported from other Soviet Republics. Further to the disintegration of the USSR and consequent collapse of the potato research and development system, stocks of valuable Russian and local varieties got lost, while conventional potato seed tubers started to be imported from abroad and then fed into the formal and informal potato seed systems. To assist local NARS in their breeding and rehabilitation efforts, the International Potato Center (CIP) supplied a set of 34 advanced breeding clones and varieties with potential or demonstrated adaptation to long day conditions in the form of in-vitro plantlets in April 2005. The introductions included advanced selections of previously released varieties from CIP's Lowland Tropic Virus Resistant (LTVR) population, and varieties (e.g. Yagana-INIA, Achirana-INTA) from intervarietal crosses or collaborating institutions' population improvement programs (Chile, Argentina). Achirana-INTA, for instance, was introduced because of its successful performance in northern China. Main traits desired by local breeders are earliness for lowlands and medium-late maturing cycle for the

highlands (up to 120-130 days from planting), red skin color, resistance to viruses and main abiotic stresses (heat, drought), and marketability. Minitubers produced under screenhouse conditions in Tashkent were planted at a mid-elevation site in 2006, for further increase and preliminary clonal observations. In collaboration with local NARS, 22 clones selected for characters such as tuber shape, tuber eye depth, plant height, length of stolons, susceptibility to early blight (*Alternaria solani*) and viruses, were then entered in multilocation trials in 2007, 2008 and 2009. The present study seeks to provide useful guidance for potato breeding and selection programs, and the results may be valuable for recommending new varieties for specific uses. The study documents field performance of CIP clones under the long day conditions of Central Asia, and provides practical indications concerning storability.

Materials and methods

In 2007, 2008 and 2009, multilocation trials were planned under the varied agro-climatic conditions and growing seasons of Uzbekistan. Trials in the lowlands were carried out in Termez (302 m asl, 37° N, 67° E), on the bank of the Amu Darya river on the border with Afghanistan, during the first growing season, with planting in February and harvest in June, and in Tashkent (476 m asl, 41° N, 69° E), either in the first or second growing season with planting in March and July, respectively. Other trials were carried out at Pskem (1 236 m asl, 42° N, 70° E) during the highlands' single cropping season, with planting in May-June and harvest in September. In Central Asia day length and temperature vary in the course of each growing season, from short to long days and mild to high temperatures during the first growing season, and the opposite in the second growing season of the lowlands. On the other hand, in the highlands, temperature may be high during the day, especially in June, July and August, but it sensibly decreases during the night. .In each one of the three sites the choice of clones to test was made according to results obtained in 2006 after measuring earliness and bulking-based maturity of CIP advanced clones (Carli et al., 2008). Between 5 and 20 selected clones were planted in a randomized complete block design with three replications at a spacing of 70 cm between rows and 25 cm between plants in the row (57 100 plants/ha). The plot size was 2.8 x 5.0 m in all the locations. Fertilizers were applied at the rate of 117 N - 138 P_2O_5 – 225 K_2O units per hectare. Crops were dehaulmed 100 days after planting and harvested approximately ten days later to record tuber yield (t/ha). On each site, especially from April till October, furrow irrigation was provided every two-three weeks. The insecticide Confidor (imidacloprid: 200 g/l) was sprayed three times at a commercial formulation rate of 0.16 kg/ha to control Colorado potato beetle (*Leptinotarsa decemlineata,* Say). Dutch var. Sante, class Elite, was used as a control check.

Storability of the selected clones was assessed both in a cellar in a traditional farm house and a cold store in the town of Tashkent, where potato tubers are kept at a temperature of 2-4°C from February till June. In the traditional cellar, mean maximum ambient temperature ranged from 14.1°C in November 2008 to 10.5°C in January 2009, while mean minimum temperature varied from 6.5°C in November 2008 to 3.6°C in January 2009. The traditional cellar is normally used for seed tubers planted at the beginning of March; it is, in fact, problematic under those conditions to keep the seed viable till June-July because of the high temperatures that occur from March onward. Therefore, in this case, pre-sprouting starts towards mid-January, that is about three to three and a half months after harvest. On the other hand, poorly maintained cold stores of a capacity of about 5 000 tons are used to keep seed tubers that are planted towards mid-May in the highlands, or mid-July in the lowlands. As a consequence, pre-sprouting should start towards mid-April or mid-June, five and a half and seven and a half months after harvesting, respectively. In both stores, seed tubers of a calibre ranging from 35 to 55 mm were kept in trays containing 30 tubers each. The trial was replicated three times. Observations were made once a month in the case of the cold store tubers, and more regularly in the case of those stored traditionally. Observations concerned: (i) percent weight losses, (ii) dormancy period measured as number of days from haulm cutting to sprouting of 80% of the tubers with at least one sprout longer than 2 mm (van Ittersum and Scholte, 1992), (iii) dormancy status of the clones as percentage of tubers that were dormant at the end of storage, (iv) number of sprouts per tuber counted every fifteen days after release of dormancy in the traditional store, and (v) length of the longest sprout measured in the traditional store at 10 day intervals and in the cold store at the end of storage. Tubers were stored on October 24, 2008. Haulm killing occurred on October 01, 2008, at 100 days after planting, followed by harvest, 10 days later, and a two-week curing period. Storage observations were completed by February 16 (traditional store) and April 13 (cold store).

The obtained data were statistically processed using MSTATC (1993). The statistical analysis covers the following indicators: mean value (x), and Coefficient of Variation (CV). A two-way analysis of variance (ANOVA-2) was then computed as well as an LSD test for the level of significance of α=0.05. Correlations between different storability parameters were computed on the basis of mean value of one year (2008-2009).

Results and discussion

Last developments of the LTVR population of CIP

The development and orientation of the LTVR population of CIP in the last thirty years was documented by several authors (Cubillos and Plaisted, 1976; Plaisted, 1987; Mendoza, 1990; Mendoza et al., 1996; Mihovilovich et al., 2007). About nine years ago, CIP's breeding program intensified efforts to improve the adaptation of LTVR population to northern temperate regions including parts of China, Central Asia and the Caucasus. Controlled-cross families were evaluated for tuberization and yield in a series of surrogate environments including extended day length in the warm summer of La Molina (12° 06' S) and the coastal desert site of Majes (16.5° S) in Peru and natural long day conditions in Osorno, Chile (41° S). This enabled the identification of superior progenitors for adaptation to long days which were in turn tested in the form of progeny in 3 locations from Central to North China. Information on stability of performance among lowland and highland sites in Peru and progeny performance under extended day length or natural long day conditions was used to identify clones and design crosses for provision to Central Asian and Caucasus countries as in vitro clones and true seed families, respectively. The high solar radiation and temperatures of short to moderate day length locations such as Majes and Huancayo (11° 09' S) seems to have played an important role in identification of genotypes with adaptation to higher latitudes.

Field performance

CIP advanced clones tested on the mid-elevation site of Pskem showed that the yield obtained in 2008 was largely higher than that obtained in 2007 for almost all the entries due to improved irrigation facilities that increased water availability to the potato crop (Table 1). Clones 388676.1 and 390478.9 performed the best, yielding 71.7 and 43.9 t/ha in 2008 and 2007, respectively. While in 2008, the yield of 388676.1 was significantly higher than that of the other entries except for 720090 (62.0 t/ha), in 2007, 390478.9 did not perform better than 391180.6 (42.3 t/ha) and 397077.16 (41.9 t/ha) at $\alpha \leq 0.05$. Clones 391180.6, 390478.9, 392780.1 and 397077.16 had, however, the most stable yield during two consecutive years of trials with the lowest variation in percentage (5.7, 14.6, 37.8 and 38.4, respectively) reported among the tested clones (Table 1).

Table 1. Yield performance at mid-elevation (1,236 m asl), Pskem, May-September. Means of 3 reps

Entries	Yield (t/ha)		Mean yield (t/ha)	Variation 2007/ 2008
	2007 17.05-05.09	2008 06.06-24.09		(%)
388611.22	14.4 m	47.0 fgh	30.7	226.39
388615.22	29.6 efgh	51.9 cdefg	40.7	75.34
388676.1	33.1 defg	71.7 a	52.4	116.62
388972.22	27.6 fghij	60.0 bcd	43.8	117.39
390478.9	43.9 a	50.3 defg	47.1	14.58
391180.6	42.3 ab	44.7 fgh	43.5	5.67
392780.1	30.7 defg	42.3 gh	36.5	37.79
397029.21	23.0 hij	42.4 gh	32.7	84.35
397030.31	37.2 bcd	21.8 i	29.5	-41.4
397035.26	35.2 cde	61.0 bc	48.1	73.3
397073.16	33.9 def	52.5 bcdef	43.2	54.87
397077.16	41.9 abc	58.0 bcde	49.9	38.42
397099.4	22.2 ijk	46.2 fgh	34.2	108.11
397099.6	26.9 ghij	25.0 i	25.9	-7.06
397054.3	28.7 efghi	61.4 bc	45.0	113.94
720089	21.9 jkl	48.7 efgh	35.3	122.37
720090	31.8 defg	62.0 ab	46.9	94.97
720140	16.3 klm	44.7 fgh	30.5	174.23
720139	15.4 lm	45.3 fgh	30.3	194.16
720189	22.3 ijk	39.7 h	20.7	78.03
Sante	27.8 fghij	48.0 fgh	37.9	72.66
Mean	28.9	48.8	38.8	68.86
CV (%)	13.98	12.22	----	----
LSD (0.05)	6.6	9.8	----	----

In Termez, the favorable results obtained for clone 388615.22 in 2008 were confirmed in 2009. However, its yield was not significantly higher than that of Sante, 391180.6 (25.3 t/ha), 388676.1 (25.0 t/ha) and 397073.16 (24.0 t/ha) in 2007, and 397073.16 (38.9 t/ha) and 391180.6 (33.0 t/ha) in 2008. Only clones 388615.22, 391180.6 and 397073.16 performed better than the others in both years (Table 2).

Table 2. Yield performance in the lowlands (first growing season, Termez). Means of 3 reps.

Entries	Yield (t/ha)		Mean Yield (t/ha)	2008/ 2009 (%)
	2008 28.02-18.06	2009 12.02-02.06		
388615.22	36.0 a	41.8 a	38.9	16.11
388676.1	25.0 ab	27.6 b	26.3	10.4
391180.6	25.3 ab	33.0 ab	29.1	30.43
397035.26	19.1 b	27.9 b	23.5	46.07
397073.16	24.0 ab	38.9 ab	31.4	62.08
Sante	25.3 ab	20.7 bc	23.0	-18.18
Mean	25.8	31.6	28.7	22.48
CV (%)	26.37	22.1	----	----
LSD (0.05)	12.38	12.43	----	----

Table 3. Yield performance in the lowlands (first growing season, Tashkent). Means of 3 reps.

Entries	Yield (t/ha)		Mean Yield (t/ha)	2008/ 2009 %
	2008 07/03– 26/06	2009 12/03- 26/06		
388611.22	17.3 b	32.8 ab	25.0	89.6
388615.22	29.8 a	31.2 ab	30.5	4.7
388676.1	24.9 ab	35.1 a	30.0	40.9
391180.6	24.6 ab	29.5 b	27.0	19.9
397073.16	20.5 b	33.8 ab	27.1	64.9
397077.16	29.3 a	38.2 a	33.7	30.4
397099.4	28.5 a	33.3 ab	30.9	16.8
390478.9	24.5 ab	37.2 a	30.8	51.8
Sante	31.8 a	22.5 bc	27.1	-29.2
Mean	25.7	32.6	29.1	26.8
CV (%)	17.55	4.5	----	----
LSD (0.05)	7.8	7.7	----	----

Table 4. Yield performance in the lowlands (second growing season, Tashkent). Means of 3 reps.

Entries	Yield (t/ha)		Mean Yield (t/ha)	2008/ 2009 %
	2007 09/07– 30/10	2008 19/07- 13/11		
388676.1	32.6 a	21.6 d	27.1	-33.7
388972.22	23.8 e	22.1 d	22.9	-7.1
391180.6	19.5 g	13.9 e	16.7	-28.7
392797.22	33.1 a	31.7 ab	32.4	-4.2
397035.26	31.4 b	25.0 cd	28.2	-20.4
397065.28	14.1 h	28.8 bc	21.4	104.3
397073.16	24.7 d	33.8 ab	29.2	36.8
397077.16	28.9 c	34.4 a	31.6	19.0
397054.3	23.0 f	31.8 ab	27.4	38.3
Sante	23.1 f	24.2 cd	23.6	4.8
Mean	25.4	26.7	26.0	5.1
CV (%)	12.03	10.95	----	----
LSD (0.05)	0.53	5.02	----	----

In the Tashkent region's first growing season, Sante had the highest yield in 2008 (31.8 t/ha) although there were only two clones that yielded significantly less, 388611.22 and 397073.16. On the contrary, in the first growing season of 2009, 397077.16 (38.2 t/ha) was the best clone with a yield significantly higher than 391180.6 and Sante. Clone 388615.22 not only showed the most stable yield during the two-year trials with the lowest yield variation (4.7%), but it was also among the best performing entries. In the second growing season, clones 392797.22 (33.1 t/ha) and 397077.16 (34.4 t/ha) performed better in 2007 and 2008, respectively, although their yield was not significantly higher than 388676.1 (32.6 t/ha) in 2207, and than 397073.16 (33.8 t/ha), 397054.3

(31.8 t/ha) and 392797.22 (31.7 t/ha) in 2008 (Table 4). Among them, 392797.22 and 397077.16 had the highest average yield in the two years. Interestingly, all the above clones performed better than Sante.

Some negative phenological and pathologic characteristics

Among the clones tested in Pskem (Table 1), 391180.6, 392780.1, 397035.26 and 720189 showed symptoms referring to potato stolbur Phytoplasma disease, with aerial tubers and reddish, rolled leaflets on the top of plants (De Bokx et al., 1987). As reported by local scientists, this disease is occurring increasingly in Central Asia. Clones 720089, 397029.21 and 397099.6 had somewhat unattractive shape, characterized by moderately deep eyes. Finally, on all the sites, including the one at mid-elevation, seven clones, namely 388972.22, 397029.21, 397030.31, 397065.28, 397099.6, 397054.3 and 720189 developed long stolons, a characteristic which is not appreciated locally as the crop is not suitable for mechanical or semi-mechanical harvest.

Crop duration

Among the clones studied, one was early maturing, five were early bulking, six were mid-early and five were medium maturing (Tables 5 and 6).

Storability

Potato storability or keeping quality is an important feature too often forgotten in potato breeding and selection. Storability attributes studied in the potatoes stored under traditional conditions included duration of dormancy, sprouting patterns and weight loss. Table 5 shows that dormancy period ranged between 77 and 115 days, the shortest being in clone 392797.22 and the longest in clone 720150. Dormancy is considered to be a varietal character that might be affected by both preharvest and postharvest conditions (Ezekiel and Singh, 2003). In accordance with the variation in dormancy observed for the clones evaluated, those with less than 80 days duration were classified as having short dormancy, those with between 80 and 90 days as having medium, and, those with more than 90 days as having long dormancy (Table 5). There were significant differences in the dormancy period between and within different maturity classes (i.e. early, mid-early, and medium). The early maturing clone 397099.4 had a dormancy period of as long as 102 days (long dormancy) and medium maturing clone 720150 had long dormancy of 115 days (long dormancy). Hence no correlation was found between maturity class and dormancy duration as also reported by Burton (1989) and others (Roztropowicz and Wardzynska, 1974). The number of sprouts (>2 mm) per tuber also varied among the clones within and between different maturity groups (Table 5). Apical dominance was prevalent in clones 388676.1, 397073.16 and 720150, whereas clones 390663.8 and 720141 had the highest significant number of sprouts (6.3 vs. 5.7) 45 days after dormancy release. The number of sprouts per tuber is known to be a varietal characteristic (Sunoschi, 1981). The length of the longest sprout showed significant variation among the clones; 132 days after haulm killing the variation ranged from 0.8 cm (720148, 720150) to 2.3 cm (397073.16). The clones which showed greater sprout length up to 16 Feb., 2009, included 397073.16 (2.3 cm), 388676.1 (2.1 cm), 390663.8 (2.0 cm), whereas significantly lower sprout length was observed in clones 720150, 720148, 720139 and 392797.22, with less than 1 cm. The length of the longest sprout has been shown to be one of the most useful measurements to estimate sprout development in potato tubers (Wurr, 1978). The variability observed in the growth rate of the longest sprout in this study confirms earlier studies (Burton, 1989; Singh and Ezekiel, 2003) who reported that in the case of varieties with prevalent apical dominance, the length of the longest sprout was found to be the highest in comparison to the varieties where several sprouts grew simultaneously, thereby showing significant negative correlation between number of sprouts and length of the longest sprout (Singh and Ezekiel, 2003). In this study as well, 397073.16, which had prominent apical dominance, showed significantly faster growth rate of the longest sprout (Table 5). However, the correlation between the number of sprouts and length of the longest sprout was non significant ($r = -0.007$) in the present study. On the other hand there was significant negative correlation between length of sprouts and the dormancy period ($r = -0.51$) indicating that the shorter the dormancy period, the longer the length of apical sprout and *vice-versa*. Weight loss, which is an indicator of storage longevity and keeping quality of potato (Pande et al., 2007) showed significant differences among clones with 397073.16 having the highest weight loss (8.03%), while 720148 and 391180.6 had the lowest loss (5.0 and 5.07%, respectively) 116 days after the beginning of storage or 45 days after release of dormancy. The highest significant weight loss was observed in a mid-early maturity clone, while the lowest weight loss was in an early bulking and mid-early clone. The weight loss of 17 entries was positively correlated with the length of the longest sprout ($r = 0.46$), while there was no correlation between weight loss and number of sprouts per tuber ($r = -0.04$). With respect to dormancy period, the weight loss showed significant negative correlation ($r = -0.58$), in accordance with results obtained in India (Pande et al., 2007).

On the other hand, in the cold store, dormancy varied both among maturity groups and within each group (Table 6), ranging from 99 (391180.6, 397035.26, 397073.16, 397077.16) to 174 days (388615.22). The majority of clones had dormancy longer than 120 days. It is reported that within the range of 3 to 20°C, tubers stored at a lower temperature have a longer period of innate dormancy than those stored at a higher temperature (Wiltshire and Cobb, 1996). This was confirmed by the present study because clone 720150, for instance, showed longer dormancy under cold store conditions than in the store under traditional conditions (174 vs. 115 days). At the end of the storage period, that is 196 days from haulm killing, 397073.16 had the longest sprout, measuring 28.3 mm, which was significantly the longest measurement among the different clones. At the end of storage, clone 720148 showed the strongest dormancy (100%), followed by 720150 and 720141 with, respectively, 90 and 75.5% of the tubers affected. Apical dominance at the end of storage was particularly noticeable in clone 397073.16. Weight loss showed considerable variation between clones on all the study's observation dates (Table 6). After 53 days of dormancy release the range of weight loss varied from as low as 4.6% (388676.1) to as high as 8.84% (397069.11). The highest significant weight loss was observed in a medium maturity clone, while the lowest weight loss was in three mid-early clones. The weight loss of 17 CIP potato advanced clones was negatively correlated with the length of the longest sprout ($r = -0.23$). With respect to dormancy period, the weight loss showed very low correlation ($r = 0.25$).

Conclusions

The study compared advanced clones and varieties with the most popular and imported variety, Sante, under Uzbekistan's different environmental conditions. Except for one case (Table 3), where performance of the standard check matched those of some CIP clones, the latter performed significantly better than var. Sante. Results demonstrated that potato yields in the dual-cropping system of the lowlands and the single cropping system of the highlands are strongly influenced by water availability under the arid conditions of Central Asia. In spite of these stressful conditions, some advanced clones from CIP showed good adaptability and performance and can be recommended for further release as varieties. Specifically, while 390478.9, early bulking, 388676.1, 391180.6, mid-early, and 397077.16, medium maturing, show good adaptation to different environments, clone 388615.22, early bulking, and 392797.22 (UNICA), mid-early maturing, perform better in the lowlands during the first and second growing season, respectively. Clone 397073.16, when apical dominance is broken in a timely manner, shows good adaptation both in the lowlands and the highlands. The only exceptions are represented by clones 388972.22, 397029.21, 397030.31, 397065.28, 397054.3, 397099.6 and 720189 that have long stolon development. Furthermore, three clones, in particular, 397065.28, 397054.3 and 720139 have too high a plant height to be accepted by the local State Committee for Variety Testing. The study concluded that among the traits sought and evaluated, in varietal assessment, storability should be regarded as equally important as yield, disease resistance and quality. In the study the sprouting attributes of 17 CIP advanced clones previously selected for agronomic and quality characteristics, revealed abundant variability in terms of dormancy period, number of sprouts, length of the longest sprout and weight loss. For instance, 397073.16 had prominent apical dominance and significantly faster growth rate of the longest sprout, thus explaining the highest weight loss recorded when potatoes are stored under traditional conditions. It is expected that the investigation results will help CIP's breeders to improve potato adaptability to long day and storing conditions of Central Asia.

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Table 5. Potatoes stored under traditional conditions: dormancy and sprouting behaviour of CIP clones. Tashkent, Uzbekistan (October 2008-February 2009). Means of three reps.

CIP clones	Maturity	Dormancy period (days)	Length of the longest sprout (cm)					Av. No. of sprouts per tuber (days after sprout initiation)			Weight loss (%)		
			05.01. 2009	15.01. 2009	25.01. 2009	05.02. 2009	16.02. 2009	15	30	45	05.01. 2009	25.01. 2009	16.02. 2009
397099.4	Early	102	0.3	0.8	0.8	1.1	1.2	1.7	2.0	2.3	4.06	5.08	5.83
388615.22	Early bulking	98	0.3	0.6	0.9	1.3	1.4	1.7	2.0	2.0	4.15	5.66	6.46
390478.9	Early bulking	98	0.7	0.9	1.4	1.6	1.8	2.7	2.7	3.3	4.05	5.22	5.85
720087	Early bulking	107	0.1	0.4	0.5	0.8	1.0	2.7	2.7	2.7	4.29	4.87	5.59
720141	Early bulking	107	0.2	0.3	0.5	0.9	1.2	3.3	5.7	5.7	4.10	5.18	5.91
720148	Early bulking	108	0.0	0.1	0.2	0.5	0.8	0.0	1.0	2.3	3.14	4.23	5.00
388676.1	Mid-early	91	0.9	1.6	1.8	1.9	2.1	1.7	1.7	1.7	4.91	5.50	6.51
390663.8	Mid-early	95	0.7	1.0	1.4	1.8	2.0	5.3	6.3	6.3	4.13	5.04	6.14
391180.6	Mid-early	98	0.5	0.7	0.8	1.1	1.5	1.3	2.3	2.3	3.20	4.26	5.07
392797.22	Mid-early	77	0.1	0.2	0.4	0.7	0.9	2.3	4.7	4.7	5.26	6.13	6.97
397035.26	Mid-early	95	0.7	1.0	1.3	1.4	1.6	2.7	3.3	3.3	4.14	5.30	6.14
397073.16	Mid-early	87	0.9	1.3	1.8	2.0	2.3	1.7	1.7	1.7	5.60	6.64	8.03
397069.11	Medium	95	0.9	1.2	1.4	1.5	1.6	1.7	2.0	2.0	4.00	5.12	6.11
397077.16	Medium	89	0.8	1.1	1.2	1.4	1.4	2.3	3.7	3.7	3.77	4.84	5.92
388611.22	Medium	91	0.7	1.0	1.2	1.4	1.6	3.3	3.3	3.3	5.23	6.18	7.11
720139	Medium	107	0.1	0.4	0.5	0.7	0.9	2.0	3.0	3.0	4.68	5.38	6.13
720150	Medium	115	0.1	0.2	0.3	0.6	0.8	1.0	1.7	1.7	4.51	5.34	6.26
	Mean	97.6	0.47	0.75	0.96	1.22	1.42	2.2	2.93	3.06	4.31	5.29	6.18
	CV (%)	1.0	20.8	16.7	12.4	8.9	7.7	23.9	18.6	17.1	4.4	4.0	3.0
	LSD (0.05)	1.6	0.16	0.20	0.19	0.17	0.18	0.86	0.89	0.86	0.31	0.34	0.31

Table 6. Potatoes kept in the cold store: dormancy, sprouting behaviour and weight loss of CIP clones. Tashkent, Uzbekistan (October 2008-April 2009. Means of three reps.

CIP clones	Maturity	Dormancy period (days)	Length of the longest sprout at the end of storage (mm)	Dormancy (% of tubers dormant at the end of storage)	Apical dominance of tubers (%)	Weight loss (%)		
						15 days after sprout initiation (22 Jan. 2009	30 days after sprout initiation (19 Feb. 2009)	53 days after sprout initiation (13 April 2009)
397099.4	Early	139	1.0	5.5	---	3.55	4.57	5.99
388615.22	Early bulking	174	2.7	---	---	3.50	4.38	7.45
390478.9	Early bulking	104	16.0	---	---	3.52	4.93	6.87
720087	Early bulking	174	0.7	50.0	---	3.90	4.88	6.15
720141	Early bulking	174	0.5	75.5	---	4.19	4.89	6.29
720148	Early bulking	174	0.0	100.0	---	3.84	4.94	5.82
388676.1	Mid-early	109	13.3	---	---	2.85	2.86	4.60
390663.8	Mid-early	174	0.8	53.3	---	4.31	5.03	6.91
391180.6	Mid-early	99	11.3	---	---	3.12	3.13	4.76
392797.22	Mid-early	114	19.3	---	---	2.66	3.33	4.80
397035.26	Mid-early	99	13.7	---	---	4.96	5.59	7.45
397073.16	Mid-early	99	28.3	---	76.7	3.59	4.10	5.86
388611.22	Medium	104	11.7	---	---	5.06	5.52	6.73
397069.11	Medium	129	7.0	10.0	3.3	5.77	7.05	8.84
397077.16	Medium	99	10.3	---	---	3.37	4.49	5.84
720139	Medium	124	1.3	---	---	3.05	3.82	5.57
720150	Medium	174	0.5	90.0	---	4.79	5.39	6.83
	Mean	133.1	8.1	22.6	---	3.88	4.64	6.28
	CV (%)	3.5	48.8	20.4	---	5.5	2.5	2.6
	LSD (0.05)	7.79	6.59	7.66	---	0.35	0.19	0.27

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Sweetpotato breeding in Uruguay

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Introduction

Sweet potato is the second most important vegetable crop after potato, occupying more than 2.500 hectares in Uruguay (34° S 56° W) and first in number of growers involved (over1500) (Casáres et al., 2009). Approximately 60% of production is obtained in the South and 30% in the North region of the country. Average yield is about 15 tons/ha (Casáres et al., 2009) whereas specialized growers obtain more than 30 tons/ha.

Sweet potato (*Ipomoea batatas* (L) Lam.) is grown through Uruguay mainly as a seasonal cash crop. This product is traditionally consumed mainly for boiling, baking or roasting (7 kg. annually per capita) without further processing. Purple skin, yellow flesh varieties with semi humid texture (boniato type) are mostly preferred, whereas orange flesh, humid texture varieties are gaining in acceptance, mainly for baking or roasting.

In temperate countries like Uruguay, production is started at the end of winter with sweet potato roots planted in seedbeds for obtaining slip plantlets. Approximately two months later (October-November), these plantlets can be transplanted into the field. During December and January, stem vine cuttings with three or four developed nodes could be removed from growing crops for additional transplanting. The harvest period extends from January to June, providing the market with fresh product in this period and from July to December with stored product.

Crop improvement and management experimentation on sweet potato began in 1973 by former CIABB (Alberto Böerger Agronomical Research Center). Local landraces were collected and later evaluated during the 80´ along with several foreign introduced cultivars at Experimental Stations Las Brujas (south), Salto (north) and Tacuarembó (northeast) (Vilaró, 1987). From those introductions, Morada INTA and Jewel were extensively adopted in the south and north regions respectively. Beauregard, introduced in the early 90´s from USA, rapidly replaced Jewel and gained some importance in both regions. Although these varieties out yielded local landraces, they only partially fulfil crop adaptation requirements.

Breeding project was started on 1987 through germplasm introduction by means of botanical seed progenies from AVRDC and USDA-South Carolina and shortly later from North Carolina, Japan and CIP. In 1988 a national survey and workshop was realized about sweet potato production, uses and problems in Uruguay, with methodology supported by CIP (INIA-CIP, 1993). In this workshop, the importance of a local breeding program was stated and objectives discussed. Since then, several successful varieties have been released from this breeding program. They are described in this paper along with breeding methodology and perspectives.

Methodology

First local progenies were developed in 1988 at Las Brujas Research Station through polycross breeding method. Up to 20 progenitors were employed including local landraces, advanced local selections and introduced cultivars. The breeding method employed population improvement through recurrent selection for various traits. Flowering was restricted to South Carolina population, thus grafting with related *Ipomoea* species was performed to improve and promote flowering. Selection criteria was based on multiple disease and insect resistance, short growing cycle (90 to 120 days), high yield in different growing conditions, long storability and quality for diverse markets and uses.

During the last two decades, around 10.000 half sib progenies were annually planted in Salto Grande Research Station and clonally selected through two 90 days growing cycles per season. Selected clones were then

collaboratively evaluated in three INIA Research Experimental Stations involved. Later, grower participatory evaluation is performed for validating the most promising clones at different growing field conditions.

More recently, the program developed three different populations with specific objectives through corresponding polycrosses of up to 20 sweet potato parental lines. A total of 30.000 seedlings are raised annually for initial clone selection. (Rodríguez et al, 2007).

Present specific objectives are focused in developing different kind of populations:

15. A boniato type population with thick purple skin and cream flesh with long storability.
16. An orange flesh population, with high beta carotene content, early harvest, insect resistance and long storability.
17. A population with high dry matter content for different uses, including animal feed.

Two polycross nurseries are established at INIA Las Brujas Research Station, under plastic greenhouses (Figures 1 and 2) for first and third population. Corresponding seedling plants are field transplanted by the end of October and harvested by the end of March.

Figures 1 and 2

Figure 3. Field selection INIA Las Brujas

Thereafter, roots from selected clones are distributed to INIA Experimental Stations at Salto Grande and Tacuarembó for further evaluation at different growing conditions (Figure 3).

The polycross nursery at northern region (INIA Salto Grande) (Figure 4) is established to develop a second breeding population. This polycross is produced under a film shade to avoid frost damage during late autumn. The seedlings are field transplanted in September, and first selection is based on earliness (90 days). Vine cuttings from selected plants are then planted for a second 90 days growing cycle (Figure 5). Roots from selected clones are then distributed to the other Experimental Stations to continue cooperative evaluation.

Figures 4 and 5

High quality initial seed stock is obtained by hill selected plants at harvest. Although virus pressure is not a major issue, some varieties are favoured using in vitro tissue culture for multiplication.

Results

Great progress was made in sweet potato improvement during the 1990s. Several varieties of various types were released and rapidly adopted, remarkably 'INIA Arapey' (Vicente et al., 1999) (Table 1).This is a boniato type cultivar with wide adaptation and short growing cycle (100 days) which replaced Morada INTA and INIA Belastiquí. At the present time it covers about 75 % of the total area and it is being adopted in neighbour countries, reaching a marketable yield that is two or three times higher than older varieties.

In addition, several orange flesh varieties were released such as 'INIA Ayuí ', 'E 9227.1', INIA Itapebí ', and INIA Cerrillos (Vicente et al, 1996), (Rodríguez et al., 2007).

INIA-Ayuí is distinguished by its short growing cycle (90 days). INIA Itapebí and E 9227.1 with purple skin and orange flesh were released because of their long storage ability for north and south regions, respectively.

New cultivars of sweet potatoes, corresponding to different commercial types and adapted to diverse production regions and uses were recently obtained and released:

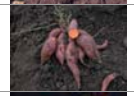
K 9818.1 and Ñ 0401.3 are two new orange flesh varieties with medium late and short growing cycle, respectively. They could replace INIA Ayuí and Beauregard for south and northern region respectively, because of higher yield, longer storability, higher multiplication rate and improved commercial quality. In addition, insect soil damage *(Chaetocnema)* is lower than Beauregard for both of them.

H 9430.23 is a red skin with cream white flesh sweet potato, adapted to northwest production region. Growing cycle is medium late (120 to 150 days) and its productivity is equal or larger than INIA Arapey. It has good storability, longer than INIA Arapey and low insect soil damage.

Finally, K 9807.1 is a sweet potato with dry matter over 30 %, suitable for processing and animal fed. It has a medium to medium late growing cycle (120-150 days) and present low insect soil damage. Its taste is quite unsweet and has a semi dry texture.

New released varieties are registered at INASE (National Seed Institute). The breeding program provides basic seed that is multiplied by grower organizations.

Table 1.

Variety Clone		Year of release or diffusion	Skin color	Flesh color	Productivity	Cycle	Storability	Dry Matter (%) ± SD	mg ß-carotene/ 100g fresh flesh ± SD
Morada Inta		**1980**	**P**	**C**	**medium**	**L**	**L**	**37.9 ± 1.7**	1.68 ± 0.04
Beauregard		**1994**	**O**	**O**	**high**	**M**	**L**	**21.5 ± 1.4**	35.50 ± 0.47
INIA Belastiquí		**1997**	**RP**	**C**	**high**	**E**	**M L**	**29.3 ± 2.5**	0.22 ± 0.01
INIA Cerrillos		**1997**	**R**	**O**	**medium**	**M E**	**P**	**25.7 ± 0.4**	29.4 ± 0.18
INIA Arapey		**1998**	**P**	**C**	**high**	**M E**	**M**	**28.2 ± 1.4**	2.15 ± 0.10
INIA Ayui		**1998**	**O**	**O**	**medium**	**E**	**P**	**20.8 ± 3.4**	23.5 ± 0.77
INIA E 9227.1		**2000**	**P**	**O**	**medium**	**ML**	**L**	**26.3 ± 1.2**	31.55 ± 1.40
INIA Itapebí		**2004**	**P**	**O**	**medium**	**M**	**M**	**23.4 ± 4.3**	30.45 ± 0.85
K 9818.1*		**2009**	**O**	**O**	**high**	**M E**	**L**	**23 ± 1.8**	55.51 ± 1.73
Ñ 0401.3*		**2009**	**O**	**O**	**high**	**E**	**L**	**22.7**	19.63 ± 0.29
H 9430.23*		**2009**	**R**	**W**	**high**	**L**	**M**	**28.9 ± 1.4**	n/d
K 9807.1*		2009	C	C	medium	M L	M L	34.8 ± 3.5	0.11 ± 0.03

Continúa …

Keys

- * Registered varieties under protection

- Skin Color
  - P (purple)
  - O (orange)
  - R (red)
  - C (cream)

  Flesh Color
  - C (cream)
  - W (white)
  - O (orange)

- Cycle
  - S (short 90 days)
  - M (medium 120 days)
  - L (long more than 140)

- Storability
  - P (poor)
  - M (medium)
  - L (long)

- Dry Matter forced air oven at 60 C° for 48 hs.

Perspectives

Polycross breeding system combined with recurrent selection allowed large progress for most traits, while maintaining enough variability. Introducing variable germplasm mainly as seed progenies became major sources for genetic improvement. Research Stations collaborative breeding program allows faster results. Wide adoption of released varieties improves crop and soil practices, having a major impact on national productivity and promotes high quality product supply of the market year around. Varieties with short growing cycle and early harvest help to extend planting season allowing a better soil use.

Through the past two years we have identified genotypes with improved characteristics in each breeding population. The development of three specialized populations is allowing faster progress for each of them.

Yield potential and quality market attributes have been remarkably improved and new processing uses are being validated. Ethanol and flour production and suitability for frozen products (puree and baking or frying) is being considered. Nutritional value such as high carotene content is being evaluated (Ibáñez et al., 2009) (Table 1). Efforts are now focusing on increasing dry matter content by inter crossing identified valuable germplasm from local and introduced accessions.

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Breeding for the future: assessing farmers' preferences for potato varieties in heat-prone Gujarat, India

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A key challenge in crop improvement research is to anticipate farmers' continuously changing preferences for varieties. Thus farmers' perspectives are now widely considered an important input in varietal development programmes. In India, potato production is increasingly constrained by abiotic stresses due to the fast-changing climate and agro-environment. Under an on-going crop improvement research project, analysis of farmers' expectations from new potato varieties in heat-prone production environment of Gujarat state was undertaken. CIP, CPRI and PRS-Deesa jointly conducted a diagnostic survey in Gandhinagar district in February 2009. The survey elicited farmers' perceptions on key traits preferred by cultivators, consumers and markets. Results revealed that a high proportion of respondents (98.5%) believed high yielding attributes; heat-tolerance (95.5%); late-blight resistance (81.5%); and drought resistance (69.0%) traits in new varieties will have the potential to further increase their potato yields. Heat susceptibility, poor yield, late maturity and late blight susceptibility were vital reasons for farmers to discard potato varieties in the past. Sizable respondents considered heat (94%) and drought (31%) as serious threats to potato production. Farmers' priority index (0-100) and percent relative importance for top ten potential attributes in new potato varieties were also listed. Heat tolerance (priority index = 92 and relative importance = 22.43%) was the top priority followed by high yield, resistance to late-blight and resistance to potato-tuber-moth etc. Survey findings are being incorporated in efforts to validate and refine the research project's key assumptions, target outputs and expected outcomes on potato farmers' livelihoods.

Keywords: Heat-tolerant potato varieties, Varietal attributes, Abandonment of potato varieties, Priority index for breeding potato varieties.

Introduction

Potato is world's fourth most important food crop after rice, wheat and maize. India is the third largest potato producer after China and Russia. Due to well developed indigenous research and development India has the highest potato productivity among the top three potato producing countries.

Importance of potato in the world's food security and poverty elevation is reflected by the statement of Jacques Diouf, the Director General, FAO "The potato is on the frontline in the fight against world hunger and poverty" (FAO, 2008). Food security issues in Indian context have been thoroughly addressed at several fora (Acharya, 2009 and Chand, et al., 2007; to mention a few). Contribution of potato in the socio-economics of Indian people has been highlighted by Shekhawat and Naik, 1999.

Among potato producing states in India, Gujarat has shown the highest potato production and productivity at annual compound growth rates during recent years (Kesari and Rana, 2008). Over the same period the share of Gujarat in national potato production has also increased. The latest official potato production data shows that Gujarat has replaced Punjab as the third largest potato producing state in India after Uttar Pradesh and West Bengal (GOI, 2009). Gujarat also has the distinction of attaining the highest potato productivity in all Indian states during 2004-05 to 2007-08.

Global warming was perceived as the biggest future threats to Indian agriculture in general and potato in particular (Lal *et al.*, 2008). Decline in potato production was estimated by (Singh, *et al.*, 2008). However, the study estimated severer reduction in potato production in states like Karnataka, Gujarat, Maharashtra and Madhya Pradesh.

Ill effects of high temperature on potato during tuber initiation and tuber bulking stages were reported by Basu and Minhas, 1991; Minhas and Kumar, 2005. Development of heat tolerant potato varieties was considered an important tool to tackle global warming. Such varieties are supposed not only to enhance potato production in warmer areas but also to extend potato cultivation to non-traditional areas. Keeping these points into consideration a project funded by GTZ "Enhanced Food and Income Security in SWCA through Potato Varieties with Improved Tolerance to Abiotic Stress" was initiated

Present paper is an outcome of a diagnostic survey targeted to understand what attributes farmers want in future potato varieties in relatively heat stressed Gandhinagar district of Gujarat.

Methodology

Gandhinagar of Gujarat being one of the hottest potato growing districts was purposively selected for this study. Premnagar, Indirapura and Nandol were randomly selected three villages in the selected district. The survey conducted in February 2009 was an attempt to know farmers' perception on potato yield enhancing attributes, desirable and undesirable characters of existing potato varieties, reasons of varieties abandonment in the past, extent of abiotic stress experienced, and priority of desirable characters in the future potato varieties.

Potato growers were divided in four farm categories viz., marginal (up to 2.5 acre potato area), small (more than 2.5 and up to 5 acre potato area), medium (more than 5 and up to 10 acre potato area) and large (more than 10 acre potato area). Overall 93 households were covered in the survey. In the process of respondents' selection care was taken that all farm categories were represented. Information on the profile of sample villages was procured from *Panchayat* (Village council) records. Before finalizing, the interview schedule was circulated among multidisciplinary team of scientists involved in the project. Personal interview method was used for data collection.

Simple mathematical and statistical techniques were used to analyse data and draw conclusions. As a guide for developing future potato varieties priority index and relative importance of desirable varietal attributes were computed. Priority index ranged from 0 to 100 where percent multiple responses were assigned weights (1^{st} response = 2; 2^{nd} and 3^{rd} responses = 1; subsequent responses = 0.5) on open ended questions. Relative importance of top ten desirable varietal attributes was simple percentage of their priority indices. For testing independence among potato farmers' categories on various factors/ attributes, chi-square test (Gupta, 2009) was applied.

Results and discussion

Yield enhancing attributes: Every respondent farmer believed that there was scope for further increasing his potato yield. Highest proportion of farmers believed that high yielding new potato varieties (98.5%) followed by heat tolerant potato varieties (95.5%), proper late blight control (81.5%), water saving technologies (especially the drip irrigation; 74.6%) and drought tolerant varieties (69.2%) can further increase their potato yield. With the help of Chi-square test it was found that farmers of different categories had perceived differential importance for role of soil reclamation, fertilizer doses, low prices of inputs and better agricultural extension services in increasing their potato yield at 1% level of significance. Marginal farmers assumed higher importance of drought tolerant potato varieties and need of better agricultural extension services for increasing their potato yields. It was found that ground water table in the study area was very deep and marginal farmers were not having assured source of irrigation. Progressive farmers, who are generally targeted by extension agencies, were found not extending information to the poor and marginal farmers.

Desirable and undesirable characters: Among the desirable characters of existing potato varieties higher yield, early maturity, desirable (large and uniform) tuber size, good storability, higher price of the output and suitability for processing were the important ones preferred by the farmers. Contrarily low yield, susceptibility to heat and late blight, late maturity, bad storability and low price of the output were important undesirable characters disliked by potato farmers. Here bad storability means higher storage losses at ambient temperature as well as during cold storage.

Reasons for abandoning varieties: Potato varieties continuously not grown by a potato farmer for last five years were considered abandoned. Low yield as a reason for abandoning varieties was reported by the highest

number of respondents. Late blight susceptibility, low yield, problem of tuber cracking during bulking stage, longer duration of maturity, low output price, heat susceptibility and poor storability were other important reasons that compelled farmers to abandon potato varieties in the past. Tubers of one of the variety (Kufri Pukhraj) fetch lower prices on account of early (pre mature) harvesting, lower dry matter and poor storability.

Heat and drought stress: Heat and drought were the highly important abiotic stress factors faced in potato cultivation in the study area. About ninety four percent respondents believed that heat was a limiting factor towards achieving higher yield levels while a lower proportion (31.5%) of respondents perceived drought as abiotic stress to their potato crop. More crucial aspect of this problem was experience of drought stress by higher proportion of small and marginal potato farmers. Small and medium farmers heavily or sometimes entirely depend on larger farmers for irrigation water which they get at relatively higher charges. Large farmers may not provide them irrigation water at the right time according to formers' personal needs. Development of potato varieties that can give normal yield at least at 2^{o}C higher minimum night temperature (i.e. 22^{o}C) than the conventional potato varieties were estimated to increase potato yield in states like Karnataka and Gujarat by at least 20%

Priorities of varietal attributes: Previous year (2008-09 crop year) was a hot year and farmers experienced significant yield losses in many states of India on account of high temperature (CPRI, 2009). The sampled farmers showed heat tolerance in potato varieties as their first priority (index = 92 and relative importance = 22.43%) followed by high yield, resistance to late-blight, resistance to potato-tuber-moth and large but uniform tubers. High potato yield was relatively less important agenda on the rating scale of large farmers as they were more concerned with quality attributes than just the higher yield. Large farmers, which are generally the trend setters, had higher focus on resistance to late blight followed by processing grade varieties, resistance to potato-tuber-moth and early maturing potato varieties. Chi-square statistics showed that respondents among different farm categories had independent preferences for high yield, resistance to late blight, resistance to potato-tuber-moth, suitability for processing, early maturity and shining skin at 1% level of significance.

India in general and Gujarat in particular have shown tremendous growth in potato processing sector (Rana and Pandey, 2007). Raw material (processing grade tubers) demand of potato processing industry in India was estimated 2.678 million MT during 2010-11 (Rana and Pandey, 2007). This demand constitutes 10.76% of Indian average potato production during TE 2007-08 (GOI, 2009). Rana and Pandey (2007) clearly indicated that proportion of processing grade tubers required (from state's production) in this state was much higher than the national one. Although the varietal attribute suggesting suitability of potato variety for processing has got seventh highest priority ranking yet, the breeders need to assign a higher importance to this attribute.

Marginal farmers owing to low volume of produce have the tendency of avoiding marketing risk and try to sell at the farm itself or storing the produce using conventional methods. Hence improved storability as an attribute in new potato varieties is likely to be more beneficial to the resource poor potato farmers having small land holdings.

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Modelling potato growth and development with parameters derived from remotely sensed data

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Abstract

Light interception models are conveniently used for simulating crop development and growth. The light interception mechanism is generally approximated using canopy cover (CC) or leaf area index (LAI). This paper introduces the use of vegetation indexes as a reliable, low-cost alternative to parameterize tuber crops models or to directly assess plant behavior. Data from experiments conducted in the Peruvian coast both within a growth chamber to generate the parameters and in the field for validation, were used to prove the concept. The growth chamber was furnished with 3 large pots 3x4x0.8m containing sand, and the air temperature was maintained between 11 and 23 ºC whereas the soil temperature varied between 10 y 20 ºC. Potato seeds were planted at a density of 4.17 plants m^{-2} and received fertigation through a solution equivalent to 215-90-370 N-P-K units. Photosynthetic active radiation (PAR) inside the chamber fluctuated between 0.77 y 7.55 MJ m^{-2} d^{-1}. Reflectance data were measured through orthogonal photographs registered with the Dycam Inc. agricultural camera at about 2 m above the canopy on 18 plants randomly selected. The digital values registered in the red and near infrared region of the spectrum were used to estimate the Normalized difference vegetation index (NDVI). The model predicted yield within the growth chamber with less than 5 % error. Results in the field trials were variable.

Keywords: Modeling, potato, remote sensing, NDVI

Introduction

Plant growth, defined as dry matter increment over time, is governed by physiological processes and can be described quantitatively, using empirical models, including regressions. The parameterization, calibration, and validation of this type of models, of simple structure, can contribute to the forecast of the expected plant growth and yield in different future scenarios (Spitters, 1990).

Monteith and Moss (1977) define the efficiency of crop production in thermodynamic terms as the ratio of energy output (carbohydrate) to energy input (solar radiation). Total production of dry matter by barley, potatoes, sugar beet, and apples is strongly correlated with intercepted radiation.

The light interception mechanism is generally approximated using canopy cover (CC) or leaf area index (LAI). However, remote sensing techniques might improve our capacity to estimate the radiant energy intercepted by the plant through the measurement of the spectral reflectance and the construction of vegetation indexes. Bouman, et al., 1992a; 1992b, highlighted the advantages of using the values of reflectance as a simple, fast and non-destructive indicator to estimate light interception by the plants. They suggested that reflectance data is more appropriate than canopy cover and leaf area index to quantify light interception by the canopy.

The spectral response of the crop, defined as the proportion of incident energy that is reflected, depends on the interaction of the electromagnetic energy with the plant canopy. This information indicates the vigor of the plants that in turn, depends on the agronomic management and on the genotype-environment interaction.

In this research, the parameters of a potato growth model, based on interception and utilization of light, were determined using canopy cover and reflectance. The predictive capacity of the potato model, parameterized with reflectance information, was compared in terms of fresh and dry matter production with the growth and yield of potato grown under controlled environment and field conditions.

Materials and methods

An experiment was carried out in a growth chamber with controlled temperature at CIP headquarters in Lima. The aim of the work was to determine the parameters of a growth model based on light interception (Spitters, 1990). Commercial seed of potato cv. Canchán was planted on June 2006. The growing period lasted 150 days, until November 2006. The crop was managed assuming potential growth conditions, that is, with no limitations of water and nutrients, and without the effect of pests or diseases of importance.

The growth chamber was furnished with 3 large pots 3x4x0.8m containing sand, and the air temperature was maintained between 11 and 23 ºC whereas the soil temperature varied between 10 y 20 ºC. Potato seeds were planted at a density of 4.17 plants m^{-2} and received fertigation through a solution equivalent to 215-90-370 N-P-K units. Photosynthetic active radiation inside the chamber fluctuated between 0.77 y 7.55 MJ m^{-2} d^{-1}.

Data collection and analysis

Temperature, radiation, and the crop's phenological stages were registered as input data every 10 days, according to Kooman et al. (1996). Canopy cover, light reflectance and the dry matter of plant organs were also measured every 10 days for monitoring the growth and development of the crop.

Canopy cover was estimated on 18 plants, using a grid adapted to the spacing between plants (Haverkort at al., 1991). The grid, of dimensions 0.8*0.3 m and 100 cells, was placed approximately 30 cm above the canopy. The cells with more than 50% coverture of green plant material were counted.

In order to obtain reflectance data, orthogonal digital photographs were taken with an agricultural camera Dycam, Inc. placed some 2.10 m above the plants. The information recorded in the red (635-667 nm) and near infrared (835-870 nm) bands, were calibrated and used to calculate the normalized difference vegetation index (NDVI), using the software ENVI.

Plant dry matter weight was obtained from 6 plants, taken at random in each sampling date. The dry weights of leaves, stems, roots, and tubers were obtained periodically and the energy partitioning was estimated as the ratio of the organ DM to total DM.

Model parameterization

The growth model, based on light interception and utilization as proposed by Spitters (1987, 1990) and Kooman (1995), was used to simulate the daily accumulation of dry matter, through the following general equation:

$\Delta Wt = ft * PARt * E$

Where:
ΔWt = the growth rate at day t (g DM m^{-2} d^{-1})
ft = the fraction of PAR intercepted by the foliage
PARt = the incoming amount of photosynthetically active radiation (MJ m^{-2} d^{-1})
E = the average light utilization efficiency (g DM MJ^{-1} PAR)

The model uses 10 parameters that describe the principal processes involved in the capacity of intercepting light, the efficiency of light utilization and the partition of assimilate to the tubers.

A logistic function describes the capacity of the leaves to intercept light, from emergence to maximum canopy cover. The parameters were in turn estimated using a non-linear regression between the measured canopy values and the cumulative thermal time. The decline in light interception, during foliage senescence, was described by a linear function.

The light use efficiency was determined as the slope of the linear regression between the total dry matter weight and cumulative intercepted PAR radiation, passing through the origin.

The dry matter partition to tubers was estimated as a function of the cumulative thermal time from emergence. The parameters were estimated through a non-linear regression.

Highlands field data

The commercial potato cv. Canchán was planted in field plots in the highlands of Peru in order to obtain data to validate the previously parameterized model. The crop was grown under non-limiting conditions of water and nutrients, between January and April 2008. During the growing period, minimum temperatures of 6º C and maximums of 19º C and average levels of global solar radiation of 18 MJ m^{-2} d^{-1} were recorded.

Plant population was 3.7 pl m^{-2}. No pests or diseases of economic importance were observed.

Temperature, radiation and NDVI, calculated on the basis of the reflectance measured in field were used as input variables for simulating the growth of the crop.

Results and discussion

Table 1 shows the coefficients obtained for the parameterization of the model. Differences in the parameters associated with the capacity of the plant to intercept light and the light use efficiency, with predictions based on canopy cover or NDVI, are noteworthy.

Table 1. Parameters for the model

Potato cv. Canchán	GC1	NDVI 1	NDVI 2
Maximum fraction of radiation intercepted (fcl)	0,973	0,807	0,760
Initial light interception capacity (f0)	0,006	0,002	0,002
Initial relative leaf growth rate (R0)	0,007	0,013	0,013
Duration of leaf senescence (od)	612	907	907
Time when light interception was reduced to 50% (t50)	1718	1718	1718
Light utilization efficiency (AND)	5.5	6.3	6.3
Asymptotic maximum of the harvest index (M)	0.8	0.8	0.8
Initial slope of the harvest index curve (b)	-2.4	-2.4	-2.4
Thermal time at the initial harvest index curve (A)	722.6	722.6	722.6
Tuber dry matter content (DMc)	0.2	0.2	0.2

1 Growth chamber (CIP, Lima)
2 Field (Huancayo, Peru)

The results of the simulations under controlled conditions showed that a greater prediction approximation to yield was found using NDVI (Figure 1). On the other hand, when canopy cover was used as estimator of the light interception capacity, yield was slightly overestimated. This can be explained by the fact that reflectance provides not only estimates of canopy cover but it is also affected by the vigor of the plant, which might be the end effect of many factors. Overall, both approaches provided adequate probabilistic yield estimates, shown by the overlapping confidence intervals. Fresh tuber average yields were 80 kg $10m^{-2}$, 89 kg $10m^{-2}$, and 77 kg $10m^{-2}$ for measured, canopy cover based prediction and NDVI based prediction, respectively.

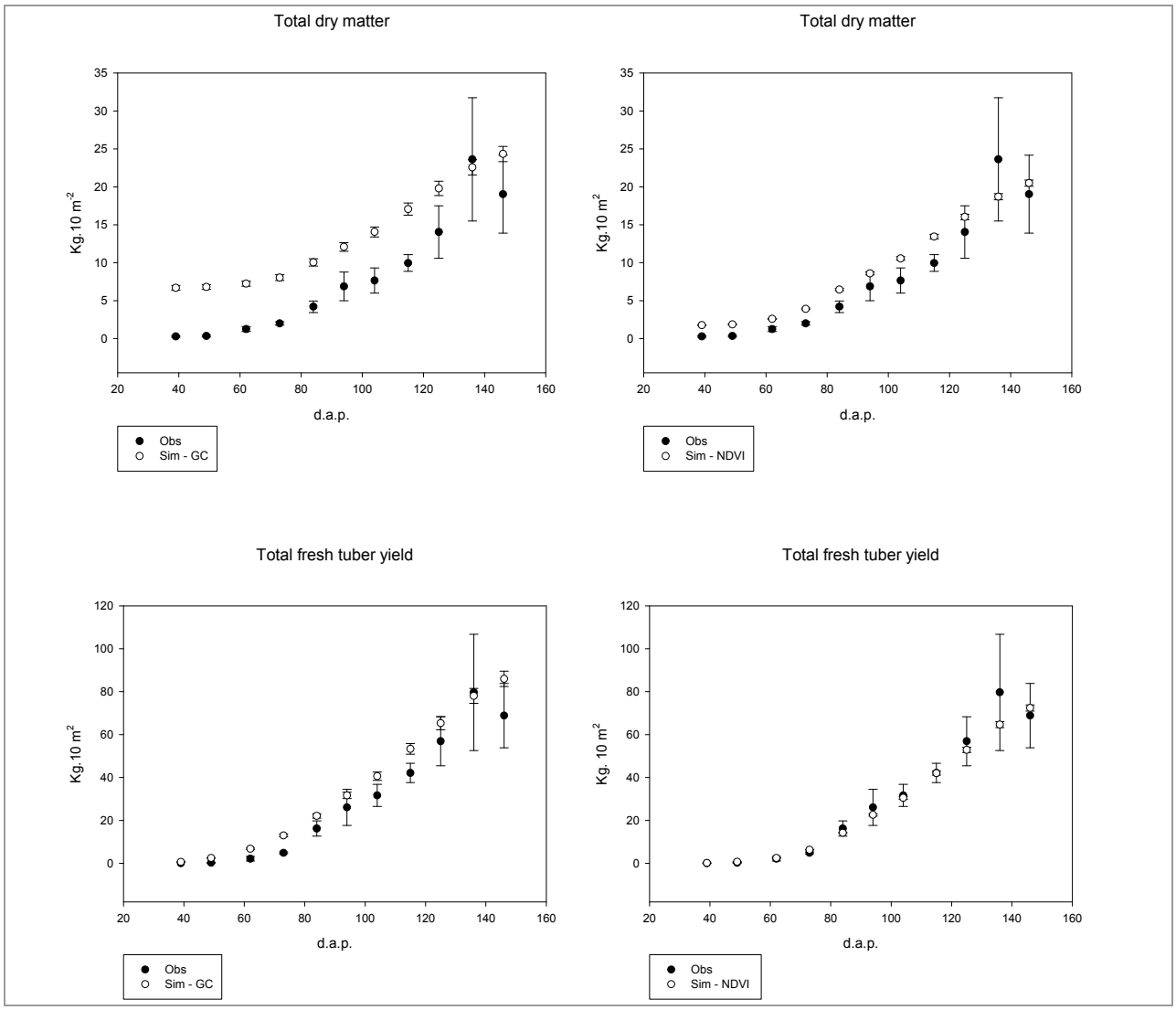

Figure 1. Estimating potato growth and tuber yield under controlled conditions, using simulation models

The model parameterized with NDVI was further validated with data from a field in the highlands of Peru. Measured fresh yield 105 d after emergence was 40 t ha^{-1} whereas the simulated yield was 44 t ha^{-1}. The 99 % confidence interval worked out by the simulation model includes the measured yield (Figure 2).

Results have shown the adequacy of light interception based models parameterized with remotely sensed data from potato crops without significant biotic and abiotic stressors. Our lab is conducting research to streamline the same concept for improving our capacity to estimate yield under the stresses faced by the potato crop in different parts of the world.

Conclusions

The growth and yield of potato grown under non-limiting conditions in both controlled growing chambers and in the field was satisfactorily estimated by means of a light interception based model. All ten parameters needed to drive the model were adequately inferred from remotely sensed data. Yield predictions were improved when the light harvesting capacity of the plants was estimated on the basis of the normalized difference vegetation index calculated throughout the phenology of the crop.

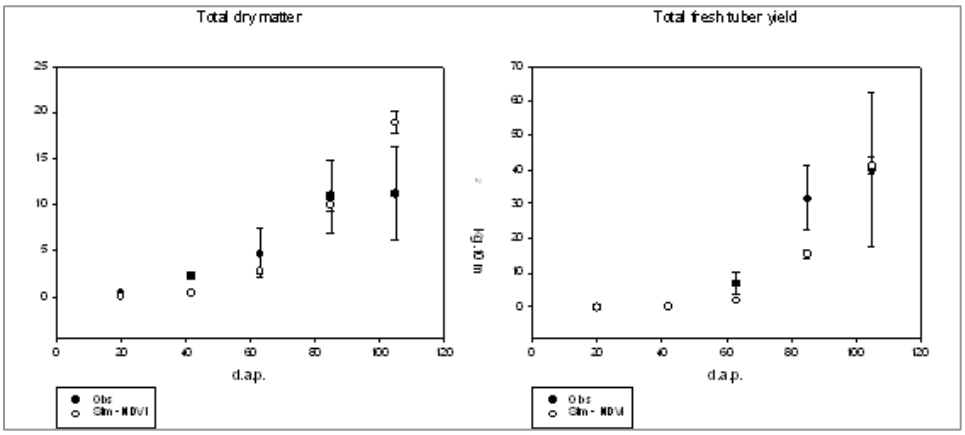

Figure 2. Estimating potato dynamics and tuber yield under field conditions, using simulation models

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New sweetpotato cultivars from INIA´s breeding project in Uruguay

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Abstract:

Sweetpotato ranks second among vegetable crops in Uruguay. This is a very traditional consumption product with the widest country coverage and largest number of growers. It is planted mainly for fresh marketable use as a seasonal crop. 60% of production is obtained in the south and 30% in northwest regions. The most widely planted, is represented by 'INIA Arapey', released in 1998. This "boniato" type cultivar is distinguished by its thick purple skin, cream flesh and semihumid texture after cooking. Secondarily, there is an increasing preference for orange cultivar types with humid texture, represented mainly by 'Beauregard'.

Main objectives of INIA´s sweetpotato breeding activities would be the development of adapted cultivars resistant to main pests for diverse market uses and with good storability. Four promising sweetpotato cultivars have been developed recently. 'Ñ0401.3' is a medium early variety (3 to 4 months), copper skin, orange flesh, good storability, reduced soil insect damage. It could over yield 'Beauregard' in the northern region. 'K9818.1' is a main season cultivar (4 to 5 months), copper skin, deep orange flesh and very good flavor. It could over yield 'Beauregard' in the southern region. 'H9430.23' is a main season cultivar (4 to 5 months), deep red skin, cream flesh, good storability, reduced soil insect damage. Last, 'K 9807.1' is another main season genotype (4 to 5 months) cream skin and flesh with very good storability. Because of its higher dry matter (30%) it is mainly recommended for processing purpose (flour, alcohol) and feeding.

Keywords: *Ipomoea batatas*, clones, orange flesh, purple skin, dry matter.

Introduction

Uruguay Sweet potato crop ranks second on planted area and first in growers number. It is a very traditional crop, having very wide country coverage. It is mainly grown as a cash crop for fresh domestic consumption. Harvest season extends from January to June, whereas annual availability is supported through rustic stores for up to 6 months. Main production specialized areas are located at South (60%) and North (30%) supplying capital major market. Other scattered production, mainly in the Northeast, supplies smaller cities. This last crop is grown more extensively and self consumption is quite common.

'INIA Arapey' is the main planted cultivar, country wide (Vicente et al 1999). It is a purple skin, yellow flesh and semi humid texture, most commercially preferred root type ("Boniato"). It is a medium season cultivar (100 to 120 days) with medium storing ability (3 to 4 months). More recently, there is a growing demand for orange flesh humid textured cultivars because of taste preferences and health considerations (high beta carotene content). 'Beauregard' and local cultivars: 'INIA Ayuí', 'INIA Itapebí', 'E 9227.1' supplies this demand (Rodriguez et al 2007).

INIA´s crop improvement project general objective is the development of pest resistant cultivars, adapted to local growing conditions and diverse market types and uses (Vilaro et al 2005). Moreover, sweet potato specific breeding objectives would be the development of adapted cultivars with improved storing ability. Recurrent selection method through half sib polycross families is been routinely peformed for over 20 years. More recently, three breeding populations were assembled for fulfilling diverse requirements. Preliminary clonal selection is performed in two cycles (North) or one (South) per year. Advanced clones are evaluated collaboratively through comparative trials conducted by three Experimental Stations (Salto Grande, Las Brujas and Tacuarembó) located at North, South and Northeast. Performance of most promising clones is validated at farm level by participatory evaluation at each region.

In this article four new cultivars developed by the project are presented. They cover various market types and adaptation to specific production regions in the country.

New developed cultivars

'Ñ 0401.3'

This cultivar was developed from 2004 polycross. Seed bed sprouting is medium, earlier than 'Beauregard' and planting vigor is good. Foliage vigor is larger than 'Beauregard' and vine length is medium. Growth cycle is early to very early (90 to 120 days), adapted to early and or late planting date. Productivity is high, superior than 'Beauregard', similar to 'INIA Ayuí' and 'INIA Arapey'. Root shape is fusiform, medium to large size, rosy smooth skin, light orange flesh and high marketable grade. Insect soil damage (*Chaectocnema sp.*) is smaller than 'Beauregard'. It shows humid texture and taste is good to very good, surpassing 'INIA Ayuí'. It has very good storing ability, similar to 'Beauregard', larger than 'INIA Ayuí' and 'INIA Arapey'. This cultivar is a large improvement in comparison to other orange flesh sweet potato available cultivars for Uruguay northern region.

'K 9818.1'

This cultivar was developed from 1998 polycross. Seed bed sprouting is medium, earlier than 'Beauregard' and planting vigor is good. Foliage vigor is larger than 'Beauregard' and vine length is medium. Growth cycle is medium to medium late (120-150 days). Productivity is high, higher than 'Beauregard'. It produces regular fusiform shape roots, medium size, smooth copper skin, deep orange flesh with very high carotene, doubling 'Beauregard' content (50 mg/100 g fresh weigth). Insect soil damage (*Chaectocnema sp.*) is smaller than 'Beauregard' in heavy soil. It shows humid texture and taste is very good. It has a good storing ability, similar to 'Beauregard'. This cultivar is a large improvement in comparison to other main season orange flesh sweet potato available cultivars for southern region. It also grows well on northern heavy textured soils.

'H 9430.23'

This cultivar was developed from 1994 polycross. Seed bed sprouting is very good and planting vigor is good. Foliage vigor is very good and vine length is medium. Growth cycle is medium to medium late (120-150 days). Productivity is equal or larger than Arapey. It produces regular fusiform shape roots, medium size, smooth red to purple skin, cream flesh. Taste is good with semi humid texture. Insect soil damage (*Chaectocnema sp.*) is low. Storing ability is quite good, longer than 'INIA Arapey'. This cultivar is a large improvement in comparison to other main season "boniato" type available cultivars for Uruguay northeast region.

'K 9807.1'

This cultivar was developed from 1998 polycross. Seed bed sprouting is very good and planting vigor is very good. Foliage vigor is quite high with medium to long vines. Growth cycle is medium to medium late (120-150 days). Productivity is similar to Arapey. It produces regular round fusiform roots, large size, cream skin and flesh. Insect soil damage (*Chaectocnema sp.*) is low. Taste is quite unsweet with semi dry texture. Dry matter is estimated over 30%, surpassing most cultivated varities. Storing ability is quite good, longer than 'INIA Arapey'. This cultivar has a wide country adaptation being a large improvement for processing and animal feed types.

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Detection of a quantitative inherited resistance to SPCSV by crossing DLP3163 with OFSP clones

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Abstract

Sweetpotato is a tropical crop considered as the seventh most important crop of the world. However, Sweetpotato virus disease (SPVD), produced by the co-infection of the *Sweet potato clorotic stunt virus* (SPCSV) and *Sweet potato feathery mottle virus* (SPFMV), results in serious yield looses in most regions of the world. No resistance to SPCSV has been identified and proofed so far, but a clone DLP3163 (CIP 420269) from CIP germplasm collection was recently considered as a source of resistance to SPCSV in a previous screening. The objectives of this study were to confirm the resistance of DLP3163 and to determine if this resistance is inherited. In total 103 clones of the population "Jewel I" were crossed with DLP3163. All parents (N = 104) and the offsprings (N = 707) were propagated and grown under greenhouse conditions. Parents and offspring were grafted with scions of *Ipomoea setosa*. For each genotype three plants were used. Symptom expressions and ELISA test evaluations for both viruses were carried 1 month after grafting and repeated three times on each plant replication. Visual ELISA reactions were recorded. The mean across each repeated measurement and plant replication was calculated by genotypes. DLP3163 was not negative for SPCSV across all ELISA tests, but it showed a low mean and median for recorded ELISA scores. Significance tests revealed significant lower SPCSV scores in the offspring group compared to the parental group. The most striking result of this study was that some new genotypes were found, which were tested negative across all SPCSV ELISA tests. In conclusion, DLP3163 is not immune but exhibit a quantitative inherited resistance to SPCSV and we might have found several new clones with resistance to SPCSV.

Introduction

Sweetpotato *Ipomoea batatas* (L.) Lam, with a mean annual production of 132 million tons between 1991-2000, is ranked among the top ten most important food crops globally (Woolfe 1992; International Potato Center 1999; FAO 2000). There are more than 20 viruses known to infect cultivated sweetpotato worldwide (Loebenstein et al, 2003), the whitefly-borne *Sweet potato chlorotic stunt virus* (SPCSV) is the main constrain in the crop because of synergism with other sweetpotato viruses, especially the aphid-borne *Sweet potato feathery mottle virus* (SPFMV). The SPCSV in co-infection with other sweetpotato viruses – mainly SPFMV – causes the sweetpotato virus disease (SPVD). SPVD is the most damaging disease of the crop in many regions of world, in particular in East Africa. This disease, first describe in East Africa, reduces severely the yield (up to 90%) of affected plants. Today SPCSV and SPFMV occur worldwide and their damage is considerable when they are infecting together. No clone has been reported so far that shows resistance to SPCSV. However, several clones have been identified that exhibit resistance to SPFMV, but this resistance breaks when a co-infection of SPCSV occurs. It is assumed that SPCSV breaks the sweetpotato resistance mechanism against viruses by RNA silencing.

SPVD induces severe mosaic, chlorosis, stunting and leaf reduction and deformation. These symptoms are typical for the disease and easily to be recognized. Grafting is the universal way to transmit viruses independently of the concentration of the virus in the tissues used as virus source. In this way, transmission (when inoculating) or infection (when detecting) of viruses is assured. NCM-ELISA is a sensible test and reliable in detecting SPCSV and SPFMV infected and susceptible genotypes, respectively. In sweetpotato plants affected with SPVD, titer of SPFMV increases several times making its detection quite easy. In 2006 the virology group at CIP identified a Peruvian landrace (DLP 3163), which had not been infected by SPCSV after inoculations and this clone was named "Resistan". This clone was the only SPCSV resistant clone found in a screening among 2000 germplasm clones and it was assumed that this SPCSV resistance is qualitative and recessive inherited with very low gene frequencies in sweetpotato populations. Provided that this assumption is true nearly no resistant clones can be found in the offspring after a one- way crosses with "Resistan" and only by backcross step or successful auto-fertilizations many resistance genotypes might be found.

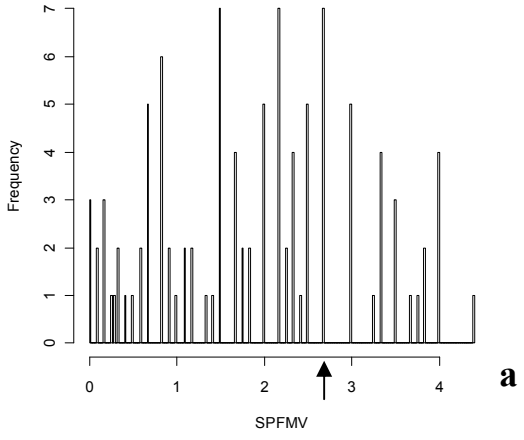
There were two objectives of this study. The first was to use "Resistan" (DLP3163) to develop a pre-breeding population, which carries the resistant allele at low to medium gene frequencies. This pre-breeding population is the prerequisite to develop a backcross population in which a clear segregation of resistant and susceptible clones can be expected. It should be noted that sweetpotato is hexaploid, so that recessive alleles must occur at higher frequencies before there is a chance to observe corresponding recessive homozygous genotypes. The second objective was to confirm the resistance of the "Resistan" clone and to determine if this resistance is inherited.

Materials and methods

In total 103 clones of the population "Jewel I" (breeding code PJ05.__) were crossed with DLP3163. All parents (N = 104) and the offsprings (N = 707) were propagated and synchronically grown under greenhouse conditions at the experimental station San Ramón. Parental and offspring clones were grafted with scions of *Ipomoea setosa* or sweetpotato plants infected with SPVD (SPCSV and SPFMV). For each genotype three plants were used. Symptoms expression and ELISA test evaluation for both viruses were carried 1 month after grafting and repeated three times on each plant replication. Visual ELISA reactions were recorded as 0 = no reaction, 0.5 = unclear positive reaction (threshold), 1 = positive reaction, 2 = strong positive reaction, 3 = very strong positive reaction, 4 = extreme positive reaction. The mean across each repeated measurement and plant replication was calculated by genotypes. The female parents and off-spring group was compared by the T-test and the Wilcoxon test.

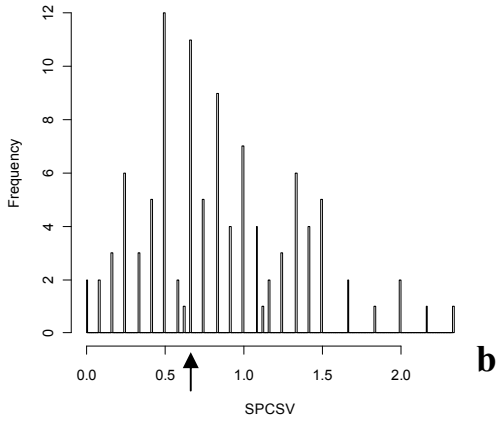
Results

The ELISA titer means (mainly represented as the mean of 9 titers that came from 3 repetitions by 3 observations) for both SPVD viruses were calculated. Among the orange fleshed female parents the titers for both viruses nearly had normal or "bell" shaped distribution (with mean and median around 1.9 and 0.8 for SPFMV and SPCSV respectively). Unfortunately, the DLP3163 clone, formerly considered as resistant, resulted susceptible with a mean of 2.83 and 0.78 for SPFMV and SPCSV, respectively. However, the offspring ELISA titers were considerably lower for SPFMV and SPCSV compared to female parents and male parent (Fig. 1).



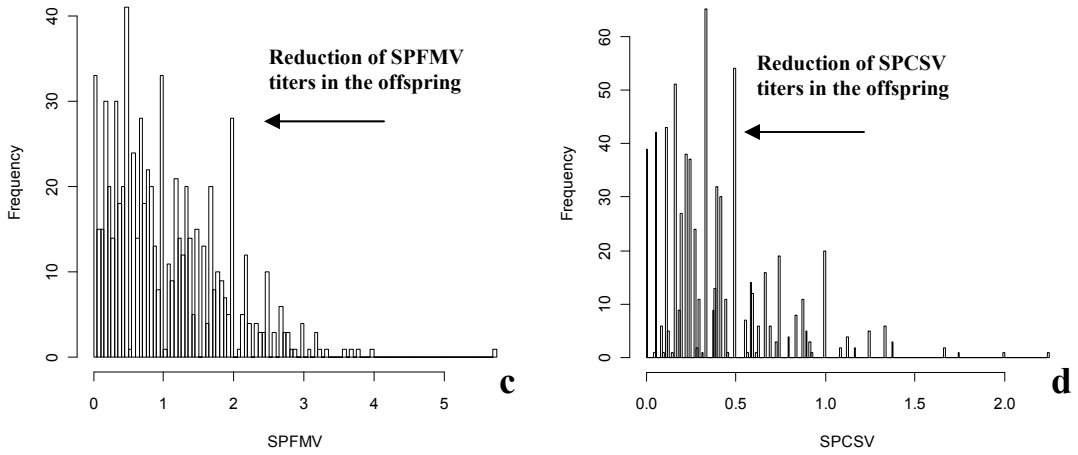
a

Average of ELISA titers for SPFMV in female parents (PJ05.__ clones)



b

Average of ELISA titers for SPCSV in female parents (PJ05.__ clones)



Average of ELISA titers for SPFMV in the offspring (PJ05.__ x DLP3163)

Average of ELISA titers for SPCSV) in the offspring (PJ05.__ x DLP3163)

Figure 1. Distribution and of ELISA titers for SPVD viruses among parental (a,b) and offspring material (c,d); [SPFMV among female parents (a), SPCSV among the female parents (b), SPFMV in the offspring (PJ05.__ x DLP3163) (c), SPCSV in the offspring (PJ05.__ x DLP3163) (d); arrows in (a) and (b) present the mean for SPFMV (2.83) and SPCSV (0.78) in the male parent (DLP3163)].

The observed difference in ELISA titers between parents and offsprings for both SPVD viruses was highly significant, according to the T-test and Wilcoxon rank sum test (table 1). These results demonstrate an inheritable quantitative or for horizontal resistance to both SPVD viruses in the clone DLP3163. On the basis of SPVD ELISA titers four groups were formed among parents and offspring clones (group 1: resistant to SPCSV and SPFMV, group 2: resistant to SPCSV and susceptible to SPFMV, group 3: susceptible to SPCSV and resistant to SPFMV, and group 4: susceptible to SPCSV and SPFMV) for further real time PCR virus detection and molecular marker studies. The first group consisted of 10 clones (Table 2); remaining groups are not presented. It appears that new material has been found which is much more attractive for SPCSV resistance studies compared to the clones DLP 3163. The new material is currently crossed in a diallel and it turned out that PJ05.064 is self-compatible and so far 34 seeds form auto-fertilizations have been developed.

Table 1. Comparison of SPCV and SPFMV infection between the parental and the offspring population by T-test (A) and Wilcoxon Rank Sum Test (B)

	ELISA score Mean (A)		ELISA score Median (B)	
Population	SPCSV	SPFMV	SPCSV	SPFMV
Parents	0.841	1.966	0.778	2.111
Offspring	0.436***	1.091***	0.333***	1.000***

*** significant lower than the parental group p <0.0001

Table 2. ELISA titer means for SPFMV and SPCSV in group 1 (ELISA titer means zero or close to zero) compared to the DLP3163 clone; PJ05. designate clones from the CIP breeding population Jewel 1 and VJ08. designate offspring clones between PJ05. clones and DLP3163

	Female parent	Male parent	Breeder code	SPFMV ELISA titer mean	SPCSV ELISA titer mean	SPFMV number of repeated measurements	SPCSV number of repeated measurements
1	-----	-----	PJ05.064	0	0	6	6
2	PJ05.154	DLP3163	VJ08.618	0.111	0	9	9
3	PJ05.072	DLP3163	VJ08.054	0	0.042	12	12
4	-----	-----	PJ05.019	0	0.083	6	6
5	PJ05.023	DLP3163	VJ08.286	0	0.111	9	9
6	PJ05.064	DLP3163	VJ08.684	0	0.111	10	9
7	PJ05.115	DLP3163	VJ08.330	0	0.111	9	9
8	PJ05.405	DLP3163	VJ08.277	0	0.111	9	9
9	PJ05.072	DLP3163	VJ08.049	0.111	0.055	9	9
10	PJ05.127	DLP3163	VJ08.401	0.111	0.055	9	9
Check	-----	-----	**DLP3163**	**2.833**	**0.777**	6	6

Discussion

SPVD is a disease that causes serious looses in the production of the seventh most important food crop of the world. There is a great interest in making sweetpotato clones resistant to both SPVD viruses. Basically, there are two ways to achieve this goal: one is by plant breeding and the other is by RNA silencing. Plant breeding needs at least one resistant clone. The DLP 3163, which were selected as resistant by the virology group in 2006 at the International Potato Center was found to be susceptible in the same year by Milton Untiveros and Heidi Gamarra (*personal communication*). Our results confirm the susceptibility of the clone DLP 3163 for both SPVD viruses, but it shows inheritable quantitative genetic components for resistance to both viruses. However, it appears that we have found new material, namely PJ05.064, VJ08.618, VJ08.054, PJ05.019, VJ08.286, VJ08.684, VJ08.330, VJ08.277, VJ08.049 and VJ08.401, which might be muchbetter suited for SPVD resistance studies compared to the clone The DLP 3163. Since the clone PJ05.064 is self-compatible we expect to develop abundant seed for dissemination to test the resistance in different regions of the world. Furthermore, it is of interest that our developed material is genetically close to the OFSP population "Jewel" and it might be possible to considerable increase the frequency of SPVD resistance in OFSP breeding populations. OFSP varieties with SPVD resistance would have an extreme advantage in dissemination this variety type in different regions of the world.

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Tuber maturity of white yam (*Dioscorea rotundata*)

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Abstract

Tuber maturity of yams (*Dioscorea* spp.) is a crucial factor in the production, marketing and consumption of the crop. A tuber that is not matured tastes poorly and does not store well. Tuber maturity, however, is difficult to measure directly, and the identification of related traits that distinguish early and late maturing accessions will be a useful tool in the genetic improvement of the crop. In this study, 10 morphological/physiological traits: time of shoot emergence, time of tuber initiation, leaf colour, plant height, shoot dry weight, tuber fresh weight, tuber number per plant, tuber colour (skin and parenchyma), tuber dry matter content and tuber dormancy period were assessed in eight accessions of *D. rotundata* during the 2008 yam growing season. Results show that attainment of stable tuber dry matter content and uniform parenchyma colour of the head, middle and tail portions of a tuber are indicators of physiological maturity in *D. rotundata*. Early and late maturing accessions could be separated by time of attainment of stable tuber dry matter content and uniform parenchyma colour within a tuber, rate of tuber bulking and length of tuber dormancy period. Early maturing accessions attain physiological maturity 5-6 months after planting while the late ones take longer. Tuber yield and tuber dry matter content correlated negatively, and tubers of high fresh weight were low in dry matter content. Regression analysis identified shoot dry weight and time of tuber initiation as major related traits to tuber fresh weight.

Keywords: *Dioscorea rotundata*; tuber maturity; tuber dormancy; dry matter content; yield related traits.

Introduction

Yams (*Dioscorea* spp) are widely cultivated throughout the humid and subhumid tropics in Africa, the Caribbean and the South Pacific Islands, with some production in the subtropics and temperate zone. Yams, of family Dioscoreaceae, are important staple food crops for over 300 million people in the tropics and subtropics. In West Africa, about 48 million tons of yams are produced annually on 4 million hectares of arable land. In this region, yams play key roles in food security and income generation, and are also integral to socio-cultural life of the people. Out of the more than 600 species, 10 are generally cultivated as food: *D. alata*, *D. rotundata, D. cayenensis, D. bulbifera, D. esculenta, D. opposita-japonica, D. nummularia, D. pentaphylla, D. transversa* and *D. trifida* (Lebot, 2009). In West Africa, *D. rotundata* is the most commonly cultivated species.

One of the major constraints to yam improvement is its long growth cycle, or maturity period, which varies from six to more than eight months depending on the species and cultivar. This slows down yam breeding and related research activities, and also restricts the supply of the crop to only once per year. The development of early maturing cultivars may result in double cropping (producing yam more than once in a year), and this will promote increased production of the crop. Changing climatic pattern also necessitates new varieties as older ones become less adaptable. For instance, long duration varieties may no longer be suitable in places where the rainy season has become relatively short and erratic. In addition, the lack of quantitative methods for determining maturity makes it difficult for a processor to establish the suitability of a batch of yams for processing and to determine optimum storage conditions. A tuber that is not matured tastes poorly and does not store well. Tuber maturity, however, is difficult to measure directly, and so far there is no clear indicator to determine physiological maturity in yam. Generally, yam is considered to be matured when the foliage (leaves or vines) is fully senesced (yellow or brown coloration). However, this could be misleading as environmental effect such as disease incidence, water or other stress conditions, may lead to early senescence of foliage. It is necessary to look for alternative indicators that may have little or no environmental influence. A change in pigmentation of leaves (e.g. green to dark green) is used as an indicator by traditional farmers to identify early maturing yam cultivars. However, previous research has shown that colour indices of leaves do not change with plant age (Akinwande 2005). The objectives of this research were to determine the state and time of

physiological maturity in *D. rotundata* yam and to identify traits that can distinguish early and late maturing accessions of this species.

Materials and methods

Plant preparation and experimental design

Eight accessions of *D. rotundata* including four breeding lines and four land races were used in the study. The land races, Ehobia, Amula, Omi Efun (all late maturing) and Akoko (early maturing) were bought from markets in Oyo North, Oyo State, Nigeria. The breeding lines (TDr 95/18949, TDr 99/02562, TDr 97/00960, and TDr 00/00403), all medium to late-maturing, were available from IITA's Yam Breeding Program. Two hundred and twenty tuber setts, each weighing 100g were prepared for every accession, and sprouted in carbonized rice husk. Fifty sprouted setts of each accession were transplanted in the field on 8th May 2008, and replicated four times in a randomized complete block design.

Trait phenotyping

Data were collected on shoot emergence, time of tuber initiation, leaf colour, plant height, shoot dry weight, tuber fresh weight, tuber number per plant, tuber colour (skin and parenchyma), tuber dry matter content and tuber dormancy period. Data collection on shoot emergence and time of tuber initiation started 10 and 50 days, respectively after planting. Data for the other traits were collected in sequence at 3, 4, 5 and 6 months after planting. Data were collected from all the plants (50/block/accession) for shoot emergence, and from five plants for all the other traits at all sampling times except for the sampling at 6 months for which data were collected from three plants because some plants were dead. The five plants were identified by selecting one out of every 10 plants along a row of 50 plants per block. Tuber number was not recorded at 3 months sampling, while plant height and shoot dry weight were not measured at 6 months sampling because the plants were all senesced at 6 months sampling time. At every sampling time, except for shoot emergence and tuber initiation, all tubers per plant were first harvested and weighed. Data were collected as follows:

Shoot emergence. This was recorded as the number of days between planting of sprouted tuber and the time the shoot emerged above the ground.

Tuber initiation. The bases of the selected clones were opened every other day until they all initiated tubers.

Leaf colour. The colour of lower leaves (first 4-5 leaves) was determined using the Methuen Handbook of Colour (Kornerup and Wanscher 1978).

Tuber number. Number of tubers per plant counted and recorded. Tuber numbers were counted during 4, 5 and 6 months harvests.

Tuber fresh weight. All tubers per plant were weighed after harvest, and recorded as tuber fresh weight.

***Tuber colour* (skin and parenchyma of head, middle and tail).** This was determined using the Methuen Handbook of Colour (Kornerup and Wanscher 1978). One tuber was cut vertically with a knife from head to tail and colours of head, middle and tail portions were recorded.

Tuber dry matter content. A representative sample of about 100 g (W1) prepared by thoroughly mixing sliced pieces of tubers was oven dried at 105°C for 48 hours and weighed (W2). Per cent (%) dry matter content was calculated as (W2/W1) x 100.

Plant height. After harvest, length of the longest vine was measured with a tape rule and recorded. Plant height was not measured during 6 month harvest as the shoots were all dried out.

Shoot dry weight. All vines and leaves per plant were oven dried at 105°C for 48 hours and weighed.

Disease incidence. Incidence of yam mosaic virus, anthracnose and leaf blight were scored 40-45 days after transplanting, and at 3, 4 and 5 months harvesting times.

Tuber dormancy period. Data were collected on tubers harvested from those plants that were assessed for tuber initiation. Plants were harvested with their corms intact, and tubers were stored in open boxes at ambient temperature in the IITA Yam barn at Ibadan. Data collection on time of tuber sprouting started three weeks after harvest and continued every other day until when 80-100% of all tubers were sprouted. A tuber was considered sprouted when it had a bud of 3 mm long. Dormancy period was calculated as length of time between tuber harvest and sprouting or between tuber initiation and tuber sprouting.

Data analysis

Two kinds of analysis were performed: (1) traits measured four times (plant height, tuber fresh weight, shoot dry weight and tuber dry matter content) were analyzed considering their change across time and the residual terms were modeled using an autoregressive (order 1) model, in a frame of repeated measures analysis; (2) traits measured only one time (tuber initiation time, shoot emergence time and dormancy) were analyzed by a simple linear model. We used a Linear Mixed Model considering replications, accessions, sampling times, and the interaction between accession and sampling time as fixed effects, and the interaction between replication by clone and the effect of plants within accessions, as random effects. The least square means for fixed effects were calculated and a Tukey (or Tukey-Kramer) adjustment was used to make the pair comparisons. The MIXED PROCEDURE from the SAS statistical package was used to do the analyses. Multiple regression analysis was performed using tuber fresh weight (tfw) as dependent variable and all other traits as independent variables to quantify the effect and importance of each trait on the tfw variable. Type III sum of squares (SS) and partial regression coefficients were calculated to measure the effect of each trait after the effect of all other was removed from the model. The Type III SS were expressed as a percentage of the "all traits sum of squares" to get a relative measure of the contribution of each trait.

Results

The accessions were significantly ($p<0.01$) different for all the traits assessed except for tuber initiation time (Table 1) for which they were similar. The interaction between accession and time of sampling was only significant ($p<0.001$) for tuber number per plant and tuber fresh weight. Time of shoot emergence varied significantly ($p<0.001$) among accessions. The number of days a shoot took to emerge ranged from 10 to 61 days with an average of 19.9 days from time of planting (Table 1). Shoot emergence was early in TDr 99/02562 (14.2 days) and TDr 95/18949 (14.4 days), but late in Omi efun (24.4 days) and Ehobia (23.1 days). Generally, shoot emergence was earlier in breeding lines than in the land races. Time of tuber initiation was on average 52.2 days from time of planting, and was similar for all the accessions (Table 1).

Trait expression was significantly ($p<0.001$) different at each sampling time, except for plant height that was similar at 3, 4 and 5 months sampling time (Table 2), indicating that height measurement in *D. rotundata* would be ideal at three months after planting. Plant height varied significantly among the accessions and was on average highest in Amula (239 cm) and lowest in Akoko (144.7 cm) (Table 1). The accessions were significantly different in shoot dry weight at 3, 4 and 5 harvest times (Table 1). Comparing shoot dry weight at the first three harvests, it was lowest at 5 month harvest, and similar for third and fourth harvest (Table 2,). It was highest in TDr 99/02562 (101.5 g/plant) and lowest in Akoko (33.5 g/plant). The shoots were all dead by the time of the 6 month harvest.

Tuber number decreased with growth period (Table 2,), and was lowest at 6 month harvest. Some accessions, for instance, Ehobia produced more tubers during the early growth period, but tuber number was similar in all the accessions at 6 month harvest time. Tuber number increased from third to fourth month growth period in TDr 95/18949.

Fresh tuber weight increased from 3 months through to the fifth month after planting and decreased significantly afterwards (Table 2,). Fresh tuber weight of all accessions increased sharply from the third to the forth month after planting, and thereafter the increase slowed down in Akoko, TDr 00/00403 and Omi efun. Tuber bulking was fastest in TDr 95/18944 and TDr 00/00403 than in the other accessions. At 6 month harvest time, fresh tuber weight was highest in Omi efun (462.5 g), least in Ehobia (295.8 g) and similar in the other accessions. The average fresh tuber weight across sampling times was highest in TDr 95/18949 (781.80 g) and lowest in Akoko (340.23 g*).*

Table 1. Mean values of physiological traits during growth stages of eight accessions of *D. rotundata*. Means with the same letter within a column are not significantly different

Accession	Number of tubers/plant	Tuber fresh weight/plant (g)	Tuber dry matter content (%)	Plant height (cm)	Shoot dry weight/plant (g)	Tuber initiation (days from planting)	Shoot emergence (days from planting)	Dormancy period (days from harvesting)
Akoko	1.31±0.19 b	340.23±40.11 c	25.65±0.83 ab	144.67±13.13 c	33.53±7.16 d	52.44±0.69 a	21.99±0.75 a	69.48±4.33 ab
Amula	1.73±0.19 b	524.45±38.97 bc	25.95±0.81 ab	239.00±11.60 a	69.78±6.87 abc	51.58±0.65 a	22.18±0.72 a	79.85±4.48 a
Ehobia	2.78±0.18 a	350.61±38.46 c	27.93±0.80 a	174.50±11.37 bc	48.49±6.72 cd	52.22±0.67 a	23.13±0.73 a	77.45±4.49 a
Omi Efun	1.44±0.19 b	459.52±39.51 bc	24.79±0.82 ab	182.43±11.84 bc	58.53±6.97 bcd	53.17±0.66 a	24.39±0.73 a	71.84±4.46 ab
TDr 00/00403	1.58±0.18 b	559.26±38.21 b	24.55±0.80 abc	196.71±11.26 abc	70.39±6.67 abc	52.13±0.65 a	15.89±0.71 b	78.30±4.45 a
TDr 95/18949	2.00±0.18 ab	781.80±38.21 a	20.77±0.80 c	189.38±11.26 abc	81.49±6.67 ab	51.79±0.66 a	14.39±0.71 b	55.37±4.33 b
TDr 97/00960	1.60±0.18 b	479.82±38.21 bc	22.99±0.80 bc	170.99±11.26 bc	51.71±6.67 bcd	52.28±0.68 a	17.39±0.72 b	74.05±4.48 ab
TDr 99/02562	1.81±0.18 b	496.05±38.23 bc	23.06±0.80 bc	224.06±11.27 ab	101.54±6.66 a	51.99±0.66 a	14.17±0.71 b	84.52±4.30 a
Means	1.77±0.18.	499.38±38.74	24.66±0.81	185.38±11.62	59.13±6.80	52.23±0.67	19.91±0.72	72.34±4.42
P>F(comparison between accessions)	0.0005	<.0001	0.0001	0.0005	<.0001	0.8108	<.0001	0.0046
P>F(accession x time interaction)	0.001	<.0001	0.277	0.805	0.557			

Dry matter content increased significantly ($p<0.001$) with growth period (Table 2,). The increase was rapid from 3 to 5 months and slowed down afterwards. Dry matter content was similar at 5 and 6 months growth period for some accessions; for instance, it was 24% in TDr 95/18949 and 29% in Akoko at 5 and 6 months growth stages. At 6 months growth period, dry matter content continued to increase in Ehobia, Omi efun, TDr 99/02562 and TDr 00/00403, but started to decrease in Amula and TDr 97/00960. The average dry matter content was highest in Ehobia (27.93%) and lowest in TDr 95/18949 (20.77%) (Table 1).

There was no clear contrast in leaf colour at 3 months harvest from that of 4 or 5 months harvest in any of the accessions (data not shown). In all the accessions, leaf colour was generally dark green at 3 months harvest, or dark or deep green at 5 months harvest. At 4 months harvest, leaf colour was greyishgreen or dark green or deep green across the accessions. Leaf senescence started during the fifth month after planting, but was observed only in few accessions. All the leaves were completely senesced at 6 months after planting.

In general, there was no clear demarcation in colour of some of the accessions at any sampling time. Three colours were associated with tuber parenchyma; creamy, white and purple. Generally, tubers were white at the tail portion, creamy or white at the middle, and creamy at the head in most accessions, indicating an association of creamy colour with tuber maturity. At 6 months harvest time, tuber head was creamy in all the accessions, except in Ehobia, whose tubers appeared to be characteristically white across the three portions. The head, middle and tail portions were creamy in TDr 95/18949 and TDr 00/00403 at both 5 and 6 months harvest, and in Akoko at 6 month harvest. Contrarily, in TDr 99/02562, all the three portions were creamy at all sampling times, except at 6 month where only the head was creamy, while the middle and tail were white. Tuber skin colour was largely white in all accessions at 4 months sampling time, and brown or golden at 5 and 6 months sampling times, but was not distinguishable among accessions.

Tuber dormancy period measured as number of days from time of tuber harvesting to time of 80-100% tuber sprouting is shown in Table 1. Tuber sprouting time was significantly ($p <.0001$) different among the accessions, and was on average 72.3 days from time of harvest. It was early in TDr 95/18949 (55.4 days) and Akoko (79.5 days), and late in TDr 99/02562 (84 days) and Amula (80 days). When calculated from time of tuber initiation to time of sprouting, tuber dormancy period was similar (about 130 days) in all the accessions.

Simple correlation analysis of eight of the ten traits identified significant correlations among most of the traits (Table 3) e.g correlation was positive ($p<0.01$) between tuber yield (tuber fresh weight) and shoot dry weight ($r = 0.63$), but negative between the yield and tuber dry matter content ($r = -80$) . When regression analysis was performed using tuber fresh weight as dependent variable and the other traits as independent variables, shoot dry weight had positive($p<0.05$) effect on tuber fresh weight (contributing 38.72%), while tuber initiation had negative effect (contributing 20.95%) (Table 4).

Discussion

Tuber maturity

Results indicated that early and late maturing accessions can be distinguished based on speed and time of cessation of tuber bulking, time of attainment of stable tuber dry matter content, time of attainment of uniform tuber parenchyma colour of the head, middle and tail portions of a tuber, and length of tuber dormancy period. Tuber bulking was fastest in TDr 95/18949, while the period of bulking was shortest in Akoko. Fresh tuber weight increased from 3 months through to the fifth month after planting and decreased significantly afterwards (Table 2,), indicating that tuber bulking in *D. rotundata* generally terminates at five months after planting. Tuber dry matter content of TDr 95/18949 and Akoko appear to reach a stable stage at 5 months after planting, while in the other accessions dry matter content continued to increase after 6 months from planting. In other accessions, such as Ehobia, Omi efun, Amula and TDr 99/02562, dry matter content kept increasing even at 6 months growth period, suggesting that these accessions are late maturing. Assessment of dry matter content at later growth stages, for instance, at 7 or 8 months after planting, may have led to the determination of the growth stage at which those accessions attain stable tuber dry matter content levels, but the experiment was terminated 6 months after planting. As in the case with tuber bulking and tuber dry matter content, tuber parenchyma colours of the head, middle and tail portions were the same (creamy) at 5 and 6 months after planting in TDr 95/18949 and Akoko respectively, indicating that these two accessions are early maturing, and were physiologically matured 5 to 6 months after planting. In yams, the proximal end (head) of a tuber matures earlier than the distal end (tail), and this reflects differences in colour of the head, middle and tail. Although colour and

its intensity may vary among accessions, immature tuber potions are generally white in colour, hence the tail portion is mostly white compared to the other portions at all growth stages. Tuber heads of all the accessions were mostly creamy at all harvest times. Tuber parenchyma colour was generally creamy at 6 months harvest, which indicates that creamy colour of tuber parenchyma may be associated with maturity in *D. rotundata*. At the time of final harvest (6 months after planting), only the head portion was creamy, while the middle and tail were largely white in TDr 99/02562, Ehobia, Amula and Omi Efun, indicating that these accessions were late maturing and would require longer than 6 months to attain physiological maturity. However, uniformity in colour across a tuber was also observed during the early growth stages in TDr 99/02562, Omi efun and Ehobia, but this pattern changed during the advanced growth stages, ruling out tuber maturity at those early growth stages.

Tuber dormancy period measured as duration from time of harvest to time of tuber sprouting was significantly shorter in TDr 95/18949 and Akoko than in the other accessions (Table 1), indicating that early maturing accessions of *D. rotundata* may have shorter dormancy. In our investigation, tuber dormancy measured as number of days from time of harvest to time of 80-100% tuber sprouting was on average 73 days, and was short in TDr 95/18949 (55 days) and Akoko (70 days), and long in TDr 99/02562 (84 days) and Amula (80 days). This result is in agreement with findings of Craufurd et al (2001) who observed, based on dormancy assessment of 286 *D. rotundata* accessions grown in the field and stored in a yam barn, that the duration from harvesting to sprouting ranged from 60 to >110 d, with the greatest number of accessions sprouting between 70 and 80 d after harvest.

The rate of tuber bulking, dry matter content, tuber colour and tuber dormancy are traits that can only be measured after the crop is harvested or by destroying the tuber while the crop is still growing on the field. They are not visible traits that can be used to select early or late maturing crops from a field of growing crops. Further evaluation of these accessions based on time of leaf senescence is necessary to validate these results. Generally, yam is considered to be matured when the foliage (leaves or vines) is fully senesced (yellow or brown coloration). However, this could be misleading as environmental effect such as disease incidence, water or other stress conditions, may lead to early senescence of foliage. In this experiment, for instance, all the accessions were completely senesced 6 months after planting, but this time (December) coincided with the onset of dry season, and may not necessarily indicate physiological maturity of the accessions. A change in pigmentation of leaves (e.g. green to dark green) is used as an indicator by traditional farmers to identify early maturing yam cultivars. However, our results show that colour indices of leaves do not change with plant age, and this has been confirmed previously (Akinwande 2005).

Tuber yield related traits

Assessment of eight traits using simple correlation and regression analyses identified shoot dry weight and time of tuber initiation as major related traits of tuber fresh weight (tuber yield) in *D. rotundata*. The effect of shoot dry weight on tuber fresh weight was positive, while that of time of tuber initiation was negative, and the correlation between shoot dry weight and time of tuber initiation was negative. The positive correlation between shoot dry weight and tuber yield had been observed earlier (Lakshmi and Eswaiamma 1980). Tuber initiation in *D. rotundata* has been reported to occur from sprouting to 84 days after sprouting (Okezie et al., 1981; Njoku et al., 1984). The timing of tuber initiation and the duration of the period of tuber formation vary within and between species, and are affected also by environmental factors (Craufurd et al 2001). In this experiment the accessions initiated tubers at similar time, and the average tuber initiation time was 52 days from time of planting. The implication of the correlation among tuber fresh weight, shoot dry weight and tuber initiation time is that high yielding cultivars of *D. rotundata* may either produce dense foliage, or initiate tubers early. Our results show that TDr 95/18949, which tuber had the highest fresh weight was correspondingly one of the accessions that had the highest shoot dry weight. Conversely, accessions with the lowest tuber yield (Akoko and Ehobia) had the least shoot dry weight (Table 1).

Tuber yield and tuber dry matter content had a strong negative correlation, and tubers of high fresh weight were low in dry matter content. For instance, Ehobia with the least tuber fresh weight (350.6 g) had the highest dry matter content (27.9%), while TDr 95/18949 with the highest tuber fresh weight (781.8 g) had the lowest dry matter content (20.8%) (Table 1). The implication is that developing a cultivar for increased tuber yield based on fresh weight will be disadvantageous to those in tuber processing industries, e.g. flour processing, who prefer accessions with high dry matter content.

Peak yield values, expressed as tuber fresh weight were highest at 5 months after planting for all the accessions. This is in agreement with findings of Akinwande (2007), who obtained peak yields at 6 months after vine emergence. The decrease in tuber fresh weight at 6 months after planting could be as a result of tuber losses due to pests and diseases during tuber development. However, tuber fresh weight at 4, 5 and 6 months after harvest did not change in Akoko (about 400 g), indicating that this accession might have reached physiological maturity at 4 months after planting, and may be resistant to pests and diseases of yams.

Tuber number decreased with growth period (Table 2,), and was lowest at 6 month harvest, indicating that some tubers died before the 6 month harvest. Although some accessions, for instance, Ehobia produced more tubers during the early growth period, tuber number was similar in all the accessions at 6 month harvest time, which suggests that Ehobia may be prone to high tuber rot. An increase in tuber number from third to forth month growth period was observed in TDr 95/18949, indicating that this accession can form new tubers over an extended period of time.

Conclusions

Attainment of stable tuber dry matter content and uniform parenchyma colour of the head, middle and tail portions of a tuber are indicators of physiological maturity in *D. rotundata*. Early and late maturing accessions of *D. rotundata* may be separated by the rate of tuber bulking, time of attainment of stable tuber dry matter content and uniform parenchyma colour of the head, middle and tail portions of a tuber, and the length of tuber dormancy period. Among the eight traits assessed shoot dry weight and time of tuber initiation were identified as major related traits of tuber fresh weight in *D. rotundata*. Tuber yield and tuber dry matter content correlated negatively and high fresh weight tubers were low in dry matter content.

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Table 2. Mean values of physiological traits at different growth stages from time of planting of *D. rotundata*. Means with the same letter within a column are not significantly different

Sampling time after planting (months)	Number of tubers/plant	Tuber fresh weight/plant (g)	Tuber dry matter content (%)	Plant height (cm)	Shoot dry weight/plant (g)
3		216.93±25.53 d	16.68±0.39 d	180.69±7.18 a	69.98±3.43 a
4	2.26±0.09 a	564.07±26.61 b	23.59±0.40 c	199.88±7.21 a	69.15±3.57 a
5	1.88±0.09 b	814.88±24.56 a	27.89±0.38 b	190.08±6.65 a	54.17±3.30 b
6	1.19±0.11 c	400.00±31.44 c	29.67±0.47 a		
Means	1.78±0.10	498.97±27.04	24.46±0.41	190.22±7.01	64.43±3.43
P>F (comparison between time measures)	<.0001	<.0001	<.0001	0.1805	0.0007

Table 3. Coefficients of correlation among physiological traits in *D. rotundata* assessed in 2008

	Ntubers[†]	tfw	dm	ph	sdw	tubini	emer
tfw[‡]	-0.02ns						
dm	0.30*	-0.80**					
ph	0.09ns	0.40**	-0.12ns				
sdw	0.09ns	0.63**	-0.56**	0.78**			
tubini	-0.32*	-0.47**	0.19ns	-0.57**	-0.47**		
emer	0.04ns	-0.66**	0.79**	-0.27ns	-0.69**	0.50**	
dorm	0.05ns	-0.54**	0.51**	0.46**	0.17ns	-0.06ns	0.11ns

[†] ns: non significant, *: ($p<0.05$), **: ($p<0.01$)

[‡] Ntubers: Number of tubers per plant, tfw: Tuber fresh weight per plant (g), dm: Tuber dry matter content (%), ph: Plant height (cm), sdw: Shoot dry weight per plant (g), tubini: Tuber initiation time (days from planting), emer: Shoot emergence (days from planting), dorm: Dormancy period (days from harvesting)

Table 4. Regression analysis to determine tuber yield related traits in *D. rotundata* assessed in 2008

tfw related traits	Regression Coefficients	Standard Error	t Value	Pr > |t|	contribution %
sdw	3.815	1.134	3.36	0.005	38.72
tubini	-20.862	8.435	-2.47	0.027	20.95
ntubers	43.22	38.182	1.13	0.277	4.39
dm	-7.205	8.487	-0.85	0.41	2.47
ph	-0.532	0.666	-0.8	0.438	2.19
emer	-7.659	7.807	-0.98	0.343	3.29
dorm	1.544	1.379	1.12	0.282	4.29
R-Square	Coeff Var	Root MSE	tfw Mean		
0.9422	9.51	47.55364	499.789		

Ntubers: Number of tubers per plant, tfw: Tuber fresh weight per plant (g), dm: Tuber dry matter content (%), ph: Plant height (cm), sdw: Shoot dry weight per plant (g), tubini: Tuber initiation time (days from planting), emer: Shoot emergence (days from planting), dorm: Dormancy period (days from harvesting