Potato quality traits: variation and genetics in Ecuadorian potato landraces

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Contents

This thesis dedicated
to my beloved parents
and my sister

Chapter 1

General Introduction

General Introduction

Potato Importance

The potato (*Solanum tuberosum* L.) is one of the world´s major staple crops, which produces more dry matter and protein per hectare than the major cereal crops (Burton, 1974; Storey, 2007). It is the world's third most important food crop after wheat and rice with 324 million tons fresh weight of tubers produced in 2010 from 18.6 million hectares of land (http://www.faostat.fao.org).

The potato is one of the main traditional crops cultivated in Ecuador. For 2010 the harvested area was 44,245 ha, with a total production of 386,798 tons, giving an average yield of 8.7 $ton.ha^{-1}$ (http://www.faostat.fao.org), with more than 82,000 producers involved. Cultivation is largely undertaken by small-scale farmers, 76% of farmers in the country grow potatoes in areas smaller than 5 ha (Devaux et al., 2010; Monteros, 2011).

Production is oriented principally towards internal consumption, approximately 81% of the national production is commercialized fresh for household consumption and potato processing industries use the rest to make crisps and French fries. Potato planting and harvesting are done year round, which means that Ecuador produces enough to satisfy its domestic demand. Nevertheless, it is important to note that there are seasons when climatic factors cause the supply to rise or fall (Devaux et al., 2010).

Potatoes are produced in the highlands with higher yields (12-14 tons per hectare) at altitudes between 2,900 and 3,300 meters (Mancero, 2007), (See Figure 1 for example of an Ecuadorian potato field).

The potato is carbohydrate-rich, it also provides significant amounts of protein, with a good amino acid balance, vitamins C, B6 and B1, folate, the minerals potassium, phosphorus, calcium, and magnesium and the micronutrients iron and zinc. The tuber is high in dietary fiber, especially when eaten unpeeled with its skin, and is rich in antioxidants comprising polyphenols, vitamin C, carotenoids and tocopherols. Fresh potatoes are virtually free of fat and cholesterol (Camire et al., 2009; Storey, 2007).

The nutrient-rich potato can contribute to improved diets, thus reducing mortality rates caused by malnutrition. It can improve food security and health, especially among women and children. Increases in potato yields are essential to improve the livelihoods and food security of poor farmers. While average potato yields in North America and Western Europe often exceed 40 $ton.ha^{-1}$, yields in developing countries are usually half that amount. Increase in productivity will depend on improved potato varieties with higher yield potential and resistance to pests and diseases, greater use of quality seed potatoes, and improved pest and disease management (Lutaladio and Castaldi, 2009).

Figure 1. Potato field planted by small farmers in the Ecuadorian highlands.

Potato origin

The Andes are a center of origin and diversity for numerous crop species (National Research Council, 1989), including the potato (Spooner et al., 2005). Potatoes were domesticated between 10,000 – 7,000 years ago, likely around Lake Titicaca, in the Andes between Peru and Bolivia (Spooner et al., 2005).

The wild species progenitors of the modern potato (*Solanum tuberosum* L.) have been the subject of much discussion. Recently Spooner et al., (2005) provided molecular taxonomic evidence for a single domestication in the highlands of southern Peru from the northern group of members of the *S. brevicaule* complex of diploid species. The result of domestication was a diploid cultigen *S. tuberosum* group Stenotomum (Dodds, 1962) from which all of the other cultivated potatoes were derived.

Potatoes were first recorded in 1,537 in Sorocata town in Peru (Hawkes, 1990). The first record of cultivated potatoes outside South America is their export in 1,567 from

Gran Canaria in the Canary Islands to Antwerp in Belgium (Hawkes and Francisco-Ortega, 1993). These authors concluded that the potato was first introduced from South America into the Canary Islands around 1,562, and from there to mainland Europe.

Genetic resources

Potatoes may contain more genetic diversity than any other crop and this may reflect the ability of potatoes to grow in remarkably divergent environments, from arid alpine highlands to tropical rainforests to permafrost soils just below the Arctic Circle (Hawkes, 1990). This genetic diversity is a valuable resource towards further improvement of tuber nutritional content, especially when taking into account that modern varieties are estimated to contain less than 1% of the available genetic diversity of wild species (Navarre et al., 2009).

The genetic diversity of potatoes *Solanum* Section Petota (Solanaceae) may be grouped in wild and cultivated potatoes; this last could be grouped in native potatoes and improved potatoes (Salas et al., 2010). The cultivated potatoes *S. tuberosum* are tetraploid (2n=4x= 48), while the native are highly diverse, diploids (2n=2x=24), triploids (2n=3x=36), tetraploids (2n=3x=48), pentaploids (2n=5x=60) and hexaploids (2n=6x=72) (Huaman and Spooner, 2002).

Cultivated potatoes

The world catalogue of potatoes 2009/2010 (Pieterse and Hils, 2009), shows more than 4,500 varieties of 102 countries from around the world. Besides, several data bases of modern varieties are available for example the data base (www.europotato.org) with information of 4,201 varieties and the potato pedigree data base of the Laboratory of Plant Breeding of Wageningen University (van Berloo et al., 2007) with pedigree information of more than 8,100 accessions.

The International Potato Center (CIP) assembled a collection of more than 15,000 accessions of potato from nine countries in Latin America: Argentina, Bolivia, Chile, Colombia, Ecuador, Guatemala, Mexico, Peru and Venezuela. Subsequently duplicate accessions were identified and the number of individual varieties was reduced to 3,527 of which 552 were diploids, 128 triploids, 2,836 tetraploids (2,644 group Andigena, 144 group Tuberosum, and 48 hybrids), and 11 pentaploids (Huaman et al., 1997).

In Ecuador INIAP holds the most important gene bank of the country with 17,920 accessions of approximately 200 different plant genera (Tapia et al., 2009). For potato approximately 350 varieties are conserved that belong to *S. andigenum, S. phureja, S.*

chaucha and *S. stenotomum* (Cuesta et al., 2005a). Large variation for tuber shape, eye depth, skin color and reaction to some diseases has been observed in these varieties. These potatoes are highly valued by scientists and farmers, because of their cooking quality and resistance to biotic and abiotic stresses. Attributes that could be used in breeding for developing new potato varieties (Cuesta, 2010).

Wild potatoes

Wild tuber-bearing *Solanum* species are distributed from the southwestern USA (38◦N) to central Argentina and adjacent Chile (41◦S) (Hawkes, 1990; Spooner and Hijmans, 2001). In the southwestern USA and in Central America wild species generally occur at medium to high altitudes. In South America they are found along the Andes from Venezuela to northwest Argentina and also in the lowlands of Chile, Argentina, Uruguay, Paraguay, and south eastern Brazil. The adaptive range among the different species is very great and includes the high Andean regions from 3,000 - 4,500 m (Bradshaw and Bonierbale, 2010).

The World Catalogue of Potato Varieties 2009/2010 (Pieterse and Hils, 2009), establishes that the International Potato Center (CIP) has a collection of wild potatoes composed of 1,917 accessions and consists of representatives of 141 species with 67 from Peru, 29 from Bolivia, 13 from Mexico, 13 from Ecuador, and 10 from Argentina.

Potato quality traits

In the case of tuber potatoes, quality can be defined as the sum of favorable characteristics of the tuber, which is a subjective and dynamic concept that depends on consumer’s tradition lifestyles, food habits (Poats, 1982; Richards et al., 1997) and the industrial process used. A complex set of external and internal quality traits are required for fresh and processed potatoes. External quality traits include tuber shape, eye depth, skin and flesh color (Jansky, 2009). Besides, dormancy and greening are additional important quality traits (Werij, 2011). These characters are especially important for fresh market potatoes, but they may also impact processing quality. Internal quality includes the content of dry matter, reducing sugar, glycoalkaloids, enzymatic discoloration and nutritional quality (Storey, 2007).

Fresh market

Tuber shape, eye depth, skin and flesh color are crucial aspects for consumers, as they are immediately obvious while making the purchase (Werij, 2011). Tuber shape is a syndrome of many characters, that considers the length/width ratio for describing the overall shape, it varies from compressed/round to long (van Eck, 2007; Werij, 2011), a single locus on chromosome X with a dominant allele *Ro* conferring round tuber shape (van Eck et al., 1994b), other reports mention quantitative trait loci (QTLs) on chromosome II, V and XI (Bradshaw et al., 2008), II and XI (ŚLiwka et al., 2008) and VII and XII (Sørensen, 2006). However, there are more factors controlling this trait, probably depending on the genetic background of the respective populations used on their researches (ŚLiwka et al., 2008; Werij, 2011). An example of tuber shape variation is shown in Figure 2.

Eye depth is an important trait of tuber quality because deep eyes affect the appearance of tubers and add to the cost of peeling in processing factories. As for tuber shape, contradictory hypotheses were formulated to explain the inheritance of eye depth (Li et al., 2005). Eye depth appears to be controlled by a single locus *Eyd/eyd*, which closely linked with *Ro* locus at chromosome X at a distance of 4 cM (Li et al., 2005). This result was confirmed by (ŚLiwka et al., 2008), where at least four QTLs on chromosomes III, V and X were identified. In Figure 3 an example of tuber eye depth differences is shown.

Figure 2. An example of tuber shape variation in Ecuadorian potato

Figure 3. An overview of the variation for tuber eye depth in Ecuadorian potato landraces.

One of the most easily noticeable traits of potato tubers is the skin color. This character ranges from white-cream to blackish (Figure 4). The tuber skin color is controlled by different genetic systems that control the presence and absence of red and blue pigments The potato *R* locus is required for the production of red anthocyanins, which have been shown to be derivatives of pelargonidin, while *P* is required for the synthesis of purple pigments, which are typically derived from petunidin (De Jong, 1991; Dodds and Long, 1955; Lewis et al., 1998). A third locus, I, is required for the synthesis of red or purple anthocyanins in tuber skin (Dodds and Long, 1955). All three of these loci have been mapped in the potato genome (van Eck et al., 1993; 1994a).

Several studies (reported by De Jong et al., 2004) suggest that *R* corresponds to dihydroflavonol 4-reductase (*dfr*), that *P* codes for flavonoid 3´,5´-hydroxylase (*f3´5´h*), and that *D* encodes an R2R3 MYB transcription factor similar to *Petunia an2*. Besides, Jung et al., (2009) evaluated the expression of flavanone 3-hydroxylase (*f3h*), dihydroflavonol 4-reductase (*dfr*) and flavonoid 3´,5´-hydroxylase (*f3´5´h*). All three genes were expressed in the periderm of red- and purple-skinned clones, while *dfr* and *f3´5´h* were not expressed, and *f3h* was only weakly expressed, in white-skinned clones.

Tuber flesh color varies from white to purple (Figure 5); it is due to the accumulation of two different classes of pigment anthocyanins and carotenoids (Lewis et al., 1998). Anthocyanin accumulation leads to red, blue or purple flesh colors (Hung et al., 1997).

Red and purple-fleshed potatoes have acylated glucosides of pelargonidin while purple potatoes have, in addition, acylated glucosides of malvidin, petunidin, peonidin, and delphinidin (Brown, 2005; Lachman et al., 2009).

Colored potatoes may serve as a potential source of natural anthocyanin pigments, since they are low-cost crops (Jansen and Flamme, 2006), and also are a significant source of potato antioxidant micronutrients (Andre et al., 2007; Nayak et al., 2011).

Thus, purple and red-fleshed potatoes could be used as novel sources of natural colorants and antioxidants with added value for the food industry and human health (Reyes et al., 2004). Antioxidant values (ORAC) for red-fleshed types ranged as high as 300% of the white flesh, while for purple fleshed antioxidant values reached 250% of the white flesh (Brown, 2005). Several studies have indicated that anthocyanins have high free-radical scavenging activity, which helps to reduce the risk of chronic diseases and age-related neuronal degeneration (Teow et al., 2007).

Carotenoid levels determine whether the tuber flesh is white, yellow or orange it is controlled by the single dominant allele at the *Y* locus on potato chromosome III (Bonierbale et al., 1988) and by association analysis of potato natural diversity, the yellow fleshed tubers which accumulate high levels of zeaxanthin were found to be controlled by a combination of the dominant beta-carotene hydroxilase 2 (Chy2) allele and homozygous recessive *Zep* allele (Wolters et al., 2010).

Figure 4. An overview of the variation of skin tuber color of Ecuadorian potato landraces.

Figure 5. An example of the variation of flesh tuber color in Ecuadorian potato landraces.

Other obvious quality traits are greening and tuber dormancy. Greening is a process that involves the transformation of amyloplasts in the outer layers of the tuber to chloroplasts (Edwards et al., 1998; Jakuczun and Zimnoch-Guzowska, 2004). Greened tubers are associated with an accumulation of glycoalkaloids, which are poisonous for humans and animals. However, there is no direct metabolic link between chlorophyll biosynthesis and total glycoalkaloids content (Edwards et al., 1998; Griffiths et al., 1998; Percival, 1999).

Many factors can influence tuber greening, such as light (Buck and Akeley, 1967; Griffiths and Dale, 2001; Griffiths et al., 1998), maturity of tubers (Buck and Akeley, 1967), time and temperature of storage (Griffiths et al., 1998), production treatments (Lewis and Rowberry, 1973) or tuber size (Parfitt and Peloquin, 1981). Although tuber greening is affected by environmental factors, variability among varieties has been reported by (Buck and Akeley, 1967; Reeves, 1988) and Reeves (1988) reported polygenic inheritance for this character.

Tuber dormancy (resting period) of potato tubers is the physiological state after harvest, during which tubers do not sprout (Wiltshire and Cobb, 1996) even when stored under conditions favorable for sprouting (van den Berg et al., 1996). Two molecular mapping studies detected a number of QTLs for tuber dormancy and demonstrated the complex character of this trait (Freyre et al., 1994; van den Berg et al., 1996). According to Werij (2011) in potato the genes involved in breaking dormancy and the following sprouting action, can be divided in several categories. A first group concerns the genes coding for homeotic proteins and transcription factors (Bachem et al., 2000; Faivre-Rampant et al., 2004). A second class of genes regulates hormone metabolism and hormone response. Abscisic acid and ethylene are mentioned as requirement for dormancy induction, while abscisic acid maintains dormancy and cytokinins are involved in loss of dormancy (Suttle, 2004). The third group of genes is involved in metabolism of reserve storage molecules (Agrimonti et al., 2007; Horvath et al., 2002). Recently a fourth gene category was discovered, involved in DNA replication (Senning et al., 2010).

Another important attribute that affect the taste of the tubers is glycoalkaloid content. Glycolalkaloids are naturally occurring components in all parts of the potato plant; they are secondary plant metabolites that at appropriate levels may be toxic to bacteria, fungi, viruses, insects, animals, and humans (Friedman, 1997).

The predominant glycoalkaloids in potato are α–solanine and α-chaconine (Nema et al., 2008), both trisacharides of the common aglycone solanidine. These two compounds comprise about 95% of the glycoalkaloids in potato tubers (Friedman and Levin, 2009), α-solanine is composed of a branched β-solatriose (α-L-rhamnopyranosyl-β-D-glucopyranosyl-β-galactopyranose) side chain also attached to the 3-OH group of the same aglycon, whereas α –chaconine has a branched β-chacotriose (bis-α-L-rhamnopyranosyl-β-D-glucopyranose) carbohydrate side chain attached to the 3-OH group of the aglycon solanidine (Friedman, 2006).

The glycoalkaloid content can increase during storage and transportation and under the influence of light, heat, cutting, slicing, sprouting, and exposure to phytopathogens. Their presence at low concentrations may contribute to the flavor characteristics of processed potato, but at levels above 15 mg per 100 g fresh weight a bitter taste may be detected (Sinden and Webb, 1972). The consumption of large amounts of glycoalkaloids by humans could produce toxication symptoms ranging in severity from nausea to, in extreme cases, death (Friedman and Levin, 2009; Friedman et al., 1997). The majority of glycoalkaloids in the potato tuber are located within the first 1 mm from the outside surface and decrease toward the center of the tuber (Friedman, 2006).

Processing market

Tuber shape and eye depth are critical aspects of selection for the processing market, varieties with long tubers are used for French fries, while varieties with round tubers are preferred for crisps (Kirkman, 2007; Van Eck et al., 1994b) to minimize waste during peeling shallow eyes are the ideal for the processing process (Li et al., 2005).

For the processing industry dry matter content (DMC) is also a critical component for the processing industry, it is a measure of the tuber internal quality, starch is the principal compound, which is a polygenic trait and the effects are located on all chromosomes (Gebhardt, 2005b; van Eck, 2007; Werij et al., 2012). Kirkman (2007) established that a DMC below 19.5% for French fries and 20% for chips potatoes is not acceptable. Similarly, a DMC of more than 25% for French fries manufacturing are not adequate. The DMC and distribution has implications for bruise susceptibility during harvest and effects on cooking type, e.g. a waxy or mealy texture when boiled, organoleptic characteristics and in processed potatoes the final product texture (Taylor et al., 2007).

Dry matter content is affected by environmental factors during growth of the crop, such as solar radiation, soil temperatures, soil moisture, fertilizers and haulm killing (Haverkort, 2007; Hughes, 1974). In general, cold climate and short growing seasons reduce DMC, whereas the contrary occurs in warm, sunny locations with long growing seasons and an adequate water supply. DMC accumulates during growth of the crop, and tuber DMC often declines from a peak after defoliation of the haulm if the root systems remain active in wet soils (Hughes, 1974; Storey, 2007).

The level of sugars in potato tuber is an important factor affecting quality in potatoes, because at high temperatures, reducing sugars glucose and fructose interact with free amino acids in the Maillard reaction, which affect the color, flavor and it has also been related to acrylamide formation in fried products (Kumar et al., 2004; Xiong et al., 2002). Sugar levels in a potato tuber are conditioned by several factors, which include genotype, the environmental conditions and cultural practices during growth, and several post-harvest factors including storage (Kumar et al., 2004). The main sugars present are the monosaccharides, glucose (0.15–1.5%) and fructose (0.15–1.5%), which are reducing sugars, and sucrose (0.4–6.6%), a non-reducing disaccharide (Storey, 2007).

The level of reducing sugars that are generally acceptable for processing for chips is 0.2–0.3% and for French fries is 0.3–0.5%. The sugar content of the harvested crop is also important for the fresh market, and sucrose levels above 1% fresh weight (FW) are reported to give an unacceptably sweet taste to the boiled potatoes (Storey, 2007).

Molecular analysis has identified between one and three putative QTL regions per chromosome and a total of 24 QTL for sugar content in potato were located on all potato chromosomes and most of the QTL for glucose content were mapped in the same positions as QTL for fructose content (Menendez et al., 2002). Besides, several candidate genes involved in carbohydrate metabolism have been mapped (Chen et al., 2001; Werij et al., 2012).

Another important trait is enzymatic discoloration (ED), which is a widespread phenomenon that causes loss of quality and is of major economic importance (Coetzer et al., 2001), that is caused by the oxidation of phenolic compounds by the enzyme tyrosinase (polyphenol oxidase, PPO) to quinones, followed by transformation of the quinones to dark pigments (Friedman, 1997). This discoloration results in deterioration of flavor, color and nutritional quality that produce considerable economic losses for the food processing and retail industry (Werij et al., 2007).

Several methods have been developed to inhibit browning during processing including the use of chemical additives. However, because of adverse health effects, some chemicals have been restricted (Coetzer et al., 2001).

Three QTLs for ED were found in a diploid (CxE) population, for cholorogenic acid and tyrosine levels a QTL was identified on parental chromosome C2 and C8 respectively and a candidate gene PPO for ED was identified on chromosome VIII. None of the QTLs overlap, indicating the absence of genetic correlations between these components (Werij, 2011; Werij et al., 2007).

Nutritional quality

Potatoes are uniquely positioned to be a valuable source of dietary vitamins, minerals, and phytonutrients because of their per capita consumption. In most parts of the developed world, potatoes are by far the most eaten vegetable. Because of this high consumption the vitamin and phytonutrient content of potato will have much more dietary relevance and impact than foods eaten in low quantities (Navarre et al., 2009).

Potato is considered as a good source of antioxidants, such as polyphenols, carotenoids and vitamin C (Brown, 2005). After oranges and apples, potatoes are the third largest contributor of antioxidants in American diet because of the high consumption (Chun et al., 2005). Diets rich in antioxidants have been associated with a lower incidence of atherosclerotic heart disease, certain cancers, macular degeneration and severity of cataracts (Cook and Samman, 1996). Furthermore, Andre et al., (2007), established the considerable high diversity offered by native Andean potato germplasm to contribute to the dietary antioxidant intake and suggest that native potatoes offer a new opportunity to promote the nutritional quality of potato.

One of the most important potato antioxidants are polyphenols which are secondary metabolites, They are known to have a wide range of physiological activities related to protection against various forms of environmental stress like UV radiation, pathogens and herbivores (André et al., 2009a). Polyphenol compounds are produced through the phenylpropanoid pathway and encompass a wide range of chemical classes, including phenolic acids such as benzoic and hydroxycinnaic acids, flavonoids such as flavonols and anthocyanins, stilbenes, and lignans (Andre et al., 2009b).

Several epidemiological studies have suggested a protective role of food polyphenols on human health (Arts and Hollman, 2005). Indeed, polyphenols may also offer indirect protection by activating endogenous defense systems and by modulating cellular signaling processes (Yang et al., 2001). This compound is important in the human defense system against reactive oxygen species (ROS), which are known to be involved in the pathogenesis of aging and many degenerative diseases such as cardiovascular diseases and cancers (Akbari et al., 2006; Yang et al., 2001).

Carotenoids are present in the flesh of all potatoes, (Storey, 2007); yellow-fleshed potatoes are generally characterized by higher contents of lutein, violaxanthin and total carotenoids (Nesterenko and Sink, 2003). Lu et al., (2001), examining 11 diploid clones of a hybrid breeding population and two tetraploid varieties, Yukon Gold (yellow flesh) and Superior (white flesh), showed that both total and individual carotenoid contents are positively correlated with tuber yellow intensity. Yellow-fleshed varieties obtain their color from xanthophyll carotenoids.

Many carotenoids have been identified, including lutein, violaxanthin, neoxanthin, antheraxanthin and β-cryptoxanthin, with deep yellow pigmentation due to the presence of zeaxanthin (Brown et al., 2005; Nesterenko and Sink, 2003) and recently Wolters et al., (2010) investigated the genetic and molecular biology of orange flesh color in potato. They hypothesized that only genotypes combining presence of the dominant beta-carotene hydroxilase 2 (*Chy2*) allele with homozygositiy for the recessive zeaxanthin epoxidase (*Zep*) allele produced orange-fleshed tubers that accumulated large amounts of zeaxanthin.

Breeding for quality traits

Many Andean varieties were produced by farmer selection from naturally occurring variation (Bradshaw, 2007). Domestication must have involved selection of less bitter and hence less toxic tubers, and Andean farmers maintained a large variation for tuber shapes and skin and flesh colors compared with wild species (Simmonds, 1995). Subsequent selection for early maturity, appropriate dormancy and resistance to abiotic and biotic stresses must have occurred in many environments (Bradshaw, 2007).

Most efforts of plant breeding in potato have been focused on increased yield and resistance to late blight (Bradshaw, 2007); breeding for quality has been a second priority (Werij, 2011). Conventional potato breeding refers to the development of new varieties from sexual crosses between pairs of parents with complementary features followed by clonal propagation and selection based on several traits (Brown, 2011). A potato breeder's most important decision is which parents to use in crosses. Based on experience, breeders choose parents and parental combinations that result in a relatively high proportion of desirable offspring (Jansky, 2009).

Before making the crossing, it is necessary to measure the genetic variation available for a trait of interest, within cultivated species. For potatoes a large variation for quality traits has been reported for Andean potatoes (Andre et al., 2006; Andre et al., 2007; Brown et al., 2007; De Haan, 2007; Monteros, 2011). This genetic variability can be exploited by breeders to improve the quality of the crop for the fresh and processing market.

Unraveling the genetics underlying the variation is classically done by setting up a population using two extreme phenotypes as parents, phenotyping this population and performing a quantitative trait loci (QTL) analysis in order to understand the genetic locations influencing the trait of interest (Werij, 2011).

In potato, genetic studies have predominantly been performed using diploid populations (Menendez et al., 2002; ŚLiwka et al., 2008; Śliwka et al., 2012a; Werij et al., 2007). Tetraploid potatoes have been used less frequently (Meyer et al., 1998). A new method arisen from the human genetics has recently been used. Association mapping has been performed in potato using a set 221 tetraploid varieties looking for the genetic components of several quality traits (D'hoop et al., 2008; D'hoop et al., 2010).

Molecular maps and the DNA markers are the current backbone of genome analysis in cultivated potato and related tuber-bearing *Solanum* species (Gebhardt, 2005a). Markers linked to QTL can be used to more rapidly incorporate the desirable regions into agronomically superior genotypes. This will be further enhanced by the use of the recently published genome sequence (Potato Genome Sequencing Consortium, 2011) which provides a new resource for use in breeding.

For some traits, such as tuber shape or eye depth, selection of required genotypes is an easy task. However, selection for high or low contents of some traits requires vast and time consuming efforts. Currently two basic genetic approaches utilized to improve quality traits are: 1) exploitation of natural genetic variation, either through direct selection, traditional breeding or through the mapping of (QTL) and subsequent marker assisted selection and 2) generation of transgenic plants to introduce novel genes or alter expression levels of existing genes to affect the contents of some quality traits.

Scope of the thesis

Ecuador has a large variability of landraces; most of this variation is conserved at INIAP germplasm bank and in farmers' fields (Monteros, 2011). Despite the large variability little information about quality characteristics is available and the use of these varieties in breeding has been minimal (Cuesta et al., 2005a).

The objective of this thesis is to characterize quality traits in a representative group of Ecuadorian landraces, identify superior landraces for use in breeding and to identify QTLs for tuber shape, eye depth, skin and flesh color, in a diploid population (CHAR-01) using DArT markers. This obtained information will be consequently used for the development of new potato varieties with enhanced quality traits that approach the ideal potato for each Ecuadorian region and actor in the chain.

In **Chapter 2** we identify the ideotype of potato demanded by farmers, traders and consumers of the main Ecuadorian regions. Information necessary for the design of the potato breeding scheme for selecting new potato varieties that satisfy the demands of the different users for the fresh market is presented.

In **Chapter 3** a group of representative landraces of the Ecuadorian potato collection was characterized for tuber shape, eye depth, skin and flesh color, dry matter content, enzymatic discoloration, reducing sugars and glycoalkaloid content. Several landraces were selected. For some traits, most of the observed variation was genetic variation that can be used in breeding for the development of new improved varieties.

In **Chapter 4** we characterize representative potato landraces from three areas of Ecuador for potato tuber dry matter and antioxidant content (polyphenols and carotenoids) large variation was identified and several landraces with the highest contents were selected for direct use or in breeding. Furthermore, we determine if farmer preferences for certain landraces are based on characteristics related to nutritional value.

Chapter 5 describes the identification of QTLs for shape, skin and flesh color in a diploid population (CHAR-01) resulting from a cross between two Ecuadorian landraces.

The general discussion **(Chapter 6)** integrates the data from the four experimental chapters and puts them in a broader perspective and makes several recommendations for the INIAP potato breeding program to improve potato tuber quality.

Chapter 2

Potato preferences in the Ecuadorian Highlands

Potato preferences in the Ecuadorian Highlands

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Abstract

Farmers, traders and consumers of three Ecuadorian highland areas were interviewed to obtain information about preferred agronomic traits as well as potato tuber quality and processing characteristics to identify the ideotype of potato for each Ecuadorian region.

There were differences among areas and chain actors for potato preferences. In general, farmers in all areas were concerned about the characteristics related to agronomic aspects; consumers were interested in potato tuber quality and processing characteristics while the traders were interested in marketability of potatoes, tuber health and for the rest criteria were shared with other actors. Differences in preference among areas were mainly related to tuber skin color and eye depth; criteria related with the improved varieties cultivated in these areas.

The preferred ideotypes in the Northern and Central region of Ecuador were quite similar: round tuber shape, red or pink skin color, shallow eyes, big or mean size, mealy consistence and fast cooking, while in the South the ideal potato should have a yellow skin color, mean depth of eyes, big size, suitable of “locro” soup and soft consistence. In all cases the ideal potato should be resistant to late blight, be high yielding and early maturing. Furthermore, good taste, yellow flesh and suitability for several cooking applications are preferred.

Finally the prospects of the INIAPs breeding program to develop the required potato based on the ideotype identified per each Ecuadorian region are discussed.

Key words: Preference, farmer, trader, consumer, potato, ideotype.

Introduction

Potato production in Ecuador is located in the highlands at an altitude range between 2,700 to 3,400 meters above sea level, divided over three production zones: Northern (Carchi, Imbabura and Pichincha), Central (Cotopaxi, Tungurahua, Bolivar and Chimborazo) and Southern regions (Azuay and Cañar)(Andrade, 2002; Herrera et al., 1998). In Ecuador 76% of the potatoes for the fresh market is produced by smallholder farmers in production units smaller than 5 ha (Devaux et al., 2010; Monteros, 2011) and more than 90% of the commercial production is for fresh consumption by the households (Devaux et al., 2010).

Potato is grown all year round and most of the farmers sell the product directly to traders who usually tend to control and fix prices. Traders play a crucial role in the potato marketing system of Ecuador by facilitating potato transactions, linking farmers to consumers.

A value chain encompasses the full range of activities and services required to bring a producer service from its production to its end use (Kaplinsky and Morris, 2001). The value chain includes direct actors which are commercially involved in the chain (farmers, traders and consumers) and indirect actors which provide services or support to the functioning of the value chain. These include financial or credit agencies, business services, providers of services, government, researchers and extension agents (Emana and Mengistu, 2011). In our study we only considered direct actors.

The "preference" of a consumer or a group of consumers for a product means that in a given situation that product is the most desirable of two or more alternatives (Rhodes, 1955). In the case of potato several traits influence the preference of the farmers, traders and consumers. These characters are mainly agronomic, tuber quality and tuber processing related characteristics (Espinosa and Crissman, 1997). These traits identify the ideotype of potato.

Idiotype is derived from the Greek word *idios,* meaning one's own, personal, separate, distinct (Zeven, 1975). The word ideotype was coined by Donald (1968) who defined it as a biological model which is expected to perform or behave in a particular manner within a defined environment. The term has been co-opted by plant breeders to describe the idealized plant type with a specific combination of characteristics (Peng et al., 2008).

The information available to characterize the ideal potato is limited; most of the data is qualitative and comes mainly from participatory research performed with farmers (Danial et al., 2007, Cuesta et al., 2007b) and surveys including a small number of consumers (Espinosa and Crissman, 1997). Furthermore, there is no quantitative information on the preferences of the main actors involved in the potato production, marketing and consumption per region of the country, information that is necessary to focus the potato breeding objectives of the National Agricultural Research Institute of Ecuador (INIAP) to develop the ideal potato for each region.

The objectives of this study were 1) to determine the main selection criteria and preferences of farmers, traders and consumers in three highland regions of Ecuador, and 2) to identify the ideotype of potato for each Ecuadorian region.

This information will be useful for the development of new potato varieties and allow a better response to the demands of these actors. The results will also help to understand the success or failure of introductions of new potato varieties.

Materials and methods

Location

For this research the Ecuadorian Highland was divided in three areas, each one consisting of several Provinces according to the Ecuadorian territorial division (Andrade, 2002):

- The North: Carchi, (main potato production area in Ecuador) and Pichincha, where Quito (the capital) is located.
- The Central region: Cotopaxi, Tungurahua and Chimborazo.
- The South: Cañar and Azuay.

These provinces account for 78 percent of the total potato production in Ecuador (Annex 1).

Participants

For the present study farmers, traders and consumers were considered as the main actors in the Ecuadorian potato value chain. During 2007, meetings with representatives of the chain were organized in each area to identify key issues and criteria for the selection of the people representing the different actors to be interviewed about potato preferences for the fresh market. Based on the information obtained a survey was designed and pretested with representatives of farmers, traders and consumers in each zone.

The Survey

The Survey was oral; interviews were questionnaire-based (Annex 7) and conducted face-to-face by interviewers of INIAP.

The survey respondents were asked questions concerning various socio-economic factors such as, gender, age, number of children and education level. In a second level of questioning, respondents were asked about potato preferences, which were grouped in: 1) Agronomic characteristics, 2) Potato tuber quality traits, 3) Tuber processing characteristics and 4) Varieties preferred (Table 1). Each question about a specific trait preference had several options and the respondent was asked to choose one. If the respondent was not interested in the options it was marked as indifferent.

For variety preference, respondents identified their favorite potato variety from a series of six options (Annex 5). However, when the respondent had a preferred variety that was not among the options, an additional list of varieties described in Table 1 was utilized.

Selection of the participants

In each study area farmers were selected based on the results of previous studies conducted by the Ministry of Agriculture (MAGAP), INIAP and information regarding: farm size, farm location, easy access to the farm, growing potato as main crop and experience in potato production, to ensure that a representative group was chosen.

Farmers interviews were conducted, either in their homes or in the farmer´s field. Representative potato traders were selected based on information provided by farmers, MAGAP and market managers. Traders were interviewed on the markets of Tulcan and San Gabriel (North), the markets of Latacunga, Ambato and Riobamba (Center), and Cuenca and Gualaceo (South).

Consumers were selected according to age, gender, income status and knowledge about cooking potatoes. We performed the consumer survey only in the urban areas of the main cities of each region, in the Northern area Quito, in the Center Ambato and Riobamba while in the South the interviews were conducted in Cuenca. Respondents were interviewed in the supermarkets, grocery stores and outdoor markets.

The preference criteria:

Interviewers of INIAP were previously trained in the management of the survey instrument and in the meaning of each character according to the following description:

A variety was considered late blight resistant when it required less than five fungicide applications during the cycle to produce potatoes under favorable conditions for the development of the pathogen.

The term high production refers to the total weigh of tubers expressed in tons per ha, which at harvest should be more than 30 tons ha^{-1}.

Earliness refers to the duration of the life cycle of the crop. It must be less than 120 days to be considered early.

Good plant size denotes a potato plant with vigorous development in the field.

Potato tubers that can be sold easily in the market are considered as marketable tubers. While potato tubers free of defects and diseases were considered as healthy tubers.

For potato tuber size small was considered a tuber of less than 60 g, for mean size between 60 g and 90 g and big size larger than 90 g. While for tuber eye depth, the reference variety for shallow eyes was INIAP-Fripapa, for mean eyes the variety INIAP-Estela and for deep eyes the landrace Chaucha roja (Annex 8).

For tuber shape, tuber skin and flesh color the description of Gómez (2000) was used.

The taste refers to consumer´s appreciation of a cooked potato tuber. For this study we consider “good taste” a potato that is very flavorful without bitterness, while if the potato is tasteless or bitter we consider it as “poor taste”.

The characteristic fast cooking refers to the time needed for cooking takes less than 25 minutes for a mean tuber size (since potatoes are placed in boiling water until a stainless steel probe easily penetrate the tuber) (Burgos et al., 2011).

The term tuber consistence refers to the variation from firm (waxy consistence) to mealiness (mealy consistence) of a tuber after cooking.

The interview:

There were 500 interviews planned, which were distributed according to the region and population size in each region, 200 for the North and 150 for the Center and South. For the analysis of the data some surveys were eliminated due to missing data or inconsistencies in the information (for example respondents mentioned that they prefer a yellow flesh tuber and selected a white flesh variety as the preferred one), finally a set of 409 interviews were used for the evaluation.

Table 1. Grouping of potato characteristics and quality traits used in the survey.

Agronomic characteristics		*Tuber quality traits*		*Tuber processing characteristics*		*Varieties preference*	
1	Late blight resistance	7	Small size	22	Good taste	32	Superchola
2	Earliness	8	Mean size	23	Poor taste	33	INIAP-Gabriela
3	High Production	9	Big size	24	Other taste	34	INIAP-Cecilia
4	Good plant size	10	Round shape	25	Fast cooking	35	Bolona
5	Healthy tubers	11	Long shape	26	Waxy consistence	36	INIAP-Fripapa
6	Marketable potatoes	12	Other shape	27	Mealy consistence	37	Unica
		13	Shallow eyes	28	Locro soup	38	Capiro
		14	Mean eyes	29	Fried	39	Rosada
		15	Deep eyes	30	Cooked	40	Violeta
		16	White-cream skin	31	Several Uses	41	Roja
		17	Yellow skin			42	Limeña
		18	Pink skin			43	Leona negra
		19	Red skin			44	Chaucha amarilla
		20	White-cream flesh			45	Jubaleña
		21	Yellow flesh			46	Uvilla
						47	Preference for new varieties

Analyses of data

For each zone and actor the preference criteria were established, the relative frequency was calculated per actor group and region and a correspondence analysis was carried out (Greenacre and Blasius, 1994; Greenacre, 1988), using SPSS version 16.0 (SPSS Inc, 2007). This analysis examines the relationships between preference criteria and actors by measuring the association of the chi-square. In this analysis the proximity in the mathematical sense among criteria of preference indicates their level of association (Clausen, 1988, Hill, 1974).

RESULTS

Socio economic characteristics

A total of 409 surveys were completed over the three regions. The vast majority (> 88%) of the respondents has attained some level of education, while between 3% – 9% of farmers and 11% – 12% of traders did not have any level of education for the Center and South region respectively. Between 19% – 70% of the farmers and traders from all regions had completed primary school, while 33% of the consumers from the Northern region had secondary school and those from the Center and South (40% – 44%) mentioned that they have completed University education (Annex 3).

The distribution of the respondents over region, actor and age group can be found in Annex 4 and the responses about agronomic and quality traits classified by the age are described in Annex 5 and 6.

For most of the agronomic and quality characteristics per each region the responses were consistent with the number of respondents per each age group. However, for consumer preference about tuber processing characteristics there were differences among age groups (Annex 6).

Preferences by actor

Agronomic traits

For farmers from all three areas late blight resistance, marketability of the potato and high production were the most important attributes. Good plant size and healthy tuber were the least important characters (Supplementary Table 1).

For traders marketability of the potatoes and healthy tubers were the most important characters for 18% and 14% of respondents respectively, while 8% of traders expressed late blight resistance as important trait. Consumers did not seem to be interested in any of the agronomic traits with exception of high production that was selected by a small number of respondents (Table 2).

Potato tuber quality traits

A round tuber with yellow flesh color was preferred by most of the farmers, traders and consumers of all the three regions. While, white-cream flesh color, long shape and small tuber size, were the least important attributes (Table 2).

Additionally, an important number of farmers from the South region (54%) were interested in tuber yellow skin (Supplementary Table 2), while some traders (14%) preferred tuber red skin and 20% of consumers preferred mean tuber size (Table 2).

Small and mean tuber size were not mentioned by any farmer, while tuber yellow skin and mean tuber size were not reported by traders and mean depth of eyes was not selected by any consumer (Table 2).

Tuber processing characteristics

Good taste and mealy consistence were the criteria most mentioned by the respondents (Table 2) with the exception of the South that preferred waxy consistence (Supplementary Table 3). In relation to tuber processing most of the respondents were interested in a potato variety with the quality to be useful in different ways of preparation (cooked or fried).

Table 2 . Preference of farmers, traders and consumers for agronomic, tuber quality and processing traits. Data is expressed as average percentage from three regions.

	Farmer (113)*	**Trader** (107)*	**Consumer** (189)*
Agronomic traits			
Late blight resistance	68	8	0
Marketable potato	48	18	0
High Production	40	0	3
Earliness	30	0	0
Good plant size	13	0	0
Healthy tubers	4	14	0
Tuber quality traits			
Yellow flesh	53	41	46
Round Shape	44	17	8
Pink skin	22	4	4
Yellow skin	19	0	5
Shallow eyes	18	2	6
Big Size	12	7	6
Mean depth of eyes	10	7	0
Red skin	10	14	12
Mean size	0	0	20
White-cream flesh	4	6	4
Long Shape	1	2	3
Small Size	0	1	3
Tuber processing characteristics			
Good taste	34	23	47
Mealy	25	16	26
Fast cooking	11	5	23
Waxy texture	0	7	22
For “locro” soup	0	0	11
Several uses	3	7	9
Cooked	3	1	4
Poor taste	7	0	1
Fried	1	1	3

* Total number of respondents.

Ideal potato per region

Based on the preference of the respondents about the agronomic, tuber quality and processing traits, we selected the top four traits for each group; the character with the highest percentage of preference was rated as 1 (most important) to 4 (less important). The results are presented in Table 3.

The agronomic characteristics that received the highest scores by farmers in all regions were late blight resistance, marketable potato and high production; these traits were rated as the most important. The character earliness was rated in the first places only in the Southern region. While, good plant size and healthy tubers were rated as the least important (Table 3).

Tuber yellow flesh color was rated in the first place in all three regions and depending on the region, round shape was rated in second place in the Southern and in third place in the Northern and Center, while yellow skin was in third place in the Southern region (Table 3).

Table 3. Rating of the most important characteristics indicated by farmers, traders and consumers in the three Ecuadorian regions.

North (181)*	**Score****	**Center** (156)*	**Score**	**South** (72)*	**Score**
Agronomic traits					
Late blight resistance	1	Late blight resistance	1	Late blight resistance	1
High Production	2	Marketable potato	2	Marketable potato	2
Marketable potato	3	High Production	3	Earliness	3
Earliness	4	Earliness	4	High production	4
Tuber quality traits					
Yellow flesh	1	Yellow flesh	1	Yellow flesh	1
Red skin	2	Big Size	2	Round Shape	2
Round Shape	3	Round Shape	3	Yellow skin	3
Pink skin	3	Pink skin	4	Mean eyes	4
Tuber processing characteristics					
Good taste	1	Mealy consistence	1	Good taste	1
Mealy consistence	2	Good taste	2	For “locro” soup	2
Fast cooking	3	Fast cooking	3	Waxy consistence	3
Several uses	4	Waxy consistence	4	Fast cooking	4
Preferred varieties					
Superchola	1	I-Gabriela/I-Cecilia	1	Bolona	1

* Total number of respondents.
** Score 1 is the most important and 4 the least important

Preferences

For tuber processing characteristics, good taste, mealy consistence and fast cooking were rated in the first places in all three regions with the exception of the Southern region where, the characteristic for “locro” soup and waxy consistence were rated in second and third place respectively (Table 3).

Preferred varieties

In the Northern region the improved variety Superchola was preferred by farmers, traders and consumers. In the Central region the improved varieties INIAP-Gabriela, INIAP-Cecilia were the favorite, while in the Southern region the landrace Bolona, was important (Table 3). In addition, there were a large number of respondents that would be interested in trying new varieties (Supplementary Table 4).

Correspondence analysis

The Correspondence analysis showed significance at $P<0.001$ for the chi square test, which means that there was no independence among variables. There was a relationship between actors in the chain and preference criteria.

Total inertia values measure the total variation explained by the two dimensions model that in our study had values of 63.1%, 69.6% and 54.6%, for the Northern, Central and Southern region, respectively (Annex 2). Figure 1 shows the correspondence analysis for the three areas in Ecuador; it shows that in all three regions farmer, trader and consumer were located far from each other, because most of them had different preference criteria. But, they also have a few preferences in common as good taste and yellow flesh color. In the North the varieties Capiro, Unica, Violeta and Rosada were associated with the traders, while INIAP-Gabriela and Superchola were close to consumers, as were the varieties Superchola and Roja. In the Center traders were more related to INIAP-Gabriela and INIAP-Cecilia, consumers were associated with Superchola and INIAP-Cecilia and farmers with INIAP-Gabriela, whereas in the South Bolona was more associated with traders and consumers preference.

The agronomic characteristics were plotted close to farmers, whereas quality and processing attributes were clustered next to consumers; marketability of potatoes and healthy tubers were located close to traders. A more detailed analysis can be found in Annex 2.

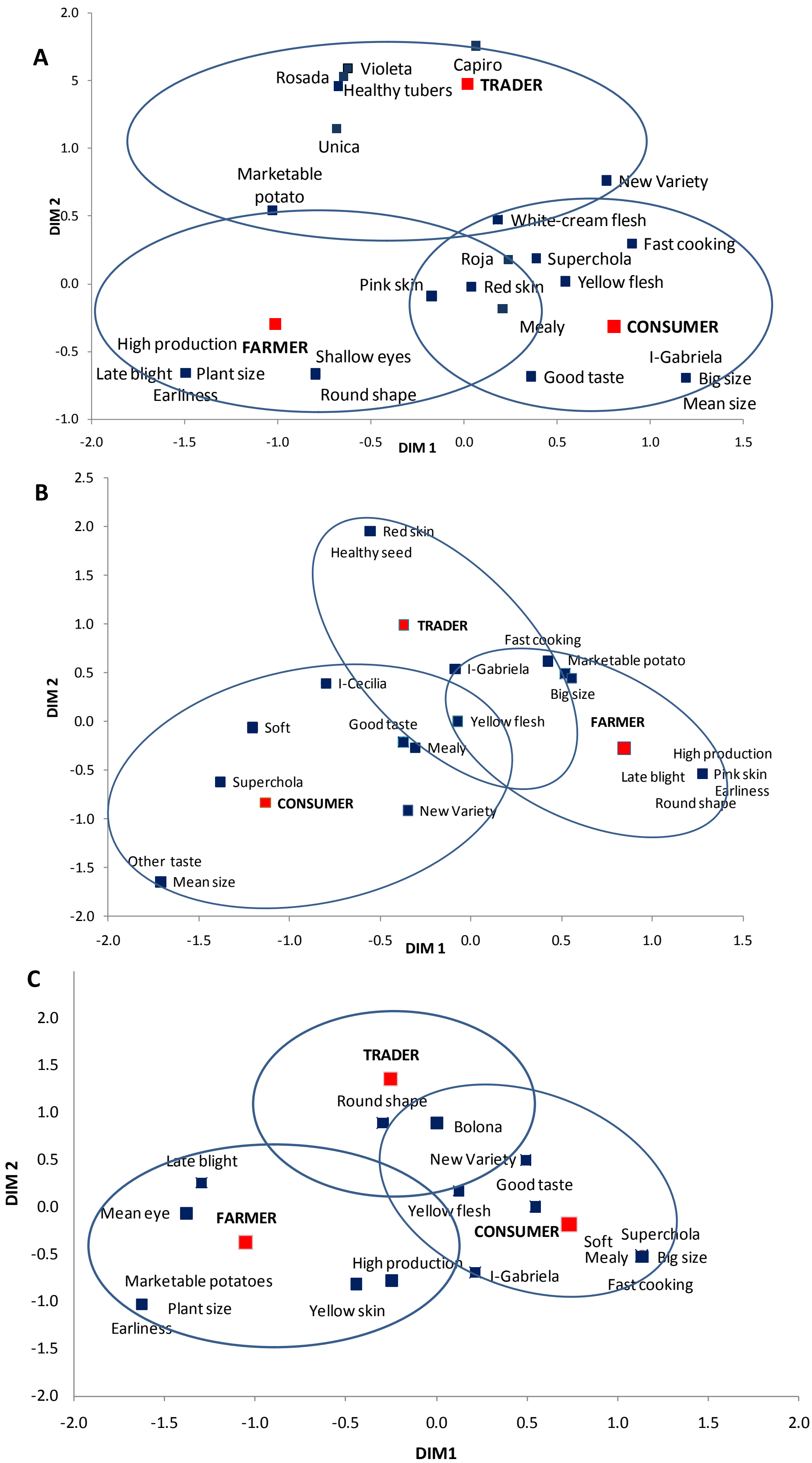

Figure 1. Biplot showing the correspondence analysis for the Northern (A), Central (B) and Southern region (C), to identify the preferences of the three main actors in the potato agri-food chain in Ecuador.

Discussion

In Ecuador the ideotype of potato varies according to the region of the country and the preference of the actors in the chain (farmer, trader and consumers). The most important factors were the tuber quality, processing characteristics and the commercial varieties more cultivated in each region. Furthermore farmers were interested in varieties with late blight resistance, high yield and marketable potato.

Socio economic characteristics

Our study showed that all the consumers and most of the farmers and traders had some level of education. Depending on the region, only 3% - 12% of farmers and traders did not have any level of education. These values are similar to those reported by the government that mentions a range between 1% – 14% of Ecuadorian people without any level of education for 2010 (http://www.inec.gov.ec). The high percentage of consumers with a completed university study in the Center and Southern region is due to the fact that we perform the survey only in the main cities of each region where most of the potato production is marketed (Herrera et al., 1998; Mancero, 2007). Besides, we applied the survey to people, that are used to buy fresh potatoes in the supermarkets, grocery stores, etc. and also individuals with knowledge about cooking potatoes, as suggested by Watts and colleagues (Watts et al., 1992).

Farmers and traders from the South were relatively older compared to those from the other regions. This could be an effect of migration, which is an important phenomenon in the country and that is most evident in the Southern region where it started already a long time ago, but was very strong in the last decade, because of the severe economic crisis, which was accentuated by the phenomenon of dollarization (Jokisch and Pribilsky, 2002).

When responses about the different agronomic and quality traits were related to the age of the respondents, there was no clear correlation. The age group does not seem to have an effect on the preference for the different traits. Results that differ from those reported by Jemison et al., (2008) studying consumer preferences of fresh potatoes in Maine, they found differences among age groups regarding to the use of potatoes, e.g. French fries potatoes were preferred choice for younger group.

For consumer preference according to the age group we found differences in preference among regions. In The North and Center region consumers preferred tubers with mealy consistence, the preference by age group was consistent with the number of respondents. While soft consistence was the preferred attribute in the South, especially by consumers (<35 years). The difference between regions about tuber consistence is related with consumer's tradition and food habits (Poats, 1982). In South area the preference is for the landrace Bolona which is usefulness in traditional dishes as "locro" soup.

Importance of a characteristic depends on the actor

Our analysis established that each actor had a different preference profile as shown by the percentage of preference established and the correspondence analysis. In general for the three regions each actor was more related to a group of preferences. The agronomic attributes late blight, earliness and high production were more frequently associated with farmers, while the characteristics related to tuber processing quality, consistence, good taste and fast cooking, were more related to consumers.

Furthermore, attributes healthy tubers and marketability of potatoes were more frequently associated with traders. Similar results about farmer preferences were reported by previous investigations using participatory plant breeding (PPB) approaches (Cuesta et al., 2007b) or surveys about demand for potatoes (Yanez and Cuesta, 2006; Ofiagro, 2009).

Farmers were more concerned about biotic limitations such as late blight. During the last years the number of incidence of late blight has raised in the Ecuadorian highlands as consequence of the increased amount and distribution of the rainfall (Perez et al., 2010, Seo and Mendelsohn, 2008), new and more complex races of *P. infestans* have been reported in Ecuador (Delgado et al., 2013).

Agronomic characteristics

Late blight resistance, high production, marketability and earliness were the main criteria mentioned by farmers of all three regions. Late blight resistance ranked as the most important trait demanded by farmers since this biotic stress limiting potato production in the Ecuadorian highlands requires more than 20 control sprays on susceptible varieties (Yanez and Cuesta, 2006) and most of the commercial varieties cultivated in the highlands are susceptible (Cuesta et al., 2009).

An important number of respondents especially those from Southern region expressed a strong need for earliness in potato varieties, which we interpret as early bulking. Earliness serves several purposes, including allowing for increase in cropping intensity as well as reducing the crop's exposure to pests and diseases (Fuglie, 2007). Farmers of Bolivia and Peru, evaluating breeding clones and improved varieties, also had similar preference criteria (Bejarano et al., 2009; Danial et al., 2007; Thiele et al., 1997).

The consumers were not interested in agronomic characteristic, because they are not directly involved in the potato cultivation. The same applies to traders; they were interested in healthy tubers and marketability of potatoes. In the Center several traders were interested in late blight; this is because some traders are also involved in the potato production (Mancero, 2007).

Tuber quality

For tuber quality the ideotype of potato as defined by the actors in the chain had a round tuber shape, pink-red skin color and yellow flesh color, while in the Southern region farmers and traders preferred yellow skin tubers. This is related to the preference for white cream and yellow skin potatoes similar to the landraces Bolona and Jubaleña which have been the favorites in this region in the last years (Yanez and Cuesta, 2006).

Comparable results of farmers preference related to tuber quality were already reported for Ecuador and Bolivia by (Danial et al., 2007) measuring farmers preferences using (PPB) approach. Bejarano et al., (2009) also found similar results in Peru when evaluating farmer preferences. The main difference is that in Peru and Bolivia farmers had preference for varieties with deep tuber eyes and in Bolivia white and cream tuber fleshed varieties were more preferred (Thiele et al., 1997).

Consumers' requirements regarding tuber quality for fresh market potatoes are often associated with the visual characteristics of the product; in the case of potato the shape and appearance of the tuber (Storey, 2007). In our study tuber size, skin and flesh color were the preferred characteristics by consumers.

While, the character most mentioned by all actors in the chain was yellow flesh color, a trait that usually has been associated with potatoes that taste good and cook well. This character is related with carotenoid content (Andre et al., 2007), the deeper the yellow color the higher the level of carotenoids that are natural antioxidants (Haynes, 2000).

The other high ranking potato characteristic was skin color. Purple and red-skinned potatoes contain twice the concentration of anthocyanins a natural antioxidant compared with white-skinned tubers (Ezekiel et al., 2012). Then indirectly, farmers, traders and consumers have been selecting for high antioxidant content in potatoes, especially those from the Northern and Center region.

Tuber processing characteristics

The ideotype of potato for processing characteristics were defined mainly by farmers and consumers. Both considered good taste, mealy consistence and fast cooking as the most important. In the Southern region the characteristics waxy consistence and for “locro” soup were also important. Variations in potato texture can be explained by determining the degree of a tuber´s mealiness or waxiness. Mealiness has been associated with potatoes with high dry matter content (Jansky, 2008).

Most of the consumers prefer a variety suitable for several types of food preparation (soups/’locro’, fries, mashed potato, salad or cooked). However, to get a variety with all these characteristics is a difficult task because each food preparation has specific requirements regarding tuber quality. For example for fried potatoes a variety with high dry matter content (DMC) and low reducing sugar content is necessary (Storey, 2007), while, potatoes for soups or stews should maintain their consistence after cooking then a low dry matter content potato is required (Taylor et al., 2007). Culinary uses of potato varieties are related to their texture (Jansky, 2010).

According to (Espinosa et al., 2002; Yanez and Cuesta, 2006), improved varieties as Superchola, INIAP-Gabriela and INIAP-Fripapa are suitable for several food preparation, and can be used as fries, mashed or cooked since these varieties have high DMC. This characteristic could explain why these varieties have better acceptance in the North and Center region but not in the South.

In the South consumers preferred a potato suitable for “locro” (potato soup), which is a traditional dish in this region. The potato variety suitable for this preparation should have a waxy consistence (low dry matter content) to avoid the disintegration during the cooking process. This is the reason that waxy consistence was considered important only in this region compared to the other places that preferred mealy consistence.

Good taste was the most important characteristic mentioned by all the actors in the chain, with the higher percentages for consumers, this characteristic is the result of the interaction between several volatile and nonvolatile compounds (Taylor et al., 2007).

This result was expected because this trait is of primary importance for consumption of potatoes (Werij, 2011) and the development of potato varieties with enhanced taste would have the potential to increase consumer interest in the consumption potatoes (Jansky, 2010).

Regional differences in the potato ideotype

Based on the preference of farmers, traders and consumers, the ideotype for the North and Center region are very similar; it must include the following characteristics: late blight resistance, high production, marketable potato, yellow flesh color, red/pink skin, round tuber shape, shallow eyes, big/mean size, good taste, mealy consistence and fast cooking.

The difference between these two regions is in the order of importance of the traits and in the preferred variety. In the North red/pink skin color was more important than mean tuber size while in the center region big/mean tuber size was more important than skin color.

Moreover, mealy consistence in the Center region was more important than good taste, however both traits are related, since texture is an important component of taste (Kaur et al., 2002). Texture is one of the most important quality attributes of potato tubers, that is easily recognizable by consumers who tend to have distinct preferences (Jansky, 2010).

In the Southern region the ideotype should have characteristics of late blight resistance, marketable potato, earliness, yellow flesh color, round tuber shape, yellow skin, mean depth of eyes, big size, good taste, suitable for “locro” soup and waxy consistence.

The ideotype in the Southern region differs from the other places mainly in the characters related to tuber quality (yellow skin color, mean depth of eye) and tuber processing characteristics (tuber with waxy consistence and suitable for “locro”soup). Furthermore, among agronomic traits earliness was more important than high production compared with the other areas. These unique characteristics of this region are influenced by the preferred variety Bolona that has specific characteristics of texture.

Preferred varieties

We found that in each specific region one or two varieties were preferred and have maintained this status for years. In the Northern area the preferred variety was Superchola, which is an improved variety released in 1987 and planted in most Ecuadorian regions, with emphasis on the North area (Andrade and Hardy, 1998). This variety meets the preference criteria for tuber quality and processing demanded by the actors in the chain, but it does not fulfill all agronomic requirements as it is susceptible to late blight and has a long life cycle (Cuesta et al., 2002).

In the Central area, the varieties INIAP-Cecilia or INIAP-Gabriela are preferred. INIAP-Cecilia is an improved variety that is planted only in this region because of the high preferences of consumers and traders as well as the environmental conditions, which are ideal for its development (Cuesta et al., 2002).The preference for this variety is associated with the marketability, it gets a higher price in the market compared to other varieties. However, this variety is susceptible to late blight and has long life cycle (Albornoz et al., 2011).

INIAP-Gabriela is an improved variety that has been widely planted in all Ecuadorian regions since the 90´s (Herrera et al., 1998; Ramos et al., 1993). However, because of its susceptibility to late blight and low yield this variety has gradually been reduced in acreage and in some areas like Chimborazo province it has been replaced completely by other varieties like INIAP-Fripapa (Yanez and Cuesta, 2006). INIAP-Fripapa is an improved variety released in 1995 with late blight resistance and quality for the fresh and processing market (Andrade and Hardy, 1998).

For the Southern region the most preferred variety was Bolona in terms of tuber quality and processing characteristics, but similar to the other regions it is necessary to include late blight resistance, earliness and high production in it. Bolona, is a landrace (*S. andigenum*) mostly planted in the Chimborazo Province (Central region) and in most of the locations of the Southern region (Herrera et al., 1998; Ramos et al., 1993; Yanez and Cuesta, 2006).

Consequences for the potato-breeding program

There is a continued need for new improved varieties (Bradshaw, 2007) to get more economic benefits through higher yield at lower production costs. New varieties should include resistances to pests and diseases that give environmental benefits through reduced use of pesticides and fungicides. They also must meet consumer demands for convenience foods, improved nutritional and health benefits, improved flavor and novel products (Walker, 1994), some of these characteristics are common for most of the breeding programs in developing countries (Fuglie, 2007). However, the quality and processing characteristics demanded are different in each country and they could differ within country as is the case in Ecuador.

The priority needs about agronomic traits identified in this research late blight resistance, high yield and earliness are consistent with results from previous surveys on potato. In a survey of potato farmers conducted by INIAP in 2006 (Yanez and Cuesta, 2006), respondents from three provinces listed yield, late blight resistance and marketability as their three top agronomic priorities. A survey of potato farmers from five provinces conducted by (Ofiagro, 2009) found high yield, late blight resistance and marketability as the highest priority needs of farmers.

Before this research we thought that each region has a different ideotype of potato and that farmer preferences represent the criteria of the other actors (Mancero, 2007). However, this study established that the ideotype in the Northern and Center are quite similar, while in the Southern region is different, a potato variety suitable for locro is required. Moreover, the main commercial varieties cultivated in each region influenced the preferences of the different actors. Since the tuber quality and processing characteristics of the ideotype defined were similar to those of the preferred varieties.

Since the agronomic traits were quite similar in the three regions with few differences in the Southern the potato breeding program should develop varieties with late blight resistance, high production and earliness for all regions but with specific quality and processing characteristics for the North-Center and South. Theses varieties could have a good chance of being adopted by the market.

Despite farmer participation in the breeding process to increase the probability of adoption of new varieties (Danial et al., 2007) in Ecuador, only two of the more than 10 varieties that have been released were successful in terms of adoption. Not including traders and consumers in the selection probably influenced in the acceptability and diffusion of new varieties as describe (Johnson et al., 2003). Therefore, if the potato breeding program decides to continue with the PPB approach to select new varieties, traders and consumers must be included in this scheme, because they have criteria that differ from those of farmers as was demonstrated in this study.

Our study established that the ideotype of potato in Ecuador was affected by the preferences of the actors in the chain and was influenced by the region of the country. Therefore potato breeding program of Ecuador to obtain new varieties should focus in the ideotype defined for the North-Center and South region, large variation for quality and processing traits are available in the Ecuadorian germplasm. Then a selection of progenitors with complementary characteristics would be good options for approaching the ideal potato.

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Supplementary Table 1. Preference of farmers, traders and consumers in the Northern, Central and Southern region of Ecuador for agronomic characteristics, data expressed in percentage (%). Values calculated are based on the total of respondents in each area per actor.

	Northern			**Center**			**Southern**		
Preference Criteria	**Farmer** (52)*	**Trader** (38)*	**Consumer** (91)*	**Farmer** (47)*	**Trader** (53)*	**Consumer** (56)*	**Farmer** (14)*	**Trader** (16)*	**Consumer** (42)*
	%	**%**	**%**	**%**	**%**	**%**	**%**	**%**	**%**
Late blight resistance	62	0	0	62	0	0	79	25	0
Indifferent	*38*	*100*	*100*	*38*	*100*	*100*	*21*	*75*	*100*
Earliness	21	0	0	26	0	0	43	0	0
Indifferent	*79*	*100*	*100*	*74*	*100*	*100*	*57*	*100*	*100*
High Production	52	0	0	40	0	0	29	0	10
Indifferent	*48*	*100*	*100*	*60*	*100*	*100*	*71*	*100*	*90*
Good plant size	17	0	0	0	0	0	21	0	0
Indifferent	*83*	*100*	*100*	*100*	*100*	*100*	*79*	*100*	*100*
Healthy tubers	12	18	0	0	25	0	0	0	0
Indifferent	*88*	*82*	*100*	*100*	*75*	*100*	*100*	*100*	*100*
Marketable potato	31	18	0	57	36	0	57	0	0
Indifferent	*69*	*82*	*100*	*43*	*64*	*100*	*43*	*100*	*100*
TOTAL	*29*	*21*	*50*	*30*	*34*	*36*	*19*	*22*	*58*

* Total number of respondents

Preferences

Supplementary Table 2. Preference of farmers, traders and consumers in the Northern, Center and Southern Ecuador area for potato tuber quality traits, data expressed in percentage (%). Values calculated based on the total of respondents of each area per actor.

	Northern			Center			Southern		
Preference Criteria	**Farmer** (52)*	**Trader** (38)*	**Consumer** (91)*	**Farmer** (47)*	**Trader** (53)*	**Consumer** (56)*	**Farmer** (14)*	**Trader** (16)*	**Consumer** (42)*
	%	**%**	**%**	**%**	**%**	**%**	**%**	**%**	**%**
Eye depth									
Shallow eyes	29	3	5	17	2	4	7	0	10
Mean depth of eyes	0	3	1	0	0	0	29	19	0
Indifferent	*71*	*94*	*94*	*83*	*98*	*96*	*64*	*81*	*90*
Shape									
Round Shape	38	0	8	43	0	0	50	50	17
Long Shape	2	3	1	0	2	2	0	0	7
Other Shape	4	8	3	2	0	0	0	0	0
Indifferent	*56*	*89*	*88*	*55*	*98*	*98*	*50*	*50*	*76*
Skin color									
Pink skin	23	11	12	43	0	0	0	0	0
Red skin	29	18	22	0	23	14	0	0	0
Yellow skin	0	0	0	0	0	0	57	0	14
Indifferent	*48*	*71*	*66*	*57*	*77*	*86*	*43*	*100*	*86*
Flesh color									
White-cream flesh	12	18	12	0	0	0	0	0	0
Yellow flesh	23	34	53	57	40	29	79	50	55
Several	2	3	1	0	0	2	0	0	2
Indifferent	*63*	*45*	*34*	*43*	*60*	*69*	*21*	*50*	*43*
Tuber size									
Big Size	0	0	5	36	21	0	0	0	14
Mean size	0	0	23	0	0	36	0	0	0
Small Size	0	0	1	0	4	2	0	0	7
Indifferent	*100*	*100*	*71*	*64*	*75*	*62*	*100*	*100*	*79*
TOTAL	*29*	*21*	*50*	*30*	*34*	*36*	*19*	*22*	*58*

* Total number of respondents

Supplementary Table 3. Preference of farmers, traders and consumers in the Northern, Center and Southern Ecuador area for tuber processing characteristics, data expressed in percentage (%). Values calculated based on the total of respondents of each area per actor.

	Northern			Center			Southern		
	Farmer (52)*	**Trader** (38)*	**Consumer** (91)*	**Farmer** (47)*	**Trader** (53)*	**Consumer** (56)*	**Farmer** (14)*	**Trader** (16)*	**Consumer** (42)*
	%	**%**	**%**	**%**	**%**	**%**	**%**	**%**	**%**
Fast cooking	0	16	20	32	0	23	0	0	26
Waxy	0	0	11	0	21	25	0	0	29
Mealy	19	11	20	57	38	48	0	0	10
Indifferent	*81*	*73*	*49*	*11*	*41*	*4*	*100*	*100*	*35*
Tuber taste									
Good taste	33	13	48	26	19	23	43	38	69
Poor taste	2	0	1	11	0	2	7	0	0
Other taste	4	0	1	0	2	9	0	0	7
Indifferent	*61*	*87*	*50*	*63*	*79*	*66*	*50*	*62*	*24*
Cooking tuber uses									
For “locro” soup	0	0	3	0	0	0	0	0	31
Fried	2	3	3	0	0	5	0	0	2
Cooked	6	0	5	4	2	4	0	0	2
Several uses	2	21	9	0	0	2	7	0	17
Indifferent	*90*	*76*	*80*	*96*	*98*	*89*	*93*	*100*	*48*
TOTAL	*29*	*21*	*50*	*30*	*34*	*36*	*19*	*22*	*58*

* Total number of respondents

Preferences

Supplementary Table 4. Preference of farmers, traders and consumers in the Northern, Center and Southern Ecuador area for preferred varieties, data expressed in percentage (%). Values calculated based on the total of respondents of each area per actor.

	Northern			**Center**			**Southern**		
Preference Criteria	**Farmer** (52)*	**Trader** (38)*	**Consumer** (91)*	**Farmer** (47)*	**Trader** (53)*	**Consumer** (56)*	**Farmer** (14)*	**Traders** (16)*	**Consumers** (42)*
	%	**%**	**%**	**%**	**%**	**%**	**%**	**%**	**%**
Superchola	23	34	37	0	4	9	0	0	12
INIAP-Gabriela	0	0	4	30	38	11	7	0	5
INIAP-Cecilia	0	0	0	9	42	27	0	0	0
Bolona	0	0	0	0	0	0	58	81	38
INIAP-Fripapa	0	0	0	9	6	5	7	0	0
Unica	12	11	1	0	2	0	0	0	0
Capiro	2	8	3	0	0	0	0	0	0
Rosada	4	5	0	0	0	0	0	0	0
Violeta	6	8	0	0	0	0	0	0	0
Roja	6	5	12	0	0	0	0	0	0
Limeña	0	0	0	6	0	0	0	0	0
Leona negra	0	0	0	9	4	4	0	0	0
Chaucha amarilla	0	0	4	0	0	0	14	13	10
Jubaleña	0	0	0	0	0	0	14	6	2
Uvilla	0	0	0	0	0	4	0	0	0
Indifferent	*47*	*29*	*49*	*37*	*4*	*40*	*0*	*0*	*33*
Preference for new varieties (Yes)	0	29	21	13	2	13	21	19	33
(No)	*100*	*71*	*79*	*87*	*98*	*88*	*79*	*81*	*67*
TOTAL	*29*	*21*	*50*	*30*	*34*	*36*	*19*	*22*	*58*

* Total number of respondents

Annex 1. Area, production and percentage of potato cultivated between 2002-2006 in three Ecuadorian Highland regions.

	Hectares	%	tons	%	$t.ha^{-1}$
North	**11166**	**26**	**134589**	**33**	**12.1**
Carchi	7030	16	90743	22	12.9
Pichincha	4136	10	43846	11	10.6
Center	**22121**	**51**	**193130**	**48**	**8.7**
Cotopaxi	5740	13	56213	14	9.8
Tungurahua	6959	16	63532	16	9.1
Chimborazo	9422	22	73385	18	7.8
South	**4533**	**11**	**35950**	**8**	**7.9**
Cañar	2127	5	18267	4	8.6
Azuay	2406	6	17683	4	7.3
Others	**5513**	**12**	**46102**	**11**	**8.4**
TOTAL	**43333**	**100**	**409771**	**100**	**9.5**

(Devaux et al., 2010) From III National Agri-cultural Census

Annex 2. Correspondence analysis for preferences of potato in three Ecuadorian areas

Correspondence analysis

In the Northern area the correspondence analysis per preference criteria shows that tuber yellow flesh color, Superchola variety and good taste were the criteria more mentioned by the actors in the chain, this is represented for the mass values 11.1%, 9.0% and 8.3%. Moreover, referring to the total variation represented by the inertia, the criteria late blight and high production had the highest values 7.9% and 6.7% (Annex 2.2).

The analysis per actor in the chain, established that consumers had the largest number of associations with preference criteria, it is expressed by the mass value of 44.5%, traders had the lowest number of associations 17.6%. Besides this, farmers accounted with the highest value 37.9% for the total variation (inertia), compared to traders that represented 17.6% (Annex 2.3).

In the Central region the analysis per preference criteria, showed that tuber mealy texture, tuber yellow flesh color, and good taste had the highest values for mass, which means that they had the largest number of associations with the chain actors, 12.5%, 10.8% and 9.1%, respectively. Moreover, referring to the total variation represented by the inertia, tuber mean size, tuber red skin and late blight resistance had the highest values of inertia 11.1%, 7.2% and 6.0% (Annex 2.5).

In the correspondence analysis per chain actor, farmers had the largest number of associations with the preference criteria, which is expressed in the mass value 44.9%. Consumers had the lower number of associations (23.2%). Besides, consumers accounted with the highest value 27.9% for the total inertia compared to traders 18.7% (Annex 2.6).

In the South consumers had the largest number of associations with preference criteria, which is shown by the mass value of 49.7%, and traders had the lowest number of associations (13.3%). Farmers accounted for the highest value (30.1%) of the total inertia compared to traders that represented 13.2% (Annex 2.8).

The correspondence analysis per preference criteria showed that tuber yellow flesh, good taste and round shape traits had the largest number of associations with the actors in the chain 16.9%, 11.6% and 8.8%, respectively. Referring to the total variation represented by inertia, the criteria marketable potatoes, late blight resistance and earliness had the largest number of association with the chain actors 7.6%, 7.5% and 5.7% respectively (Annex 2.9).

Annex 2.1. Summary of the correspondence analysis for the Northern Ecuadorian area (a).

					Proportion of Inertia		Confidence Singular Value	
								Correlation
Dim	Sing value	Inertia	Chi Square	Sig.	Accounted for	Cumulative	Standard Deviation	2
1	0.665	0.442			0.692	0.692	0.021	-0.084
2	0.443	0.197			0.308	1.000	0.034	
Total		0.631	420.597	0.000a	1.000	1.000		

a. 44 degrees of freedom

Annex 2.2. Correspondence analysis row points for the preference study in the North area of Ecuadorian highlands (a).

Criteria	Mass	Score in Dimension		Inertia	Contribution				
					Of Point to Inertia		Of Dimension to Inertia of		
		1	2		1	2	1	2	Total
Late blight	0.049	-1.492	-0.593	0.079	0.163	0.039	0.905	0.095	1
Earliness	0.017	-1.492	-0.593	0.027	0.056	0.013	0.905	0.095	1
High	0.041	-1.492	-0.593	0.067	0.137	0.033	0.905	0.095	1
Plant size	0.014	-1.492	-0.593	0.022	0.046	0.011	0.905	0.095	1
Healthy seed	0.020	-0.609	1.473	0.024	0.011	0.097	0.204	0.796	1
Marketable	0.035	-0.993	0.575	0.028	0.052	0.026	0.817	0.183	1
Fast cooking	0.036	0.948	0.227	0.023	0.049	0.004	0.963	0.037	1
Round shape	0.041	-0.791	-0.641	0.024	0.039	0.038	0.695	0.305	1
Shallow eyes	0.023	-1.492	-0.593	0.037	0.076	0.018	0.905	0.095	1
P skin	0.041	-0.146	-0.100	0.001	0.001	0.001	0.762	0.238	1
R skin	0.064	0.070	-0.042	0.000	0.000	0.000	0.809	0.191	1
W-C flesh	0.036	0.227	0.441	0.004	0.003	0.016	0.284	0.716	1
Y flesh	0.111	0.580	-0.032	0.025	0.056	0.000	0.998	0.002	1
Mean size	0.032	1.215	-0.778	0.040	0.071	0.044	0.785	0.215	1
Big size	0.008	1.215	-0.778	0.009	0.017	0.010	0.785	0.215	1
Waxy	0.015	1.215	-0.778	0.019	0.034	0.021	0.785	0.215	1
Mealy	0.052	0.293	-0.251	0.004	0.007	0.007	0.672	0.328	1
Other	0.017	1.215	-0.778	0.021	0.037	0.023	0.785	0.215	1
Good taste	0.083	0.378	-0.721	0.027	0.018	0.098	0.292	0.708	1
Gabriela	0.006	1.215	-0.778	0.008	0.013	0.008	0.785	0.215	1
Other var	0.046	0.824	0.697	0.030	0.046	0.050	0.677	0.323	1
Super	0.090	0.429	0.146	0.012	0.025	0.004	0.929	0.071	1
Unica	0.036	-0.628	1.158	0.031	0.022	0.110	0.306	0.694	1
Capiro	0.020	0.142	1.725	0.026	0.001	0.132	0.010	0.990	1
Violeta	0.021	-0.555	1.600	0.028	0.01	0.123	0.153	0.847	1
Rosada	0.014	-0.581	1.539	0.017	0.007	0.073	0.176	0.824	1
Roja	0.035	0.277	0.144	0.002	0.004	0.002	0.846	0.154	1
Active Total	1.000			0.638	1.000	1.000			

a. Symmetrical normalization

Annex 2.3. Correspondence analysis column points for the preference study in the North area of Ecuadorian highlands (a).

Actor	Mass	Score in		Inertia	Contribution				
					Of Point to Inertia of		Of Dimension to Inertia of		
		1	2		1	2	1	2	Total
Farmer	0.379	-0.992	-0.263	0.260	0.561	0.059	0.955	0.045	0.379
Trader	0.176	0.098	1.438	0.163	0.003	0.821	0.007	0.993	0.176
Consumer	0.445	0.807	-0.345	0.216	0.436	0.119	0.891	0.109	0.445
Active Total	1.000			0.638	1.000	1.000			

a. Symmetrical normalization

Annex 2.4. Summary of the correspondence analysis for the Central Ecuadorian area (a).

Dim	Sing value	Inertia	Chi Square	Sig.	Proportion of Inertia: Accounted for	Proportion of Inertia: Cumulative	Confidence Singular Value: Standard Deviation	Confidence Singular Value: Correlation 2
1	0.677	0.458			0.694	0.694	0.020	-0.068
2	0.450	0.202			0.306	1.000	0.034	
Total		0.660	446.837	0.000a	1.000	1.000		

a. 40 degrees of freedom

Annex 2.5. Correspondence analysis row points for the preference study in the Center area of Ecuadorian highlands (a).

Criteria	Mass	Score in Dimension		Inertia	Contribution				
					Of Point to Inertia		Of Dimension to Inertia of		
		1	2		1	2	1	2	Total
Late blight	0.049	1.277	-0.534	0.060	0.120	0.027	0.882	0.118	1.000
Earliness	0.020	1.277	-0.534	0.025	0.050	0.011	0.882	0.118	1.000
High production	0.032	1.277	-0.534	0.039	0.079	0.018	0.882	0.118	1.000
Healthy tubers	0.022	-0.556	1.955	0.047	0.010	0.165	0.095	0.905	1.000
Marketable potato	0.077	0.520	0.494	0.023	0.032	0.037	0.591	0.409	1.000
Fast cooking	0.047	0.426	0.621	0.015	0.013	0.036	0.380	0.620	1.000
Round shape	0.034	1.277	-0.534	0.041	0.083	0.019	0.882	0.118	1.000
Shallow eyes	0.020	1.277	-0.534	0.025	0.050	0.011	0.882	0.118	1.000
Pink skin	0.034	1.277	-0.534	0.041	0.083	0.019	0.882	0.118	1.000
Red skin	0.034	-0.556	1.955	0.072	0.016	0.254	0.095	0.905	1.000
Yellow flesh	0.108	-0.071	0.005	0.000	0.001	0.000	0.996	0.004	1.000
Mean size	0.034	-1.709	-1.643	0.111	0.149	0.179	0.586	0.414	1.000
Big size	0.047	0.557	0.443	0.014	0.022	0.018	0.673	0.327	1.000
Waxy	0.042	-1.202	-0.060	0.040	0.092	0.000	0.998	0.002	1.000
Mealy	0.125	-0.308	-0.266	0.012	0.018	0.017	0.636	0.364	1.000
Good taste	0.091	-0.372	-0.208	0.010	0.019	0.008	0.808	0.192	1.000
INIAP-Gabriela	0.067	-0.087	0.544	0.010	0.001	0.039	0.033	0.967	1.000
New varieties	0.024	-0.347	-0.911	0.012	0.004	0.039	0.159	0.841	1.000
Superchola	0.012	-1.380	-0.615	0.017	0.034	0.009	0.868	0.132	1.000
INIAP-Cecilia	0.069	-0.799	0.396	0.035	0.067	0.021	0.842	0.158	1.000
Active Total	1.000			0.696	1.000	1.000			

a. Symmetrical normalization

Annex 2.6. Correspondence analysis column points for the preference study in the Center area of Ecuadorian highlands (a).

Actor	Mass	Score in Dimension		Inertia	Contribution				
					Of Point to Inertia of		Of Dimension to Inertia of		
		1	2		1	2	1	2	Total
Farmer	0.449	0.846	-0.271	0.230	0.485	0.065	0.927	0.073	1.000
Trader	0.318	-0.368	0.992	0.187	0.065	0.617	0.152	0.848	1.000
Consumer	0.232	-1.132	-0.834	0.279	0.450	0.318	0.706	0.294	1.000
Active Total	1.000			0.696	1.000	1.000			

a. Symmetrical normalization

Annex 2.7. Summary of the correspondence analysis for the Southern Ecuadorian area (a).

					Proportion of Inertia		Confidence Singular Value	
								Correlation
Dim	Singular Value	Inertia	Chi Square	Sig.	Accounted for	Cumulative	Standard Deviation	2
1	0.647	0.418			0.767	0.767	0.031	0.244
2	0.357	0.127			0.233	1.000	0.046	
Total		0.546	146.764	0.000a	1.000	1.000		

a. 34 degrees of freedom

Annex 2.8. Correspondence analysis row points for the preference study in the South area of Ecuadorian highlands (a).

Criteria	Mass	Score in		Inertia	Contribution				
					Of Point to		Of Dimension to Inertia of Point		
		1	2		1	2	1	2	Total
Late blight	0.056	-1.295	0.253	0.062	0.145	0.010	0.979	0.021	1.000
Earliness	0.022	-1.625	-1.038	0.470	0.091	0.067	0.816	0.184	1.000
High production	0.030	-0.244	-0.782	0.008	0.003	0.051	0.150	0.850	1.000
Plant size	0.011	-1.625	-1.038	0.023	0.046	0.034	0.816	0.184	1.000
Marketable tubers	0.030	-1.625	-1.038	0.062	0.121	0.090	0.816	0.184	1.000
Fast cooking	0.041	1.137	-0.527	0.038	0.082	0.032	0.894	0.106	1.000
Round shape	0.082	-0.296	0.885	0.027	0.011	0.179	0.169	0.831	1.000
Shallow eyes	0.019	0.585	-0.629	0.007	0.010	0.021	0.610	0.390	1.000
Mean eyes	0.056	-1.378	-0.070	0.069	0.164	0.001	0.999	0.001	1.000
Yellow skin	0.052	-0.441	-0.819	0.019	0.016	0.098	0.345	0.655	1.000
Yellow flesh	0.156	0.123	0.164	0.003	0.004	0.012	0.506	0.494	1.000
Big size	0.022	1.137	-0.527	0.021	0.045	0.017	0.894	0.106	1.000
Mealy	0.015	1.137	-0.527	0.014	0.030	0.012	0.894	0.106	1.000
Waxy	0.045	1.137	-0.527	0.042	0.089	0.035	0.894	0.106	1.000
Indifferent	0.015	1.137	-0.527	0.014	0.030	0.012	0.894	0.106	1.000
Good taste	0.108	0.546	0.000	0.021	0.050	0.000	1.000	0.000	1.000
INIAP-Gabriela	0.011	0.216	-0.697	0.002	0.001	0.015	0.149	0.851	1.000
New varieties	0.074	0.494	0.046	0.012	0.028	0.000	0.995	0.005	1.000
Superchola	0.019	1.137	-0.527	0.017	0.037	0.014	0.894	0.106	1.000
Bolona	0.138	0.004	0.884	0.038	0.000	0.301	0.000	1.000	1.000
Mean	0.056	-1.378	-0.070	0.069	0.164	0.001	0.999	0.001	1.000
Active Total	1.000			0.564	1.000	1.00			

a. Symmetrical normalization

Annex 2.9. Correspondence analysis column points for the preference study in the South area of Ecuadorian highlands (a).

Actor	Mass	Score in Dimension		Inertia	Contribution				
					Of Point to Inertia of		Of Dimension to Inertia of		
		1	2		1	2	1	2	Total
Farmer	0.323	-1.051	-0.370	0.247	0.552	0.124	0.936	0.064	1.000
Trader	0.160	-0.251	1.357	0.112	0.016	0.825	0.058	0.942	1.000
Consumer	0.517	0.735	-0.188	0.187	0.432	0.051	0.965	0.035	1.000
Active Total	1.000			0.546	1.000	1.000			

a. Symmetrical normalization

Annex 3. Information about Education of the actors in the chain in three region expressed in percentage based on 409 respondents*

		No education	Incomplete Primary	Incomplete Secondary	Incomplete University	Complete primary	Complete Secondary	Complete University
Farmer	North	0.0	10.0	7.5	2.5	70.0	7.5	2.5
	Center	3.1	26.6	6.3	3.1	42.2	15.6	3.1
	South	9.1	24.2	15.2	0.0	36.4	15.2	0.0
Trader	North	0.0	0.0	5.6	0.0	61.1	33.3	0.0
	Center	10.7	25.0	7.1	7.1	32.1	10.7	7.1
	South	12.5	37.5	18.8	0.0	18.8	12.5	0.0
Consumer	North	0.0	0.0	14.8	25.9	7.4	33.3	18.5
	Center	0.0	14.3	5.7	17.1	17.1	5.7	40.0
	South	0.0	0.0	18.8	18.8	6.3	12.5	43.8

* Respondents have to choose one alternative in the survey, the higher education level that they have attended

Annex 4. Information about age of the actors in the chain of three regions expressed in percentage based on 409 respondents

	Age	<18	19-24	25-34	35-44	45-54	55-64	>65
Farmer	North	0.0	2.5	25.0	22.5	32.5	12.5	5.0
	Center	0.0	3.1	25.0	37.5	21.9	12.5	0.0
	South	3.0	6.1	3.0	18.2	24.2	27.3	18.2
Trader	North	0.0	0.0	10.5	36.8	31.6	10.5	10.5
	Center	0.0	7.4	11.1	40.7	3.7	22.2	14.8
	South	6.3	6.3	6.3	6.3	25.0	25.0	25.0
Consumer	North	0.0	11.1	14.8	11.1	33.3	25.9	3.7
	Center	0.0	2.9	37.1	20.0	17.1	14.3	8.6
	South	0.0	12.5	25.0	43.8	12.5	6.3	0.0

Annex 5. Effect of demographics on agronomic traits. Data expressed in percentage based on farmer preference.

		North		
Age	**Total***	**Yield**	**L.B. resistance**	**Earliness**
18	0	0	0	0
19-24	3	0	0	0
25-34	25	12	10	7
35-44	23	12	26	6
45-54	33	19	26	8
55-64	13	7	0	0
>65	5	2	0	0
Total	100	52	62	21
		Center		
18	0	0	0	0
19-24	3	1	4	6
25-34	25	9	25	3
35-44	38	16	21	6
45-54	22	8	4	9
55-64	13	6	8	3
>65	0	0	0	0
Total	100	40	62	26
		South		
18	2	1	0	0
19-24	5	0	0	0
25-34	7	3	0	9
35-44	21	8	21	17
45-54	30	9	32	0
55-64	21	6	21	9
>65	14	2	5	9
Total	100	29	79	43

* Total of respondents (%); L.B.= Late blight

Annex 6. Effect of demographics on tuber processing characteristics. Data expressed in percentage based on consumer preference.

		North		
Age	**Total***	**Fast cooking**	**Waxy consistence**	**Mealy consistence**
19-24	11	3	1	2
25-34	15	3	3	0
35-44	11	5	0	2
45-54	33	8	3	9
55-64	26	3	2	7
>65	4	0	1	0
Total	100	20	11	20
		Center		
19-24	3	2	0	3
25-34	37	6	10	13
35-44	20	8	5	13
45-54	17	2	5	11
55-64	14	4	5	5
>65	9	2	0	3
Total	100	23	25	48
South				
19-24	13	4	4	0
25-34	25	4	7	0
35-44	44	17	15	3
45-54	13	0	4	3
55-64	6	0	0	3
>65	0	0	0	0
Total	100	26	29	10

* Total of respondents (%)

ANNEX 7.

Survey

Date (dd/mm/yy)____________________ Pollster name:_______________________________

1. Nº survey

☐

2. Province:

- ☐ Carchi
- ☐ Pichincha
- ☐ Tungurahua
- ☐ Chimborazo
- ☐ Cotopaxi
- ☐ Azuay-Cañar

3. Canton____________________

4. Parish________________

5. Location/community name____________________________

6. Identification of the respondent

Name:____

7. Gender: Male☐ Female☐

8. Education (the highest level that you attended):

No education	☐		
Incomplete primary school	☐	Complete primary school	☐
Incomplete secondary school	☐	Complete secondary school	☐
Incomplete university	☐	Complete university	☐

9. Age:

< 18	☐	19-24	☐	25-34	☐	35-44	☐
45-54	☐	55-64	☐	> 65	☐		

10. ¿How many people live in your home?

Adult _____________ Children _____________

11. Which potato variety do you prefer?:
Súper Chola □ Gabriela □ Cecilia □ Fripapa □ Bolona □ Chaucha amarilla□

Other □ name? ________________________* (See Table 1)

12. **Would you like to test new potato varieties**? Yes □ No□

13. When the crop is still in the field which characteristic do you prefer?

High Production □
Late blight resistance □
Earliness □
Good plant size □
Healthy tubers □
Marketable potatoes □
Indifferent □

14. According to the tuber size do you prefer: (Only one option).
Small □ Mean □ Big □ Indifferent □

15. According to the shape, do you prefer: (Only one option).
Round□ Long□ Other□ Indifferent □

16. According to the eye depth do you prefer: (Only one option)
Shallow eyes □ mean eyes □ depth eyes □ Indifferent □

17. According to the tuber skin color, do you prefer: (Only one option).
White cream□ Yellow □ Pink□ Red□ Indifferent□

18. According to the tuber flesh color, do you prefer: (Only one option).
White cream □ Yellow□ Several□ Indifferent□

19. According to the tuber taste, do you prefer: (Only one option)
Good taste □ Poor taste □ Other taste □ Indifferent□

20. According to the tuber consistence do you prefer: (Only one option).
Fast cooking□ Waxy consistence□ Mealy consistence □ Indifferent□

21. According to the use of tuber potatoes do you prefer: (Only one option).
Soups/Locro□ Fries□ Mashed□ Salad □ Cooked□ Several□ Indifferent □

ANNEX 8

Figure 2. INIAP-Fripapa with shallow eyes

Figure 3. INIAP-Estela with medium eyes

Figure 4. Landrace Chaucha roja with deep eyes

Chapter 3

Variation of quality traits in Ecuadorian potato landraces

Variation of quality traits in Ecuadorian potato landraces

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Abstract

Ecuador is recognized as one of the centers of diversity for cultivated potatoes, variation that has been collected and conserved by INIAP. However, this variation has only been partially characterized and scarcely used in breeding for quality. We studied the variation of the main quality traits required for the fresh and processing market in a representative group of forty potato landraces from the Ecuadorian potato collection (EPC) in three locations of the Ecuadorian highlands and the possibility of use in breeding for quality.

For all traits evaluated, large variation was observed. Interaction effect genotype x environment was significant for most parameters, but was smaller than genotypic effect, except for total glycoalkaloid content for peeled potatoes. For some characters as greening and dormancy the estimated broad sense heritability (*H*) was high (0.76 and 0.86), therefore the selection response in a breeding scheme is likely to be greater. However, some traits were affected by the environment such as total glycoalkaloid content for peeled potatoes and yield ($H < 0.34$).

Total glycoalkaloid content in all potato landraces was lower than the upper limit considered safe for consumption (20 mg $100g^{-1}$ Fresh weigh). Besides this, most potato landraces suited the characteristics of dry matter and reducing sugar content demanded by the processing industry, while the white cream and yellow skinned potatoes showed low enzymatic discoloration compared with colored tubers.

Several potato landraces were identified as possible progenitors for use in breeding e.g. the landraces Leona blanca, Leona negra, Leona negra norte, Milagrosa, Uvilla, Chaucha amarilla and Chaucha pintada were outstanding with best characteristics for processing, while Uvilla, Leona blanca, Milagrosa, Puña, Jubaleña, Chaucha amarilla, Chaucha pintada and Bolona seemed best for use in the fresh market. This study provides useful information concerning the potential of the potato landraces to contribute to get the ideal potato for the fresh and processing market through direct use or through crop improvement for quality.

Key words: Quality traits, potato landraces, dry matter, reducing sugar, glycoalkaloids, greening, dormancy, enzymatic discoloration.

Introduction

The cultivated potato (*Solanum tuberosum* L.) is one of most nutritious crops that man currently grows (Sowokinos, 2007). Potato ranks first among vegetables in *per capita* consumption in many countries and produce more dry matter, protein and minerals per unit growing area compared with cereals (Ezekiel et al., 2012; Bamberg and Rio, 2011).

Potato landraces native to the Andes are extremely diverse ranging from diploids to pentaploids. This wide genetic diversity among potato landraces may show a considerable variability in quality traits (Andre et al., 2007).

Recent studies have shown that Andean landraces cover the largest part of the available genetic diversity of cultivated potato (Lefèvre et al., 2012). However, published data on the extent of variation with regard to quality traits within potato landraces is limited.

Despite its diversity, the improved potato varieties contain only a fraction of the potential biodiversity that is present in the Andean potato landraces (Bradshaw, 2007). For this reason, there is enormous capacity through breeding to improve quality traits in potato for the fresh and processing market using the diversity present in Andean potato landraces (Camire et al., 2009).

Ecuador has been recognized as important center of diversity for cultivated potatoes (Hawkes, 1990) and recently Monteros (2011), established a high allelic diversity among Ecuadorian potato landraces especially in the tetraploid varieties. These characteristics make Ecuadorian landraces an important genetic resource for use in a breeding programs and thus for the development of new potato varieties.

The potato breeding program of The National Agriculture Research Institute (INIAP) of Ecuador in order to generate new improved potato varieties, have a wide genetic variation represented by the potato Ecuadorian collection (EPC), it is composed of a core collection of sixty landraces with diploid, triploid and tetraploid genotypes highly diverse for shape, color and resistance to biotic and abiotic factors.

Some research has been done in characterization of morphological traits and late blight resistance. However, it is necessary to evaluate these landraces as potential sources of genes for improvement potato quality traits.

The objective of this study was to evaluate the variation of some tuber quality traits like tuber shape, eye depth, skin and flesh color, dry matter content (DMC), reducing sugar content (RSC), dormancy, greening, total glycoalkaloid content (TGA), enzymatic discoloration (ED) in forty potato landraces from the EPC, grown in three different environments and to identify superior landraces for direct use or as progenitors in breeding for the development of new potato varieties with the characteristics of quality required for the fresh and processing market.

Materials and methods

Plant material

Forty potato landraces from the (EPC) maintained at INIAP, were used for this study. The landraces were chosen to represent the range of tuber skin color, tuber flesh color and shape (Table 1 and Supplementary Table1).

The potato landraces were planted in a randomized complete block design with three replications, located in three sites of the Ecuadorian Highland between 2,850 to 3,000 meters altitude (Table 2). Each landrace was planted in two drill plots of ten tubers each spaced 30 cm apart; the distance between adjacent drills was 100 cm.

For reducing sugar and glycoalkaloid content (raw and peeled potatoes), twenty landraces that represent the morphological variation were chosen from location 1 and 2 based on the fresh tubers availability for the content analysis (Table 1). Landraces from location 3 were not included in the analysis of RSC, TGA and DMC because of the limited quantity of tubers available for analysis.

Different rates of fertilization were applied previous to the planting using the INIAPs recommendation (Annex 4) according to the chemical soil analysis that consisted of 100-250-80; 200-300-100 and 100-200-60 kg ha^{-1} of Nitrogen, Phosphorus and Potassium for location 1, 2 and 3 respectively. Most of the soils dedicated to potato in Ecuador are volcanic origin and in general 50% of the soils are low in Nitrogen and 80% are low in Phosphorus (Oyarzun et al., 2002).

For controlling late blight, five applications of fungicide for location 1, two for location 2 and four for location 3 were made exchanging between cymoxanil and dimethomorph. To avoid insects, the insecticides thiametoxam combined with lambdacihalotrina were used in rotation with profenofos, two sprays for location 1, four for location 2 and three for location 3.

Table 1. Potato landraces from the (EPC) to measure the variation of quality traits in three Ecuadorian locations and their morphological characteristics.

	Code*	Landrace	Shape	Eye depth	Skin color	Flesh color
1	HSO 146	Bolona**	Round	Medium	White -cream/Pink	Yellow(bright)
2	74p	Cacho blanco	Elongate	Shallow	White-cream	Cream
3	SOL 14	Calvache	Long-oblong	Protruding	Red	Yellow(bright)
4	ASO 802A	Carrizo**	Oblong	Deep	White-cream	Cream
5	HSO 453	Carrizo2**	Oblong	Medium	Purple/Cream	Cream/Purple
6	BOM 540	Chaucha **	Oblong	Shallow	Blackish	Cream/Purple
7	HSO 131	Chaucha amarilla**	Oblong	Medium	Orange	Yellow (intense)
8	HSO 377	Chaucha blanca	Compressed	Medium	Yellow	Cream/Purple
9	HSO 169	Chaucha negra**	Oblong	Medium	Purple	Cream/Purple
10	BOM 532	Chaucha n. camote	Eliptic	Shallow	Blackish/Cream	Cream/Purple
11	HSO 700	Chaucha pintada**	Long-oblong	Medium	Yellow	Yellow (bright)
12	HSO 369	Chaucha roja	Eliptic	Deep	Red	Yellow(intense)
13	HSO 198	Chaucha1	Oblong	Medium	Red-purple	Cream
14	HSO 213	Chaucha2	Oblong	Medium	White-Cream	Cream/Purple
15	JS 3	Coneja blanca	Long-oblong	Protruding	Yellow	White
16	HSO464	Coneja negra	Long-oblong	Medium	Blackish	Cream
17	HCS 570	Curipamba**	Oblong	Medium	Red/White-Cream	Cream
18	HX 201	Durazno	Eliptic	Deep	Orange	Yellow(intense)
19	HSO 197	Huagrasinga	Oblong	Medium	White-Cream/Purple	Cream/Purple
20	CHS 690	Hualcala**	Oblong	Medium	Red	Cream/Purple
21	HSO 272	Jubaleña	Oblong	Shallow	Red-purple/Yellow	Yellow
22	ASO 802	Leona**	Oblong	Medium	White-Cream	Cream/Purple
23	HSO 641	Leona negra**	Oblong	Shallow	Purple/Red	White/Cream
24	SOL 29	Leona n.norte**	Oblong	Shallow	Purple/Cream	Cream/Purple
25	SOL 6	Leona blanca**	Oblong	Shallow	Yellow	Yellow(bright)
26	PM 202	Macholulo	Long-oblong	Shallow	Purple	Cream
27	PM 203	Milagrosa**	Oblong	Shallow	Pink	Yellow
28	SOL 14	Moroponcho**	Long-oblong	Protruding	Red	Cream
29	115p	Norte roja**	Oblong	Deep	Purple	Cream
30	JS30	Osito**	Compressed	Medium	Purple-Cream	Cream/Purple
31	HSO 370	Puña	Round	Shallow	Red-purple	Cream
32	PM 204	Quillu	Compressed	Deep	Yellow	Yellow(intense)
33	HSO 165	Rosada **	Round	Shallow	Pink	Cream
34	PM 204	Sole negra	Long-oblong	Protruding	Blackish	Cream/Purple
35	PM 205	Sta. Rosa amarilla	Long-oblong	Deep	Yellow	Yellow(intense)
36	PM 206	Sta. Rosa blanca**	Eliptic	Medium	Yellow	Yellow(bright)
37	HSO 211	Suscaleña negra	Round	Medium	Purple-Cream	Cream
38	PM 200	Tushpa	Round	Medium	Blackish	White/Violet
39	BOM 549	Uvilla**	Round	Shallow	Yellow/Red	Yellow(bright)
40	HCS 581	Violeta	Oblong	Shallow	Yellow/Purple	White

***** INIAP-PNRT-papa codification
** Landraces chosen for glycoalkaloids and reducing sugar content analysis

Table 2. Environmental conditions of three locations to measure the variation of quality traits in Ecuadorian potato landraces.

	Location 1	Location 2	Location3
Province:	Cotopaxi	Tungurahua	Carchi
Canton:	Latacunga	Ambato	Huaca
Parish:	Alaquez	Cunchibamba	Mariscal Sucre
Place:	Simón Rodríguez	ITA-LAM	Guananguicho
Latitude:	$0^o42'47''$ S	$1^o1'30''$ S	0^o 36'29´´ N
Longitude:	$78^o26'25''$ W	$78^o35'27''$ W	77^o 76' 35´´W
Altitude (m)	2,850	3,000	2,945
Average temperature (^oC)	12.6	12.0	12.3
Rain fall (mm)	800	300	700
Humidity (%)	80	60	75
Available N (ppm)	58	10	60
Available P (ppm)	14	11	22
Available K (meq/100ml)	0.30	0.21	0.37

Morphological characterization

At harvest time for each landrace tuber shape, eye depth, skin and flesh color were assessed on five tubers of each plot.

Tuber shape was determined according to (Gómez, 2000), who described eight types of tuber shape, which were transformed into numerical scores from 1 to 8, where 1 = compressed, 2= round, 3=ovate, 4=obovate, 5= elliptic, 6=oblong, 7=long-oblong and 8=elongate.

Eye depth was scored using a 1-9 scale, where one means protruding eye and nine means very deep eye (Gómez, 2000).

Tuber skin color, was assessed visually according to a color card (Gómez, 2000), from 1–9 scale, where 1= white-cream, 2= yellow, 3=orange, 4=brown, 5=pink, 6=red, 7=red-purple, 8=purple and 9= blackish.

Tuber flesh color, was evaluated visually using the color card (Gómez, 2000), from 1–8, where 1=white, 2=cream, 3=yellow (bright), 4=yellow, 5=yellow (intense), 6=red, 7=purple, 8=violet.

Tuber Yield

All plants of the plot of each landrace were harvested and the yield of each plot per replicate was expressed in kg plant^{-1}.

Tuber Greening

After harvest, a sample of ten tubers were placed on trays and exposed to natural light. Tuber greening was evaluated weekly using the scale proposed by (Grunenfelder et al., 2006a). This scale ranges from 0 to 9 for cream/yellow potatoes and from 0 to 7 for colored potatoes, (0, no greening; 7 or 9, maximum greening). Tuber greening was considered when potatoes reached to the score 5 for cream/yellow potatoes and 6 for colored tubers, for the analysis the results were expressed in days after harvest.

Tuber Dormancy

For tuber dormancy a sample of ten fresh tubers from the field were placed on trays and stored in the potato warehouse at room temperature 7- 9^{o}C. Tuber dormancy was evaluated weekly, the length of dormancy was determined as the average number of days required for 2-mm-long sprouts to be evident for each variety (Freyre et al., 1994).

Enzymatic discoloration

For the measurement of the enzymatic discoloration (ED) a random sample of three tubers per landrace from each treatment and location of the field experiment was peeled, grated, and exposed to air in a small Petri dishes at room temperature. The degree of discoloration was measured after 30 min (ED1) and after 180 min (ED2). Based on the observed discoloration, using an ordinal scale in nine different classes (0-8), ranging from no discoloration at all to completely brown/black (Werij et al., 2007).

Tuber content analysis

Total glycoalkaloid content

At harvest 3-4 tubers, each weighing 20-30 g were selected from each treatment from the field experiment, whole tubers were ground, freeze-dried, and stored at -20 ^{o}C under nitrogen prior to extraction and analysis. For each landrace the sample was extracted in duplicate.

The total glycoalkaloid content (TGA) was measured according to the method reported by (Hellenäs, 1986). Briefly, pure α-solanine and α-chaconine were obtained from Sigma Chemical Co. (St. Louis, MO). All quantitative determinations were based on comparison with pure α-solanine, aliquots of a stock solution in methanol (1 mg ml^{-1}) were pipetted into centrifuge tubes and the methanol was evaporated under a stream of nitrogen. For the colorimetric quantification glycoalkaloid pellets or standards were dissolved in 0.3 ml 10% ortho-phosphoric acid/ethanol, 1:1 (by vol), by sonication in an ultrasonic cleaner. Fresh Clarke's reagent (3ml) [50 mg paraformaldehyde dissolved in 100ml H_3P0_4 (85% by vol)] was added and the contents were mixed carefully on a Vortex mixer. After 60 min at ambient temperature the optical densities were recorded at 408 *n*m. TGA content was determined by reference to standard curve of α-solanine (50 - 400 μg). Results were calculated as total glycoalkaloids (TGA), expressed as mg TGA $100g^{-1}$ fresh weight (FW).

Reducing sugars content

Potato tubers for reducing sugar content (RSC) measurement were harvested and stored at a temperature between 7 – 9 ^{o}C for one month. After cold storage, three to four random tubers of each landrace were sent to INIAP´s Nutrition laboratory for analysis. Reducing sugar content (RSC) was measured according to (Cronin and Smith, 1979). The fresh sample was treated with ethyl alcohol at 5%, picric acid was used to react with reducing sugars, making a mixed sample of (picric acid + sugars) of intense color, an aliquot of the sample extract was taken for spectrophotometric determination at 510 *n*m using a spectrophotometer Shimadzu UV-VIS 2201 (Shimadzu Corp., Kyoto, Japan). Results were expressed as percentage of fresh weight (FW).

Dry matter content

The total dry matter content (DMC) was calculated according to Bonierbale.,(2007). Five tubers of each treatment were chopped (about 500 g total) into small 1-2 cm cubes. They were mixed thoroughly and two sub-samples of 200 g each were taken. The exact weight of each sub-sample was recorded as fresh weight. Subsequently, each sub-sample was placed in an open container and set in an oven at 80^{o}C for 72 hours or until constant dry weight was reached. Each subsample was weighed immediately and recorded as dry weight. The dry matter content for each sub-sample was estimated with the following formula: dry matter = (dry weight / fresh weight) x 100.

Statistical analysis

To measure the variability of the different quality traits among landraces, simple analysis of variance (ANOVA) considering a randomized complete design with three replications was performed for each site, and genotypic means were compared by Tukey´s test at ($P<0.05$).

The effect of environment (Cotopaxi, Tungurahua and Carchi) and the genotype x environment interaction (GxE) were analyzed by combined ANOVA considering genotypes as fixed and locations as random effects.

The effects of peeling tubers on the glycoalkaloid content were analyzed by ANOVA considering the genotypes as random effects and the raw and the peeled tubers as fixed effects and means were compared by Tukey´s test at ($P<0.05$). All statistical tests were performed using SPSS version 18 (PASW Inc, 2010).

Prior to the analysis of variance the data was tested for normality using Shapiro Wilk test in their respective lineal model. The data for greening and dormancy were transformed to the natural logarithm (Ln) and the reducing sugar content information was transformed to (Ln+1) and subsequently subjected to analyses of variance. Whereas, the Enzymatic discoloration (ED) was transformed using the root square previous the analysis.

Broad-sense heritability (*H*) was estimated as the ratio of the genotypic (σ^2_G) to total phenotypic variance, $H = (\sigma^2_G / ((\sigma^2_{error}/re)+(\sigma^2_{GxE}/e)+\sigma^2_G)$(Holland et al., 2010), where r=number of replications and e=number of environments.

Results

Tuber Yield

The average tuber yield in kg plant^{-1} of potato landraces grown in Cotopaxi, Tungurahua and Carchi are shown in Supplementary Table 2. The yield per plant observed in the landraces grown in Cotopaxi, Tungurahua and Carchi ranged from 0.29 to 1.28 kg plant^{-1}, from 0.05 to 0.74 kg plant^{-1} and from 0.17 to 0.83 kg plant^{-1} respectively.

In Cotopaxi the landraces Osito2, Chaucha, Chaucha amarilla, Milagrosa, Violeta, Hualcala and Chaucha2 had the highest yield between 1.10 and 1.28 kg plant^{-1}, whereas the landraces Sole negra, Uvilla and Coneja negra showed the lowest yield (<0.35 kg plant^{-1}) (Supplementary Table 2).

In Tungurahua the landraces Milagrosa, Sta Rosa amarilla, Chaucha roja, Chaucha negra and Rosada had the highest yield ranging from 0.61 to 0.74 kg plant^{-1} and the landraces Sole negra, Uvilla, Suscaleña negra and Coneja blanca showed the lowest yield (<0.2 kg plant^{-1}) (Supplementary Table 2).

For Carchi, the landraces Chaucha negra and Milagrosa showed the highest yield (0.83 and 0.80 kg plant^{-1}) respectively. While, the landraces Puña, Coneja negra and Leona blanca had the lowest yield (<0.2 kg plant^{-1}) (Supplementary Table 2).

Combined analysis of variance of yield for 40 potato landraces grown in three locations (Cotopaxi, Tungurahua and Carchi) revealed significant effects due to genotype x environment (GxE) interactions (p<0.01) (Annex 1). Although the GxE significantly affects the yield values, the influence of genotype on yield was by far more important, the contribution of the Genotype (34.09%) to the variance was higher than that of the GxE interaction (26.1%) (Annex 1).

The landraces, Milagrosa, Osito 2, Chaucha, Chaucha pintada, Tushpa, Hualcala and Chaucha blanca had the highest overall yield with a range from 0.73 to 0.88 kg plant^{-1}, and the landraces Sole negra, Uvilla, Coneja negra and Puña had the lowest yield with a variation from 0.26 to 0.30 kg plant^{-1} (Supplementary Table 2).

Despite the different performance of most of landraces across locations, there was a tendency toward higher yield in Cotopaxi than Tungurahua and Carchi and the estimated broad sense heritability was 0.34.

Tuber greening and dormancy

The greening and dormancy information of potato landraces grown in Cotopaxi, Tungurahua and Carchi are shown in (Supplementary Table 3). The landrace Sta. Rosa amarilla had the lowest greening days for Cotopaxi, Tungurahua and Carchi with values of 26, 35 and 26 days respectively. In Cotopaxi the landrace Macholulo and Coneja negra had highest greening value (119 days), whereas Hualcala had the highest value in Tungurahua (110 days) and Sole negra showed the highest greening in Carchi (119 days) (Supplementary Table 3).

For dormancy in Cotopaxi, the landraces Durazno, Chaucha amarilla, Osito and Chaucha roja showed the lowest value (14 days), in Tungurahua this was Durazno (4 days) and in Carchi the landraces Chaucha amarilla and Chaucha blanca (4 days). The landraces Milagrosa and Moroponcho had the highest dormancy (112 days) in Cotopaxi and in Tungurahua while in Carchi the landrace Coneja negra showed the highest dormancy days (105 days) (Supplementary Table 3).

Analysis of variance for greening and dormancy of the potato landraces grown in three locations (Cotopaxi, Tungurahua and Carchi) established significant effects due to GxE interactions (p<0.01) (Annex 1). However, the contribution of the genotype to the variance was higher than that of the GxE interaction according to the variance component distribution analysis. The GxE interaction effect accounted for only 9 % of total variation compared with the genotype main effect that contributed 89 % of total variation (Annex 1).

For greening the landraces Sta. Rosa blanca, Quillu, Sta. Rosa amarilla, Suscaleña negra, Durazno and Leona blanca showed the lowest greening days across environments ranging from 29 to 51 days, whereas the landraces Sole negra, Coneja negra and Tushpa showed the highest greening values across locations ranging between 106 and 114 days (Supplementary Table 3).

For tuber dormancy, the landraces Durazno, Chaucha amarilla, Chaucha roja and Chaucha blanca showed the lowest values across locations with a variation from 8 to 10 days; while the landraces with the highest values in all environments were Coneja negra, Tushpa and Moroponcho having a variation from 103 to 107 days (Supplementary Table 3). The estimates of broad sense heritability were 0.76 and 0.86 for greening and dormancy respectively.

Total glycoalkaloid content

The total glycoalkaloid content of 20 landraces for raw and peeled tubers was evaluated in two locations Cotopaxi and Tungurahua; results are shown in Figure 1. In Cotopaxi the landrace Leona blanca had the highest TGA for raw and peeled potatoes with contents of 11.40 and 2.70 mg TGA $100g^{-1}$ FW respectively. The landraces Norte roja and Hualcala had the lowest contents, (2.15-2.28 mg TGA $100g^{-1}$ FW) for raw potatoes and (0.91 - 1.48 mg TGA $100g^{-1}$ FW) for peeled potatoes respectively (Supplementary Table 5).

In Tungurahua the landraces Moroponcho, Sta. Rosa blanca, Uvilla, Leona blanca, Milagrosa and Leona negra had the highest TGA contents for raw and peeled potatoes with exception of Uvilla and Leona negra peeled. The values ranged from 7.56 to 12.10 mg TGA $100g^{-1}$ FW for raw potatoes and from 2.61 to 7.66 mg TGA $100g^{-1}$ FW for peeled potatoes.

The lowest values were for Leona, Carrizo and Chaucha pintada with values ranging from 2.35 to 2.96 mg TGA $100g^{-1}$ FW for raw potatoes, whereas the landraces Chaucha amarilla, Rosada, Carrizo Leona and Bolona had the lowest content with values ranging from 1.39 to 1.57 mg TGA $100g^{-1}$ FW for peeled potatoes. Significant ($p<0.01$) differences for TGA content between raw and peeled potatoes for all landraces in both locations were identified (Supplementary Table 5).

Combined analysis of variance for TGA concentration of the 20 potato landraces grown in two locations (Cotopaxi and Tungurahua) revealed significant effects due to GxE interactions ($p<0.01$) (Annex 3). Even if the influence of GxE interaction was significant, the genotype was the main responsible factor of this variability for raw potatoes. The contribution of the genotype (79%) to the variance was approximately four times higher than that of the GxE interaction (18%) (Annex 3).

For raw potatoes the landraces with highest overall contents were Moroponcho, Milagrosa, Leona blanca and Uvilla with TGA between 9.08 and 10.96 mg $100g^{-1}$ FW and the landraces with the lowest overall contents were Leona, Chaucha pintada, Carrizo, Hualcala, Leona negra norte and Norte roja, TGA content had a variation from 2.35 to 3.11 mg $100g^{-1}$ FW.

For peeled potatoes the highest overall contents were for Milagrosa, Leona blanca, Moroponcho and Sta. Rosa blanca, with TGA from 2.33 to 4.62 mg $100g^{-1}$ FW, whereas the landraces with the lowest overall contents were Leona, Carrizo and Hualcala with TGA ranged from 1.14 to 1.66 mg $100g^{-1}$FW (Supplementary Table 6). The broad sense heritability was 0.42 and 0.04 for raw and peeled potatoes respectively.

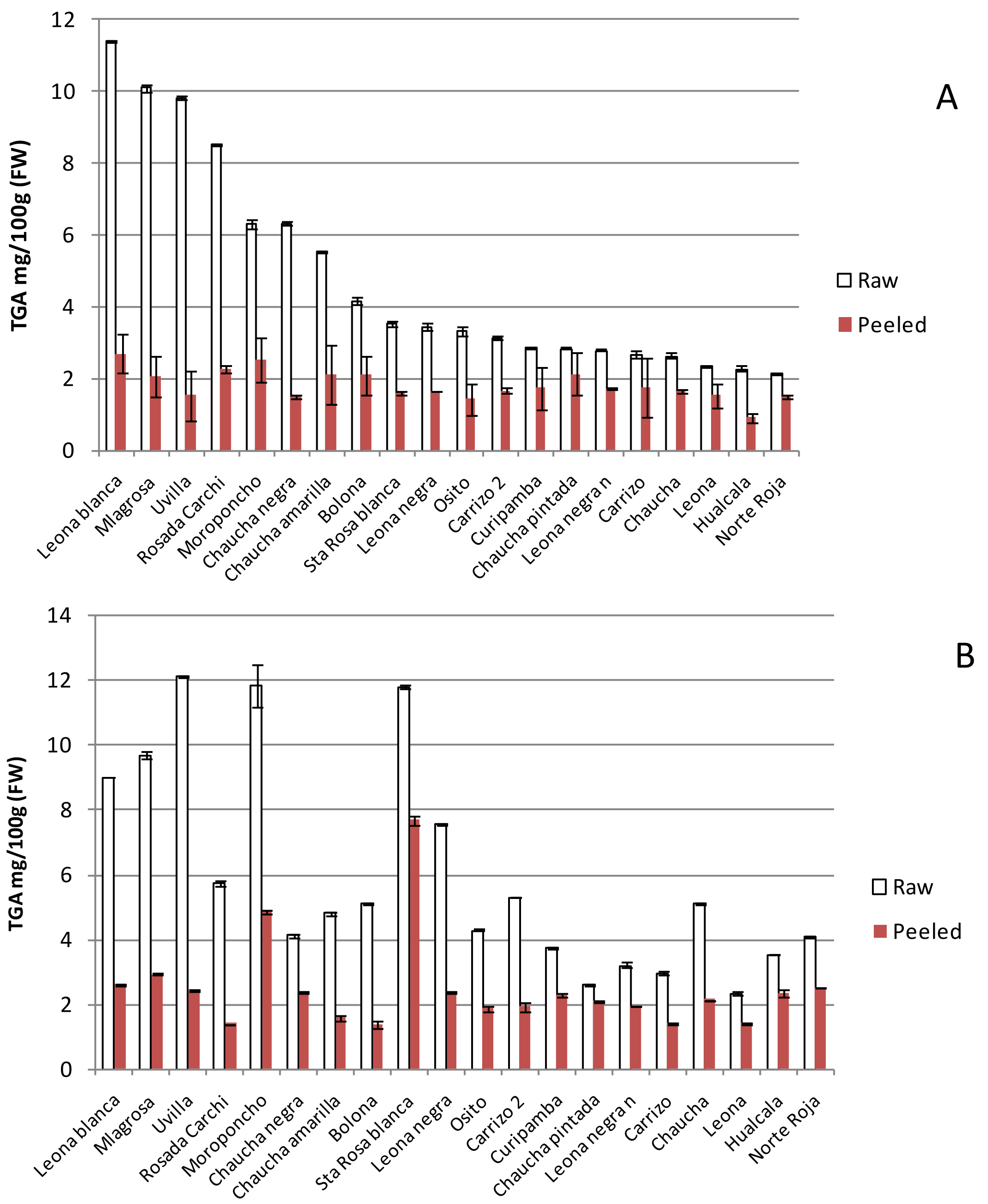

Figure 1. Total glycoalkaloids content for raw and peeled potatoes evaluated in Cotopaxi (A) and Tungurahua (B). Bars indicate mean TGA content (n=3) and standard deviation.

Reducing Sugar Content

Reducing sugar content had a range of variation from 0.01% to 0.44% FW and from 0.01% to 0.30% FW for Cotopaxi and Tungurahua respectively (Figure 2).

In Cotopaxi, the landraces Leona blanca Leona negra, Carrizo, Milagrosa, Carrizo 2, Uvilla, Chaucha, Bolona, Moroponcho, Norte roja had the lowest RSC with values from 0.01% to 0.07% FW, while the landraces Chaucha negra and Chaucha amarilla had the highest RSC from 0.37% to 0.44% FW. In Tungurahua, the landraces Chaucha pintada, Carrizo, Carrizo 2, and Curipamba had the lowest contents 0.01% FW, while the landraces Norte Roja and Sta. Rosa blanca had the highest RSC, with values from 0.17% to 0.30% FW (Supplementary Table 7).

Analysis of variance combined, established statistical differences at ($p<0.01$) for the G x E interaction. However, most of the variation for RSC was accounted for by genotype variation (64%) compared with GxE interaction (30%), (Annex 3). The variety Chaucha negra had the highest RSC 0.37% FW, while the variety Chaucha pintada had the lowest RSC 0.006% FW. The mean RSC for Cotopaxi and Tungurahua were 0.14% and 0.07% FW basis respectively (Supplementary Table 7).

The landrace Carrizo had the lowest overall RSC 0.015% FW and the landrace Chaucha negra showed the highest overall RSC 0.367% FW (Supplementary Table 7). The estimated broad sense heritability was 0.33.

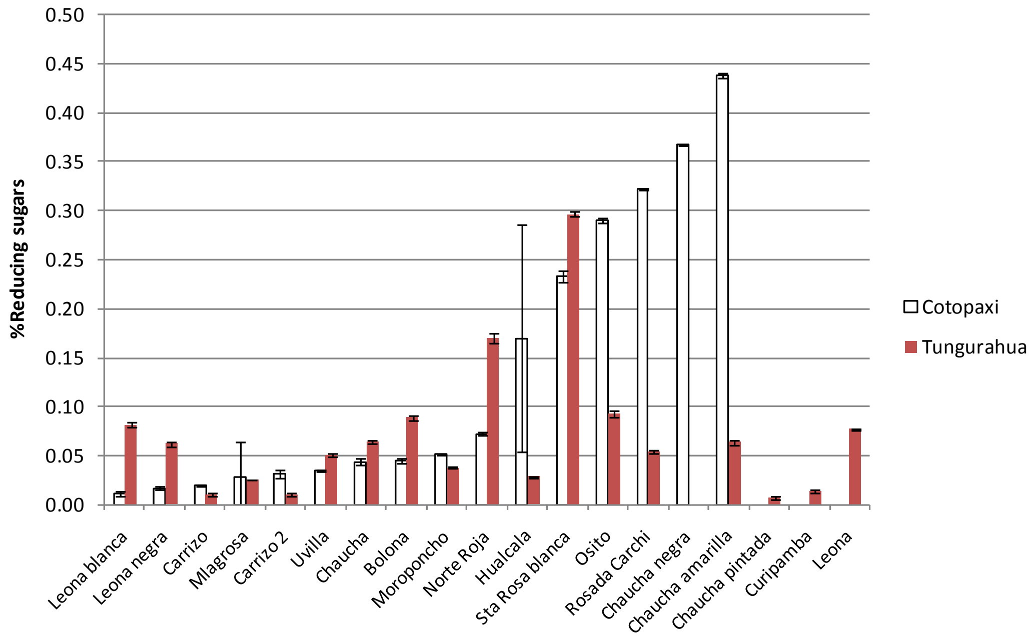

Figure 2. Reducing sugar content in potato landraces evaluated in two locations. Bars indicate mean Reducing sugar content (n=3) and standard deviation.

Dry matter content

The landrace with the lowest DMC in Cotopaxi was Violeta 18.1%, while the landrace Leona blanca had the highest DMC 23.6%. In Tungurahua the landraces Leona negra, had the highest content 24.9%, whereas, the landrace Violeta had the lowest 18.5% (Supplementary Table 8). ANOVA of DMC of potato landraces grown in two locations Cotopaxi and Tungurahua (Supplementary Table 6) revealed significant effects due GxE interactions ($p<0.01$).

In spite of the significant GxE interaction, this interaction accounted for a very small proportion (12%) of the total variation compared with the genotype (61%) (Annex 3).

The mean value of DMC proved to be different when the landraces of the two different locations were compared (Figure 3). A highest DMC was observed for most of the landraces cultivated in Tungurahua compared with the same landraces in Cotopaxi. The overall DMC mean had a variation from 18.3 to 24% for Violeta and Leona blanca respectively (Supplementary Table 8).

With the exception of Uvilla, Chaucha amarilla, Hualcala, Carrizo 2, Chaucha negra camote, Leona negra norte, which showed no differences in DMC across environments (Supplementary Table 8), three landraces (Leona blanca, Leona negra and Leona), showed highest DMC in the two environments with an average ranging from 23.3% to 24.0%. The estimated broad sense heritability was 0.64. In Tables 3 and 4 a summary of the landraces with the highest average yield, DMC, greening (among white/yellow cream skin potatoes), low RSC, ED, TGA, ED and long dormancy among *S. phureja* and short dormancy among *S. andigenum* potatoes are shown.

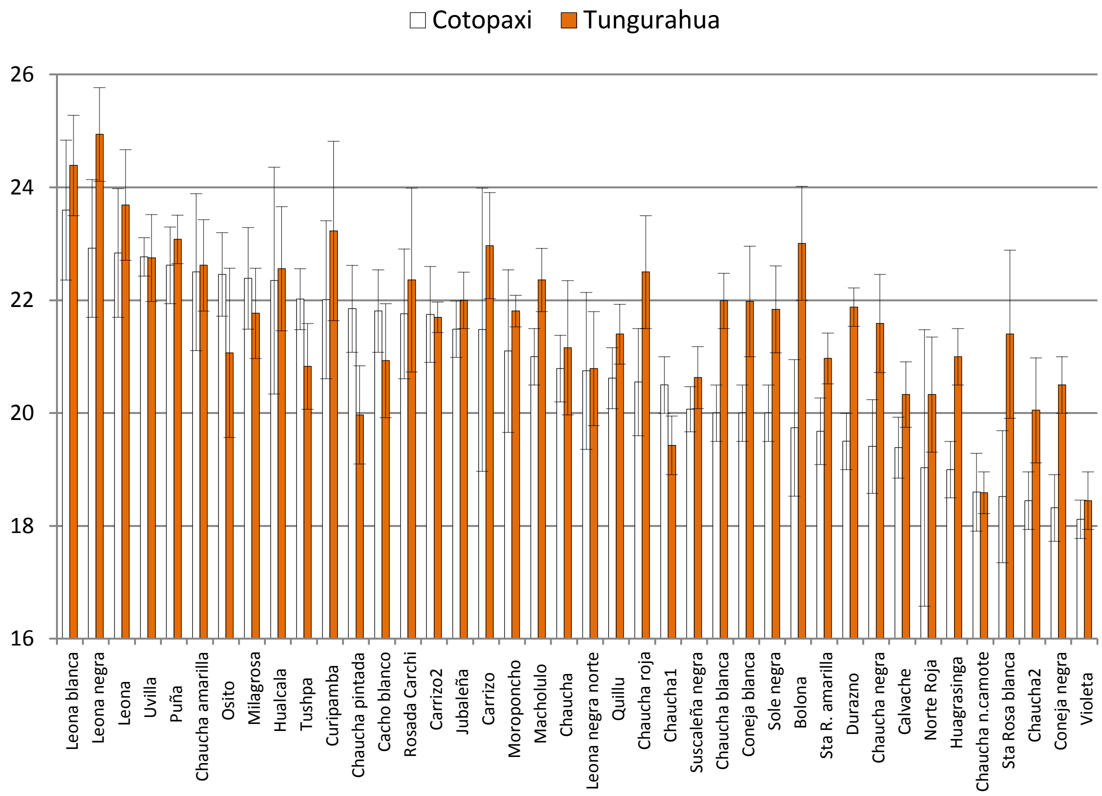

Figure 3. Dry matter content in potato landraces evaluated in two locations. Bars indicate mean DMC (n=3) and standard deviation

Enzymatic discoloration

The ED scores showed a large variation in the three locations, ranging from 1 to 4 at 30 min ED1 and from 1 to 7 at 180 min ED2, except for Tungurahua, where ED2 scores reached until 8 at 180 min (Figure 4).

The landrace Chaucha amarilla, Quillu, Durazno, Sta. Rosa blanca had the lowest values for ED at 30 and 180 min in all regions, while the landraces Chaucha, Suscaleña negra, Sole negra, Milagrosa and Cacho blanco had the highest scores (Supplementary Table 4).

Although combined analysis for ED in two locations (Cotopaxi and Tungurahua), established high significant effects due to the (GxE) interaction ($p<0.01$) (Annex 2), genotypic effect was greater than GxE interaction. The Genotype main effect contributed >53%, while the GxE interaction effect contributed <35% to total variation (Annex 2). The estimated broad sense heritability was 0.50 and 0.39 for ED1 and ED2 respectively.

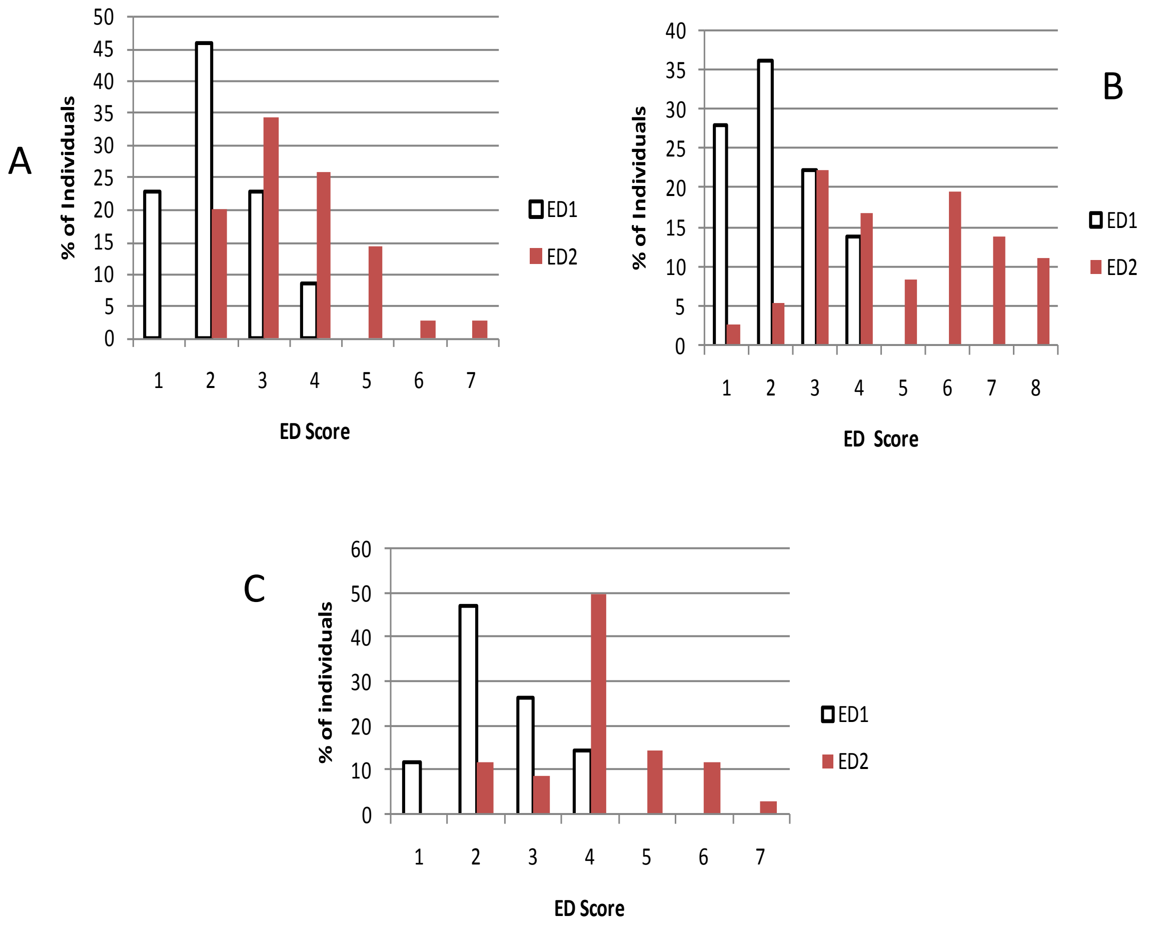

Figure 4. Distribution of Enzymatic Discoloration (ED) at two times of evaluation ED1 and ED2 in potato landraces grown in Cotopaxi (A), Tungurahua (B) and Carchi (C).

Morphological traits

The full range of tuber shape was observed from grade 1 (compressed) to grade 8 (elongate). Most of the landraces (45%) had oblong tuber shape (Figure 6a). Tuber eye depth had a variation from protruding (grade 1) to deep (grade 7), with most of the individuals (40%) with medium depth of eyes (Figure 6b).

Tuber skin color varied from white-cream (score 1) to blackish (score 9). Most of the landraces (23%) were yellow skinned (Figure 6c). Tuber flesh color had a variation from white (score 1) to yellow intense (score 5). Most of the clones (58%) had cream color (Figure 6d). In Figure 5 an overview of the morphological trait variation is shown.

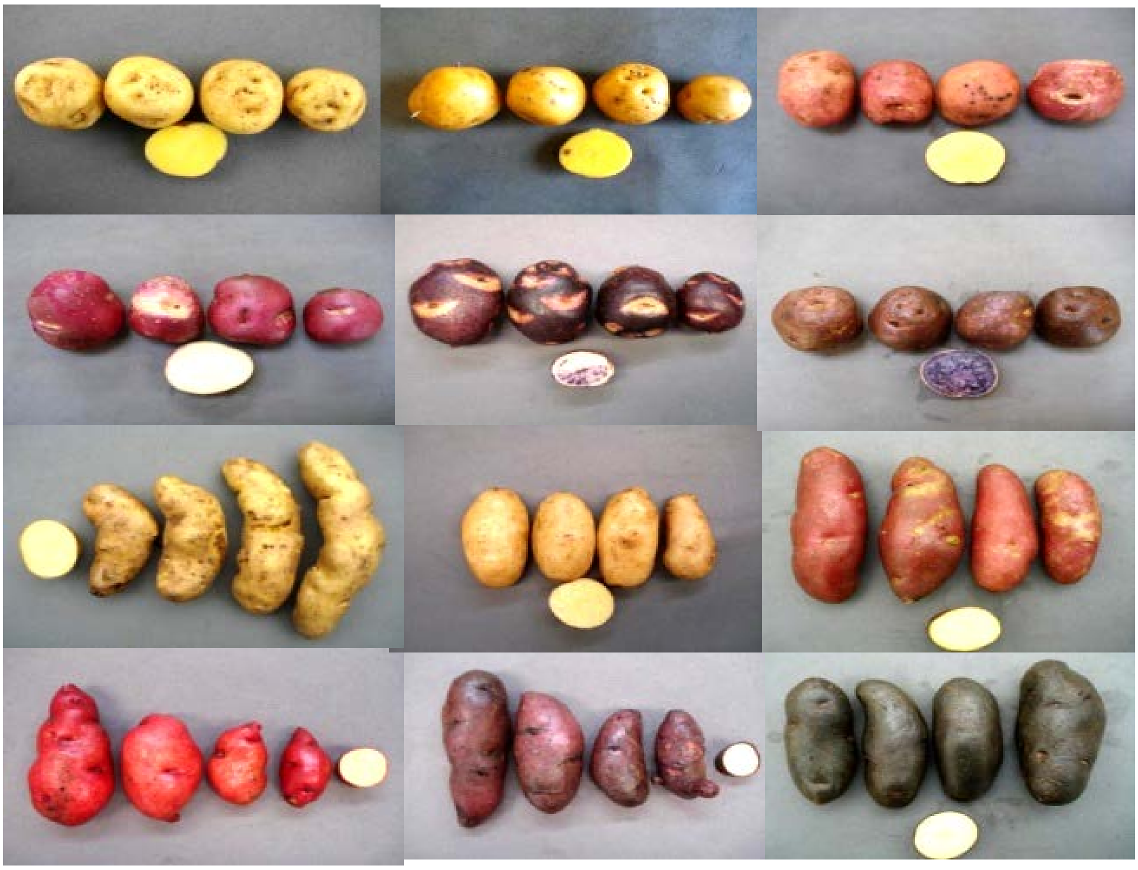

Figure 5. An overview of tuber shape, eye depth, skin and flesh color variation of potato landraces.

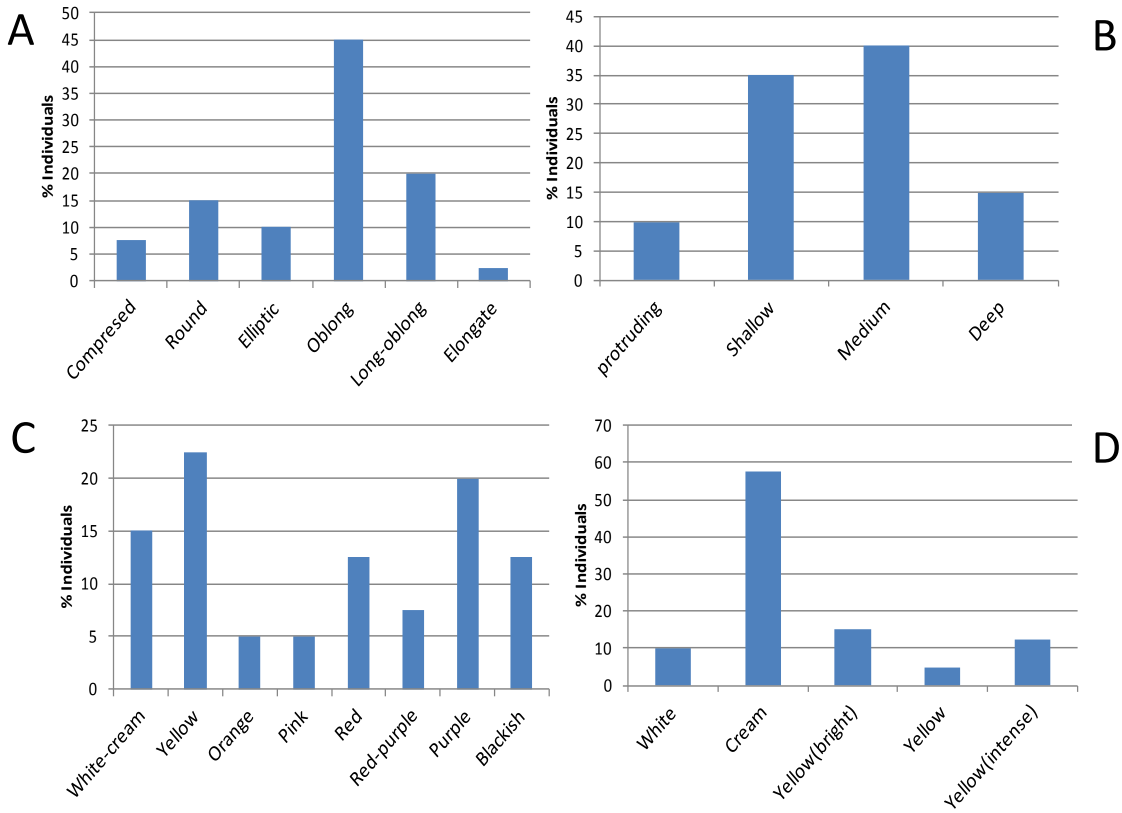

Figure 6. Distribution of tuber shape (A), eye depth (B), skin (C) and flesh color (D) in potato landraces.

Discussion

We studied the variation of most of quality parameters required for the fresh and processing market in a group of landraces from the EPC, where large variation for most of these traits was observed and for some characters as dormancy, greening and DMC, a large amount of the variation observed was genetic as the ANOVA and the estimate broad sense heritability established. This data can now be used by breeders to select for superior progenitors in the development of new improved varieties for the fresh and processing market. However, the level of yield was lower than the commercial varieties therefore other sources of genes should be included in the breeding scheme.

Quality traits for the fresh market

Consumers' requirements for the fresh market are often associated with the morphological features (shape, depth of eyes, skin and flesh color), together with greening, dormancy and taste. Furthermore these traits are also important for farmers and traders as we demonstrate in Chapter 2. These characters determine the acceptability of the tuber. However, for farmers agronomic traits as late blight resistance and yield are important to consider in the definition of the ideotype of potato for the fresh market.

Yield

High tuber yield is one of the most important selection criteria of the breeding scheme for the development of new potato varieties of INIAP and is also an important selection criterion for farmers (Chapter 2).

In our study the potato landraces showed a large variation for yield per plant, ranging from 0.05 to 1.28 kg plant^{-1}. However, most of the potatoes had lower yield compared to the improved Ecuadorian varieties and breeding clones of INIAP that produce on average yields between 0.7 and 2.0 kg plant^{-1} (Cuesta et al., 2005). The low yield obtained in the potato landraces was expected because the improved varieties arise from a selection procedure where one important criterion is high yield. Moreover, the potato landraces evaluated belong to the *S. andigenum* and *S. phureja*, species where yield potential is lower compared to the improved varieties that are hybrids mainly between *S. andigenum* and *S. tuberosum* (Cuesta et al., 2002), with a resulting heterosis effect affect that was also demonstrated by Mendoza and Haynes (1974) in progenies from crosses with *S. andigenum.*

Yield was significantly affected by the interaction GxE. The potato landraces evaluated in Cotopaxi had higher yield than Tungurahua and Carchi, this may be due to better environmental conditions especially water supply on this locality during the development of the crop; conditions that influenced the performance of the landraces.

The effect of water stress on potato development and productivity has been previously described. Loon, (1981) reports potato as a crop very sensitive to water stress compared to other species that may affect the potato plant at all developmental stages, resulting in decreased plant growth, tuber yield, number of tubers per plant, as well as tuber size and quality (Mackerron et al., 1988).

The estimated broad sense heritability was intermediate (0.34). This value is comparable to that from previous research, for example Mendoza (2008) reported heritability values between 0.14 and 0.61 for yield in Peruvian tetraploid potatoes and Gopal, et al., (1994) studying first generation potatoes estimated a heritability value of 0.33. However, is lower than the estimated reported by Yildirm and Caliskan, (1985), in eleven Turkish potato genotypes (0.87).

Hence, in the breeding scheme of INIAP for the development of new potato varieties with high yield, the more stable potato landraces across environments that had the highest yield as Milagrosa, Chaucha and Huagrasinga (Table 3) could be combined with breeding clones, improved varieties of INIAP or advanced genotypes from (CIP) with high yield.

Greening

In the Ecuadorian market, white-cream skinned tuber potato varieties are less preferred compared to red skin tubers (Chapter 2), the main reason is the susceptibility for greening of non-colored skin tubers. Storage practices have been developed to reduce greening (Reeves, 1988). However, breeding could be a better option to reduce this limitation (Sinden, 1971; Parfitt and Peloquin, 1981). Reeves (1988), reported polygenic inheritance for greening, making potato breeding an important approach toward selection of landraces with resistance to greening and it was also suggested that selection for low greening susceptibility is feasible with varietal differences with reasonably high heritability (Van Eck, 2007).

In our study the landraces showed large variation for this character, the blackish and red-skinned landraces exhibited less greening than the white-cream and yellow skinned potatoes. This relationship between colored potatoes and greening was reported by Reeves (1988) who studied a group of 144 North American improved varieties. This effect could be attributed to differences in periderm thickness, color and presence of accessory pigments, all of which interact to affect the degree of discoloration. The colored potatoes have pigments that may act as natural light filters, affecting the quality of the light penetrating the outer periderm (Grunenfelder et al., 2006b).

The variation observed for greening in this study was mainly due genetic factors since the contribution of the genotype to the total variance was higher than that of the GxE interaction.

Similar results were obtained by (Reeves, 1988; Parfitt and Peloquin, 1981) in American landraces and clones of breeding. This is supported by the estimated heritability value of 0.76 calculated in our study. This value is in the range of those reported by Parfit and Peloquin (1981), who estimated a value of 0.66 in clones from the Wisconsin breeding program.

From this it follows that the landraces less susceptible to greening among the white-cream skinned as Durazno, Sta. Rosa blanca, Sta. Rosa amarilla and Chaucha amarilla, among the *S. phureja* and Quillu, Leona blanca, Uvilla, Jubaleña, Coneja blanca, Cacho blanco, Chaucha blanca and Chaucha 2 among the *S. andigenum* are good alternatives for use in breeding as progenitors for the developing of new potato varieties with resistance to greening (Table 3).

Dormancy

The management of tuber dormancy is of great importance for the ware, pre packing and processing markets and also for the seed industry (Wiltshire and Cobb, 1996). In Ecuador short dormancy mainly affects the storage and marketability of the *S. phureja* potatoes as Chaucha amarilla one of the main potato landraces found in markets (Unda et al., 2005), but is also a difficulty in some improved varieties as INIAP-Natividad (Cuesta et al., 2007).

From our results the length of dormancy showed a large variation among potato landraces, genotypes with less than a week dormancy as Durazno, Chaucha amarilla and Chaucha roja that belong to the *S. phureja* group until landraces with long dormancy (>105 days) as Milagrosa, Moroponcho and Coneja negra all belonging to *S. andigenum*. The phureja group is characterized by short dormancy while long dormancy is generally found in genotypes from *andigenum* group (Estrada, 2000; Suttle, 2007).

Most of the variation observed was genetic; the contribution of the genotype to the total variance was higher than that of the GxE interaction, and the estimated broad sense heritability was established at 0.86, which is a value higher than previously reported by Thompson, (1980) who established a heritability of 0.57 in diploid populations. An alternative approach to increase the length of dormancy is through breeding, since tuber dormancy is under polygenic control (Simmonds, 1964) and more than three genes are involved (Freyre et al., 1994).

In our study suitable progenitors are available to increase dormancy in *S. phureja* landraces, such as Sta. Rosa blanca and Chaucha pintada with a dormancy period of about three to four weeks (Table 3), compared with other *S. phureja* landraces as Durazno with a dormancy period less than a week.

Glycoalkaloid content

An important character that affects the taste and safe consumption of potato for the fresh market is total glycoalkaloid content in tubers, which is an important criterion of selection in the potato-breeding scheme, since glycoalkaloids can be passed to progenies during breeding (Kozukue et al., 2008).

The TGA in raw potatoes had a variation from 2.15 to 12.10 mg 100 g^{-1} FW in the two locations, values that are in the same range as some previous reports. Knuthsen et al., (2009) in Danish varieties, found values of the TGA of raw tubers on a FW basis that ranged from 0.5 to 28.0 mg 100 g^{-1}. Sinden and Webb (1972) reported values from 1 to 35 mg 100 g^{-1} FW in five American varieties and one breeding clone.

Peeled potatoes had a variation of TGA content from 0.91 to 7.66 mg 100 g^{-1} FW in the two locations which are somewhat lower values than those reported by Friedman et al., (2003) who measured the TGA content in eight American varieties and found contents from 0.1 to 14.8 mg 100 g^{-1} FW.

In our study the process of peeling had a significant impact on lowering the content of glycoalkaloids in the tuber potato landraces. Peeling decreased TGA content in about 56% on average compared with the raw material. These results are in agreement with those previously found by (Friedman, 2003; Friedman, 2006; Jansen and Flamme, 2006). They established that the majority of glycoalkaloids in the potato tuber are located within the first 1 mm from the outside surface and decrease toward the center of the tuber.

Furthermore, the amount of TGA after peeling decreased by 36 – 79% compared with the raw material. These percentages are similar to those reported by (Tajner-Czopek et al., 2012) for colored potatoes.

This wide range of decreased can be explained by the differences in tuber shape and eye depth among potato landraces that affected the peeling process and the consequent volume of peeled skin. Moreover differences in the distribution of TGA content in the tuber have been reported (Friedman, 1997; Mondy and Gosselin, 1988) where the highest levels of TGA are located around the tuber eyes of the outer layer (Friedman, 2006) effect that contribute to the differences found between TGA for raw and peeled potatoes.

It is important that glycoalkaloids can be maintained at low levels in new commercials varieties, the limit established for safety consumption may not exceed 20 mg $100g^{-1}$ FW and levels higher than 14 mg 100 g^{-1} FW result in a bitter taste and disqualifies potatoes, especially those for human consumption (Friedman, 2006).

In our study, all the potato landraces evaluated had a TGA content lower than the upper limit considered toxic to human beings (Friedman, 2006; Sinden, 1984) and below the levels reported to affect quality (Friedman 2006; Ross, 1978; Sinden, 1976), thus the Ecuadorian potato landraces might be safely used directly for consumption, processing or in a potato breeding-scheme.

Despite the GxE interaction was significant for TGA for raw potatoes, the genotype was the main responsible factor of this variability, result that is agree with those reported by (Sanford and Sinden, 1972; Sinden and Webb 1972) in commercial potato varieties and breeding clones from United States.

The broad sense heritability for raw potatoes in our study had a value of 0.42, which is lower than previously reported by Sinden et al., (1984) and Sanford and Sinden (1972), who found a broad sense heritability ranging from 0.66 to 0.89 in breeding clones at Beltsville Maryland. However, our estimated heritability value was higher than those reported by Ross et al., (1978) who reported broad sense heritabilities around 0.25. For peeled potatoes the estimated broad sense heritability was very low 0.04, one reason for this might be because the peeling process was affected by tuber eye depth of some potato landraces.

Then the large genotypic variation that exists for TGA for raw potatoes together with the fact that the contribution of the genotype to the variance was significantly higher than that of the G x E interaction and of the environment means that through breeding we can select potato landraces and develop varieties with low levels of TGA. The potato landraces with the low levels across environments that could be selected for use in breeding are: Leona, Chaucha pintada, Carrizo, Hualcala and Leona negra norte with TGA lower than 3.00 mg 100 g^{-1} FW (Table 3).

This study identified large variation for tuber shape, eye depth, skin and flesh color, tuber yield, greening, dormancy and TGA for raw potatoes which are crucial aspects of selection for the fresh market (Storey, 2007; Werij, 2011). Most of the variation reported was genetic.

In Table 3 a summary of the landraces with best characteristics for the fresh market is presented, based on the results of this research is possible to select progenitors with the required characteristics for the fresh market and we expect a fast progress in breeding for those characters.

Based on these results the landraces Uvilla, Leona blanca, Milagrosa, Puña, Jubaleña, Chaucha pintada, Bolona and Chaucha amarilla could be used as possible progenitors into the breeding scheme.

Table 3. Summary of potato landraces with high yield kg ha^{-1}, long dormancy (days after harvest) in diploid potatoes and short dormancy in tetraploid potatoes, long greening (days after harvest) and low TGA for raw potatoes (mg 100g^{-1}).

2n	Landrace	Yield(1)	2n	Landrace	Dormancy(1)	2n	Landrace	Greening(1)	2n	Landrace	TGA(2)
4X	Milagrosa	0.88	2X	Sta. Rosa am.	15.6	2X	Sta. Rosa bl.	28.8	4X	Leona	2.35
4X	Chaucha	0.78	2X	Chaucha p.	18.4	4X	Quillu	37.3	2X	Chaucha p.	2.72
4X	Huagrasinga	0.78	2X	Sta. Rosa bl.	31.9	2X	Sta. Rosa am.	39.7	4X	Carrizo	2.82
2X	Ch. pintada	0.74				2X	Durazno	50.6	4X	Hualcala	2.91
4X	Tushpa	0.74	4X	Jubaleña	59.0	4X	Leona bl.	51.3	4X	Leona n.n.	3.00
4X	Hualcala	0.73	4X	Cacho bl.	59.5	4X	Uvilla	56.8	4X	Norte roja	3.11
4X	Ch. blanca	0.73	4X	Chaucha 1	70.0	4X	Jubaleña	59.1	4X	Curipamba	3.31
4X	Ch.negra	0.72	4X	Suscaleña n.	75.4	4X	Coneja bl.	63.0	4X	Osito	3.32
2X	Ch.amarilla	0.70	4X	Puña	76.2	2X	Ch. amarilla	66.1	4X	Chaucha	3.88
4X	Leona n.n.	0.69	4X	Quillu	78.6	4X	Cacho bl.	77.0	4X	Carrizo2	4.24
4X	Chaucha2	0.69	4X	Curipamba	81.7	4X	Chaucha bl.	78.6	4X	Bolona	4.64
4X	Osito	0.69	4X	Uvilla	82.4	4X	Chaucha2	91.0	2X	Ch.amarilla	5.18

(1) Mean based on 3 locations and 3 replicates; (2) Mean based on 2 locations and 3 replicates
Ch.=Chaucha; bl.= blanca; am.=amarilla; p. pintada; n.n.= negra norte

Quality traits for the processing market

For the processing market, tuber shape, eye depth, DMC, ED and RSC, are crucial traits that affect the product-manufacturing efficiency (Storey, 2007). Round tuber shape is preferred for crisps and long shape is ideal for French fries potatoes. Furthermore, shallow eyes are preferred in both cases (van Eck, 2007). But also important are yield, dormancy, greening and TGA traits that were discussed previously.

Dry matter content

Dry matter content and the level of sugar content in potato tubers are important factors that affect quality in potatoes (Storey, 2007). Despite dry matter content is strongly influenced by the environment (Laboski and Kelling, 2007), it is genetically controlled and selection of suitable varieties offers the best means of producing high DMC potatoes (Hughes, 1974).

In our study generally, lower DMC values were observed in Cotopaxi as compared to Tungurahua. Since the agronomic management of the GxE experiment was homogeneous, so principal sources of environmental variation was climate and water supply factors that probably affected the DMC. Vos and Haverkort, (2007) reported that a moderate drought at the end of the growing season usually leads to an increase of the dry matter concentration.

All the landraces except Violeta, Chaucha blanca, Chaucha 1, and Coneja negra had DMC higher than 19.5%, a value considered to be the lower limit for using potato in processing as French fries or Crisps (Kirkman, 2007). Then most of the potato landraces could be used in breeding to increase the DMC. However is necessary to consider the tuber shape, eye depth and the other traits related to quality for processing as describe (Keijbets, 2008).

For DMC the estimated broad sense heritability was 0.64, indicating that most of the variation observed was due to genetic differences among landraces. The heritability value was higher than in previous reports. Yildirim and ÇaliŞkan (1985) studying eleven Turkish genotypes reported an estimate of broad sense heritability of 0.24. However, the value is lower than those found by Ruttencutter et al., (1979), who measured the heritability of breeding clones and reported values up to 0.74 and demonstrate that this character could be increased by means of breeding.

The considerable genotypic variation that exists for DMC in the potato landraces could be used for INIAP´s potato breeding program to select genotypes and develop varieties with high levels of DMC, attribute necessary for the fresh and processing market. The landraces Leona blanca, Leona negra, Leona, Puña, Uvilla and Curipamba with the highest DMC (Table 4), are the more suitable to use as parents to improve this character.

Reducing sugar content

The concentration of RSC is genetically determined (Menendez et al., 2002), and selection for low RSC germplasm is possible through breeding evaluation. Tuber maturity, fertilization, temperature and soil moisture are some of the factors that affect the resulting sugar accumulation in newly harvested tubers (Sowokinos, 2007).

In our study the RSC in more than 84% of landraces had contents below 0.25% which is a value considered the upper limit, higher values are considered unacceptable for potato processing (Kumar et al., 2004; Rodriguez-Saona and Wrolstad, 1997).

The broad sense heritability for RSC was 0.33 and this value is lower than that reported in previous researches. Grassert et al., (1984) reported values of 0.91 after cold storage and Pereira, et al., (1994) studying three potato populations from crosses among clones and landraces developed by Agriculture Canada, Fredericton, North Dakota State University and the variety Russet describe values from 0.47 to 0.63. However, the RSC reported in our study was higher than the concentration reported by Chitzas (1983) who studied segregating populations and found heritability values of 0.21.

Generally lower RSC mean was observed in Tungurahua as compared to Cotopaxi, since the agronomic management was homogeneous for both places the difference could be explained by the fact that Cotopaxi had more water availability, factor that affect the RSC in potato landraces. However, there are divergent opinions about the role of soil moisture in sugar accumulation in potatoes. Davies et al., (1989) reported that tubers water stressed during growth (drought) had lower reducing sugar contents (Kumar et al., 2004), while Owings et al., (1978) found that moisture stress during growth caused increased reducing sugar accumulation during storage.

Based on RSC the landraces with the lowest contents as Chaucha negra camote, Carrizo, Carrizo2, Bolona, Milagrosa, Leona negra, Uvilla, Curipamba and Leona blanca (Table 4) could be selected as progenitors in the breeding scheme of potato.

In our study DMC and RSC of 20 potato landraces were significantly affected by the interaction GxE. However, the genotypic component (landrace) contributed to the largest extent to the observed variability. The predominance of the genetic background (landrace) over environment effect on RSC and DMC has also been reported in the literature for potato (Pereira et al., 1994; Grassert et al., 1984).

Enzymatic discoloration

Enzymatic discoloration, which is a significant problem in the food industry, is one of the main causes of quality loss during postharvest handling (Coetzer et al., 2001). This discoloration results in considerable economic losses for the food processing and retail industry (Werij et al., 2007).

The ED for the Ecuadorian potatoes showed large variation among landraces for both locations at 30 and 180 min. The yellow skinned and fleshed landraces Sta. Rosa blanca, Chaucha blanca, Chaucha amarilla and Durazno had the lowest scores for ED in all locations and were not affected by the time of assessment, while the colored landraces Milagrosa, Chaucha, Suscaleña negra and Sole negra had the highest scores of ED in all locations and times of measurement. Varietal differences for ED have been reported. Sapers et al., (1989) studied the ED variation in a group of American varieties, and identified that Russet Burbank is very susceptible to ED compared to Atlantic. Recently Werij et al., (2007) studying the CxE population identified large variation for this character and established that ED is a polygenic character.

In our study the white cream/yellow potatoes brown much less extensively than colored potatoes, a relation that could be explained by composition differences among landraces. The colored potatoes have a high content of anthocyanin (Jansen and Flamme, 2006), which is an important component of polyphenols (André et al., 2009a; Perla et al., 2012). The polyphenol content is directly involved in the browning of tubers (Friedman, 1997) and the relation between polyphenol content and browning has been previously reported (Mondy et al., 1985; Friedman, 1997).

The potato germplasm evaluated shows large variation for ED with relatively high heritability of 0.50 for ED1 and lower for ED2 0.39 which are lower values compared with those reported by Werij et al., (2007) who established heritability values of 0.84 and 0.82 for ED1 and ED2 respectively. Furthermore the contribution of the genotype to the variance was significantly higher than that of the GxE interaction and of the environment. Then is possible to select progenitors with low ED values to develop varieties with this characteristic. Therefore, the landraces Sta. Rosa blanca Quillu, Chaucha amarilla and Durazno (Table 4), could be selected as progenitors for use in breeding.

This research demonstrates that significant genetic diversity exists for DMC and RSC in potato landraces, the contents are in close agreement with the industry standards for French fries or crisps potatoes. This information will be useful for selecting parents for breeding programs aimed at enhancing these traits for the processing market.

In Table 4 a summary with the landraces with the best quality characteristics for the processing market is shown, the landraces Leona blanca, Uvilla, Leona negra, Leona negra norte and Milagrosa, could be selected as progenitors for use in breeding to obtain varieties with high DMC and low levels of RSC. These landraces have also the required tuber shape (long – oblong) and eye depth (shallow) (Table 1).

Furthermore, as the white cream and yellow skinned potatoes showed low ED values in both times of evaluation, the use of these landraces in the breeding scheme could assure low ED e.g. the diploid landraces Sta. Rosa blanca, Chaucha amarilla and

Durazno (Table 4). However, is necessary to improve the tuber eye depth, since most have medium tuber eye depth (Table 1).

Table 4. Summary of potato landraces with the highest yield (kg plant^{-1}), DMC (%) and low RSC (%), ED (scale 1-8) at 30 min (ED1) and 180 min (ED2).

2n	**Landrace**	**Yield(1)**	2n	**Landrace**	**DMC(2)**	2n	**Landrace**	**RSC(2)**	2n	**Landrace**	**ED1-ED2(1)**
4X	Milagrosa	0.88	4X	Leona blanca	24.0	4X	Chaucha n.c.	0.01	2X	Sta. Rosa bl.	1.0-2.3
4X	Chaucha	0.78	4X	Leona negra	23.9	4X	Curipamba	0.01	4X	Quillu	1.0-2.7
4X	Huagrasinga	0.78	4X	Leona	23.3	4X	Carrizo	0.02	2X	Ch. amarilla	1.3-2.3
2X	Chaucha pintada	0.74	4X	Puña	22.9	4X	Carrizo2	0.02	4X	Durazno	1.3-2.3
4X	Tushpa	0.74	4X	Uvilla	22.8	4X	Bolona	0.02	4X	Curipamba	1.3-2.8
4X	Hualcala	0.73	4X	Curipamba	22.6	4X	Moroponcho	0.03	4X	Chaucha bl.	1.5-2.5
4X	Chaucha blanca	0.73	4X	Chaucha2	22.6	4X	Milagrosa	0.03	2X	Sta. Rosa am	1.7-3.0
4X	Chaucha negra	0.72	4X	Hualcala	22.5	4X	Leona negra	0.04	4X	Uvilla	1.7-3.3
2X	Chaucha amarilla	0.70	4X	Carrizo	22.2	4X	Uvilla	0.04	4X	Norte roja	1.7-3.3
4X	Leona n.n.	0.69	4X	Milagrosa	22.1	4X	Leona bl.	0.05	2X	Ch. roja	2.0-2.7
4X	Chaucha2	0.69	4X	Rosada	22.1	4X	Chaucha	0.05	4X	Puña	2.0-3.2
4X	Osito	0.69	4X	Jubaleña	21.8	4X	Leona	0.08	4X	Coneja bl.	2.0-3.4

(1) Mean based on 3 locations and 3 replicates; (2) Mean based on 2 locations and 3 replicates
Ch.=Chaucha; bl.= blanca; am.=amarilla; p. pintada; n.n.= negra norte, n.c.=negra camote

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Supplementary information

Supplementary Table 1. Potato landraces from the (EPC) to measure the variation of quality traits in three Ecuadorian locations.

	Code*	Landrace	*Taxonomic Group*		Code	Landrace	*Taxonomic Group*
1	HSO 146	Bolona**	*S. andigenum*	**21**	HSO 272	Jubaleña	*S. andigenum*
2	74p	Cacho blanco	*S. andigenum*	**22**	ASO 802	Leona**	*S. andigenum*
3	SOL 14	Calvache	*S. andigenum*	**23**	HSO 641	Leona negra**	*S. andigenum*
4	ASO 802A	Carrizo**	*S. andigenum*	**24**	SOL 29	Leona blanca**	*S. andigenum*
5	HSO 453	Carrizo2**	*S. andigenum*	**25**	SOL 6	Leona negra norte**	*S. andigenum*
6	BOM 540	Chaucha**	*S. andigenum*	**26**	PM 202	Macholulo	*S. andigenum*
7	HSO 131	Chaucha amarilla**	*S. phureja*	**27**	PM 203	Milagrosa**	*S. andigenum*
8	HSO 377	Chaucha blanca	*S. phureja*	**28**	SOL 14	Moroponcho**	*S. andigenum*
9	HSO 169	Chaucha negra**	*S. andigenum*	**29**	115p	Norte roja**	*S. andigenum*
10	BOM 532	Chaucha negra camote	*S. andigenum*	**30**	JS30	Osito**	*S. andigenum*
11	HSO 700	Chaucha pintada**	*S. phureja*	**31**	HSO 370	Puña	*S. andigenum*
12	HSO 369	Chaucha roja	*S. phureja*	**32**	PM 204	Quillu	*S. andigenum*
13	HSO 198	Chaucha1	*S. andigenum*	**33**	HSO 165	Rosada **	*S. andigenum*
14	HSO 213	Chaucha2	*S. andigenum*	**34**	PM 204	Sole negra	*S. andigenum*
15	JS 3	Coneja blanca	*S. andigenum*	**35**	PM 205	Sta. Rosa amarilla	*S. phureja*
16	HSO464	Coneja negra	*S. andigenum*	**36**	PM 206	Sta. Rosa blanca**	*S. phureja*
17	HCS 570	Curipamba**	*S. andigenum*	**37**	HSO 211	Suscaleña negra	*S. andigenum*
18	HX 201	Durazno	*S. phureja*	**38**	PM 200	Tushpa	*S. andigenum*
19	HSO 197	Huagrasinga	*S. andigenum*	**39**	BOM 549	Uvilla**	*S. andigenum*
20	CHS 690	Hualcala**	*S. andigenum*	**40**	HCS 581	Violeta	*S. andigenum*

***** INIAP-PNRT-papa codification
** Landraces chosen for glycoalkaloids and reducing sugar content analysis.

Supplementary Table 2. Average yield per plant (kg) in potato landraces evaluated in three locations and overall mean.

Landraces	Cotopaxi		Tungurahua		Carchi		Overall Mean	
Sole negra	0.29	a	0.05	a	0.42	f-h	0.26	a
Uvilla	0.31	a-b	0.13	a-b	0.33	c-f	0.26	a-b
Coneja negra	0.35	a-c	0.27	a-g	0.19	a-b	0.27	a-b
Curipamba	0.41	a-d	0.37	b-l	0.51	g-k	0.43	b-i
Puña	0.44	a-e	0.30	a-i	0.17	a	0.30	a-c
Suscaleña negra	0.47	a-f	0.18	a-c	0.57	i-n	0.41	a-g
Sta. Rosa blanca	0.47	a-f	0.24	a-f	0.64	k-o	0.45	c-j
Bolona	0.49	a-g	0.46	d-m	0.27	a-e	0.41	a-g
Quillu	0.50	a-h	0.28	a-h	0.35	d-f	0.38	a-f
Moroponcho	0.52	a-i	0.24	a-f	0.24	a-d	0.33	a-e
Durazno	0.52	a-i	0.21	a-e	0.40	e-g	0.38	a-f
Chaucha roja	0.52	a-i	0.63	l-n	0.52	g-k	0.56	g-m
Jubaleña	0.55	a-j	0.58	k-n	0.44	f-i	0.52	f-l
Rosada	0.56	a-j	0.61	l-n	0.32	b-f	0.50	e-k
Sta. Rosa amarilla	0.63	a-j	0.69	m-n	0.69	n-q	0.67	l-o
Chaucha negra	0.71	a-k	0.61	l-n	0.83	q	0.72	m-p
Carrizo	0.72	a-k	0.40	b-l	0.53	g-l	0.55	f-m
Chaucha1	0.73	b-k	0.47	e-m	0.53	g-l	0.58	g-n
Calvache	0.73	b-k	0.37	b-l	0.73	o-q	0.61	j-o
Leona	0.77	c-k	0.33	b-k	0.74	o-q	0.61	k-o
Norte roja	0.81	d-l	0.36	b-l	0.73	o-q	0.63	k-o
Tushpa	0.82	d-l	--		0.66	l-o	0.74	n-p
Osito	0.82	d-l	0.51	f-n	0.73	o-q	0.69	l-o
Macholulo	0.84	e-l	0.40	b-l	0.22	a-d	0.49	d-k
Leona blanca	0.89	f-m	0.25	a-f	0.20	a-c	0.45	c-j
Chaucha negra camote	0.90	g-m	0.19	a-d	0.69	n-q	0.59	i-n
Coneja blanca	0.91	g-m	0.20	a-e	0.50	g-j	0.54	f-l
Carrizo2	0.92	h-m	0.40	b-l	0.35	d-f	0.56	g-m
Chaucha blanca	0.93	h-m	0.53	g-n	--		0.73	n-p
Leona negra norte	0.94	i-m	0.43	c-m	--		0.69	l-o
Chaucha pintada	0.97	j-m	0.56	i-n	0.68	m-p	0.74	n-p
Chaucha2	1.08	k-m	0.47	e-n	0.50	g-j	0.69	l-o
Hualcala	1.08	k-m	0.37	b-l	0.74	o-q	0.73	n-p
Violeta	1.09	k-m	0.34	b-k	0.34	c-f	0.59	h-n
Milagrosa	1.10	k-m	0.74	n	0.80	p-q	0.88	p
Chaucha amarilla	1.14	k-m	0.37	b-l	0.58	j-n	0.70	l-o
Chaucha	1.22	l-m	0.55	h-n	0.55	h-m	0.78	o-p
Huagrasinga	1.28	m	0.30	a-j	0.76	o-q	0.78	o-p
Cacho blanco	--		0.57	j-n	0.27	a-e	0.42	a-h
Leona negra	--		0.22	a-e	0.43	f-h	0.32	a-d
Mean	0.75		0.39		0.50		0.55	

Different letters indicate significant differences between landraces, according to the Tukey HSD test ($P<0.05$).
"-- " No information available.

Supplementary Table 3. Average greening and dormancy in days after harvest of potato landraces evaluated in three locations

	GREENING								DORMANCY							
Landraces	**Cotopaxi**		**Tungurahuaa**		**Carchi**		**Mean**		**Cotopaxi**		**Tungurahuaa**		**Carchi**		**Mean**	
Sta Rosa blanca	25.7	a	35.0	a	25.7	a	28.8	a	21.0	bc	39.7	hi	35.0	g-i	31.9	ij
Quillu	35.0	b	42.0	b	35.0	b	37.3	b	74.7	h-j	91.0	k	70.0	kl	78.6	n-p
Sta Rosa am.	42.0	bc	35.0	a	42.0	bc	39.7	b	21.0	bc	11.7	cd	14.0	c	15.6	bc
Curipamba	46.7	cd	74.7	gh	65.3	ef	62.2	e-g	79.3	i-k	91.0	k	74.7	k-m	81.7	n-q
Durazno	46.7	c-e	56.0	c	49.0	cd	50.6	d	14.0	a	4.0	a	6.0	ab	8.0	a
Leona blanca	51.3	d-f	56.0	c	46.7	cd	51.3	d	93.3	j-l	95.7	k	79.3	k-m	89.4	o-s
Coneja blanca	53.7	d-f	63.0	de	72.3	f-h	63.0	fg	86.3	i-l	105.0	k	91.0	lm	94.1	p-s
Jubaleña	56.0	e-g	67.7	ef	53.7	de	59.1	ef	56.0	e-h	72.3	jk	48.7	ij	59.0	lm
Violeta	56.0	e-g	60.7	cd	72.3	f-h	63.0	fg	45.0	de	--		61.7	jk	53.3	kl
Suscaleña negra	58.3	f-h	35.0	a	44.3	cd	45.9	c	72.3	h-j	81.7	jk	72.3	kl	75.4	no
Chaucha am.	60.7	f-h	72.3	fg	65.3	ef	66.1	gh	14.0	a	7.0	bc	4.0	a	8.3	a
Puña	65.3	g-i	72.3	fg	81.7	f-j	73.1	hi	65.3	f-i	91.0	k	72.3	kl	76.2	no
Moroponcho	67.7	Hi	86.3	jk	72.3	f-h	75.4	hi	112.0	l	107.3	k	95.7	lm	105.0	rs
Milagrosa	70.0	h-j	77.0	g-i	67.7	fg	71.6	hi	112.0	l	105.0	k	93.3	lm	103.4	rs
Chaucha blanca	74.7	i-k	63.0	de	98.0	j-l	78.6	ij	18.7	ab	7.0	bc	4.0	a	9.9	a
Uvilla	74.7	i-k	42.0	b	53.7	de	56.8	de	72.3	h-j	84.0	jk	91.0	lm	82.4	n-q
Chaucha 2	84.0	j-l	98.0	mn	91.0	i-k	91.0	k-n	35.0	d	28.0	f-h	21.0	cd	28.0	hi
Leona	86.3	k-m	88.7	j-l	105.0	k-l	93.3	k-o	18.7	ab	7.0	ab	28.0	e-g	17.9	b-e
Carrizo	86.3	k-m	91.0	k-m	--		88.7	kl	18.7	ab	14.0	de	--		16.3	b-d
Chaucha pint.	86.3	k-m	105.0	no	88.7	h-k	93.3	l-o	21.0	bc	14.0	de	20.3	cd	18.4	c-f
Osito	88.7	k-m	105.0	no	72.3	f-h	88.7	klm	14.0	a	23.3	fg	23.3	c-e	20.2	e-g
Chaucha neg. c.	91.0	Lm	105.0	no	95.7	j-l	97.2	m-r	21.0	bc	14.0	de	28.0	e-g	21.0	fg
Chaucha	91.0	Lm	105.0	no	93.3	i-k	96.4	l-q	20.3	bc	7.0	bc	28.0	e-g	18.4	b-e
Chaucha negra	91.0	Lm	98.0	mn	91.0	i-k	93.3	k-o	53.7	e-g	21.0	ef	30.3	f-h	35.0	ij
Chaucha 1	91.0	Lm	91.0	k-m	84.0	g-k	88.7	klm	70.0	g-j	77.0	jk	63.0	jk	70.0	mn
Norte roja	91.0	Lm	105.0	no	86.3	h-k	94.1	l-p	44.3	de	54.0	ij	42.0	hi	46.8	k
Chaucha roja	93.3	l-n	102.7	no	95.7	j-l	97.2	m-r	14.0	a	7.3	bc	5.0	a	8.8	a
Calvache	95.7	l-n	84.0	i-k	74.7	f-i	84.8	jk	86.3	i-l	103.7	k	98.0	lm	96.0	p-s
Carrizo	95.7	l-n	95.7	l-n	74.7	f-i	88.7	klm	25.7	c	35.0	g-i	14.0	b	24.9	gh
Bolona	102.7	m-o	95.7	l-n	86.3	h-k	94.9	l-p	49.0	ef	35.0	g-i	28.0	e-g	37.3	j
Hualcala	102.7	m-o	109.7	o	98.0	j-l	103.4	p-s	16.3	ab	23.3	fg	18.7	c	19.4	d-g
Huagrasinga	112.0	no	98.0	mn	95.7	j-l	101.9	o-r	21.0	bc	7.0	bc	18.7	c	15.6	b
Sole negra	116.7	o	105.0	no	119.0	l	113.6	s	103.7	kl	99.0	k	95.7	lm	99.4	q-s
Tushpa	116.7	o	--		95.7	j-l	106.2	q-s	102.7	kl	95.7	k	91.0	lm	96.4	p-s
Coneja negra	119.0	o	105.0	no	98.0	j-l	107.3	rs	105.0	kl	112.0	k	105.0	m	107.3	s
Macholulo	119.0	o	98.0	mn	86.3	h-k	101.1	n-r	90.0	j-l	97.0	k	72.3	kl	86.4	n-r
Cacho blanco	--		81.7	h-j	72.3	f-h	77.0	i	--		56.0	ij	63.0	jk	59.5	lm
Mean	79.0		80.7		76.4		79.0		52.4		53.4		50.2		51.8	

Different letters indicate significant differences between landraces, according to the Tukey HSD test ($P<0.05$).
"-- " No information available.

Supplementary Table 4. Enzymatic discoloration(ED) evaluated at 30 min (ED1) and at 180 min (ED2) in tuber potato landraces grown in three locations.

	Cotopaxi		Tungurahua		Carchi		Mean	
Landrace	ED1	ED2	ED1	ED2	ED1	ED2	ED1	ED2
Chaucha amarilla	1.0	2.0	2.0	3.0	1.0	2.0	1.3	2.3
Chaucha blanca	1.0	2.0	2.0	3.0	--	--	1.5	2.5
Durazno	1.0	2.0	1.0	1.3	2.0	3.7	1.3	2.3
Jubaleña	1.0	5.0	2.0	6.0	3.0	5.3	2.0	5.4
Norte roja	1.0	3.0	1.0	3.0	3.0	4.0	1.7	3.3
Quillu	1.0	3.0	1.0	3.0	1.0	2.0	1.0	2.7
Sta Rosa blanca	1.0	2.0	1.0	3.0	1.0	2.0	1.0	2.3
Uvilla	1.0	2.0	1.0	4.0	3.0	4.0	1.7	3.3
Curipamba	1.7	2.7	1.0	3.0	--	--	1.3	2.8
Bolona	2.0	4.0	2.0	4.0	2.0	4.0	2.0	4.0
Carrizo	2.0	3.0	2.3	7.0	3.3	4.3	2.6	4.8
Carrizo2	2.0	2.0	2.0	6.0	--	--	2.0	4.0
Chaucha negra	2.0	3.0	2.0	5.0	2.0	3.0	2.0	3.7
Chaucha roja	2.0	2.0	2.0	3.0	2.0	3.0	2.0	2.7
Chaucha1	2.0	3.0	3.0	6.0	2.0	3.7	2.3	4.2
Coneja blanca	2.0	3.0	2.0	3.3	2.0	4.0	2.0	3.4
Huagrasinga	2.0	3.0	3.0	6.0	3.0	4.0	2.7	4.3
Hualcala	2.0	3.0	1.0	5.0	2.0	4.0	1.7	4.0
Leona	2.0	3.0	2.0	7.3	2.0	3.0	2.0	4.4
Leona blanca	2.0	3.3	3.0	4.0	3.0	5.0	2.7	4.1
Moroponcho	2.0	4.0	3.0	7.0	2.0	4.0	2.3	5.0
Osito	2.0	4.0	2.0	7.0	2.0	5.0	2.0	5.3
Sta Rosa amarilla	2.0	3.0	2.0	4.0	1.0	2.0	1.7	3.0
Tushpa	2.0	3.0	1.0	1.0	3.0	5.3	2.0	3.1
Chaucha negra c.	3.0	4.0	3.0	6.0	2.0	4.0	2.7	4.7
Chaucha pintada	3.0	5.0	3.0	5.7	3.0	5.3	3.0	5.3
Chaucha2	3.0	4.0	2.0	5.0	2.0	3.3	2.3	4.1
Coneja negra	3.0	4.0	2.0	3.3	2.0	5.0	2.3	4.1
Milagrosa	3.0	7.0	3.3	7.0	3.3	6.3	3.2	6.8
Puña	3.0	4.0	1.0	2.0	2.0	3.7	2.0	3.2
Sole negra	3.0	6.0	3.0	8.0	2.0	4.0	2.7	6.0
Violeta	3.0	4.0	--	--	4.0	5.0	3.5	4.5
Calvache	3.7	4.7	3.7	6.0	3.3	4.0	3.6	4.9
Chaucha	4.0	5.0	4.0	8.0	3.3	4.0	3.8	5.7
Suscaleña negra	4.0	5.0	3.3	7.7	2.0	4.0	3.1	5.6
Cacho blanco	--	--	4.0	7.0	3.0	4.0	3.5	5.5
Macholulo	--	--	1.0	3.0	2.7	5.7	1.8	4.3
Mean	2.2	3.5	2.2	4.8	2.4	4.0	2.2	4.1
LSD at 5%	0.23	0.64	0.31	0.65	0.36	0.74	0.53	0.41

"-- " No information available.

Supplementary Table 5. Total glycoalkaloids content in mg $100g^{-1}$ in fresh weight (FW) in raw and peeled tuber potato landraces grown in Cotopaxi and Tungurahua.

	COTOPAXI									TUNGURAHUA								
Landraces	**RAW(1)**				**PEELED(1)**				**P(2)**	**RAW(1)**				**PEELED(1)**				**P(2)**
Leona blanca	11.40	±	0.01	a	2.70	±	0.56	a	**	9.00	±	0.00	c	2.61	±	0.03	d	**
Mlagrosa	10.10	±	0.10	b	2.08	±	0.57	ab	**	9.68	±	0.13	b	2.92	±	0.03	c	**
Uvilla	9.82	±	0.04	c	1.53	±	0.68	ab	**	12.10	±	0.04	a	2.42	±	0.02	def	**
Rosada	8.51	±	0.03	d	2.28	±	0.11	ab	**	5.75	±	0.09	e	1.40	±	0.00	l	**
Moroponcho	6.31	±	0.12	e	2.52	±	0.61	a	**	11.84	±	0.64	a	4.87	±	0.05	b	**
Chaucha negra	6.31	±	0.05	e	1.50	±	0.04	ab	**	4.13	±	0.05	hi	2.39	±	0.02	ef	**
Chaucha amarilla	5.55	±	0.02	f	2.10	±	0.81	ab	**	4.81	±	0.06	g	1.57	±	0.10	l	**
Bolona	4.17	±	0.10	g	2.09	±	0.54	ab	**	5.11	±	0.02	fg	1.39	±	0.10	l	**
Sta Rosa blanca	3.53	±	0.08	h	1.59	±	0.04	ab	**	11.80	±	0.08	a	7.66	±	0.13	a	**
Leona negra	3.44	±	0.09	h	1.65	±	0.02	ab	**	7.56	±	0.05	d	2.38	±	0.02	ef	**
Osito	3.32	±	0.12	hi	1.43	±	0.44	ab	**	4.29	±	0.03	h	1.86	±	0.09	k	**
Carrizo 2	3.15	±	0.04	i	1.66	±	0.07	ab	**	5.32	±	0.01	ef	1.93	±	0.15	jk	**
Curipamba	2.87	±	0.02	j	1.73	±	0.58	ab	**	3.75	±	0.01	ij	2.28	±	0.04	fgh	**
Chaucha pintada	2.84	±	0.03	jk	2.12	±	0.59	ab	**	2.60	±	0.02	mn	2.09	±	0.01	hij	**
Leona negra	2.79	±	0.02	jk	1.72	±	0.03	ab	**	3.21	±	0.09	kl	1.95	±	0.01	ijk	**
Carrizo	2.69	±	0.09	jk	1.74	±	0.82	ab	**	2.96	±	0.05	lm	1.40	±	0.04	l	**
Chaucha	2.64	±	0.07	k	1.65	±	0.07	ab	**	5.12	±	0.02	fg	2.14	±	0.00	ghi	**
Leona	2.36	±	0.03	l	1.52	±	0.32	ab	**	2.35	±	0.08	n	1.40	±	0.04	l	**
Hualcala	2.28	±	0.09	l	0.91	±	0.13	b	**	3.55	±	0.02	jk	2.34	±	0.09	efg	**
Norte roja	2.15	±	0.03	l	1.48	±	0.04	ab	**	4.07	±	0.03	hi	2.51	±	0.01	de	**
Mean	4.81	±	2.89		1.80	±	0.55			6.27	±	3.97		2.48	±	1.42		

(1) Mean values ± standard deviation (n=3). Different letters indicate significant differences between accessions for each site, according to the Tukey HSD test (P<0.05)

(2) Differences between raw and peeled for each accession: ** = significant at (P<0.01)

Supplementary Table 6. Total glycoalkaloids content in mg $100g^{-1}$ in fresh weight (FW) in raw and peeled tuber potato landraces grown in two locations.

Landraces	RAW [(1)]	PEELED [(1)]	% Reduction[(2)]
Uvilla	10.96 ± 1.25 a	2.27 ± 0.16 d	79
Leona blanca	10.19 ± 1.30 b	2.82 ± 0.23 c	72
Mlagrosa	9.88 ± 0.25 c	2.33 ± 0.65 d	76
Moroponcho	9.08 ± 3.06 d	3.36 ± 1.65 b	63
Sta. Rosa blanca	7.66 ± 4.53 e	4.62 ± 3.33 a	40
Rosada	7.13 ± 1.52 f	1.84 ± 0.49 f-i	74
Leona negra	5.50 ± 2.26 g	2.02 ± 0.40 e	63
Chaucha negra	5.22 ± 1.19 h	1.89 ± 0.27 e-i	64
Chaucha amarilla	5.18 ± 0.41 h	1.77 ± 0.35 i-k	66
Bolona	4.64 ± 0.52 i	1.98 ± 0.65 e-g	57
Carrizo2	4.24 ± 1.19 j	1.79 ± 0.18 h-k	58
Chaucha	3.88 ± 1.36 k	1.94 ± 0.49 e-h	50
Osito	3.80 ± 0.54 k	1.90 ± 0.07 e-i	50
Curipamba	3.31 ± 0.48 l	1.84 ± 0.49 f-i	44
Norte roja	3.11 ± 1.06 lm	2.00 ± 0.56 ef	36
Leona negra n.	3.00 ± 0.23 mn	1.83 ± 0.13 g-j	39
Hualcala	2.91 ± 0.70 m-o	1.66 ± 0.75 k	43
Carrizo	2.82 ± 0.16 no	1.33 ± 0.08 l	53
Chaucha pintada	2.72 ± 0.13 o	1.67 ± 0.25 jk	39
Leona	2.35 ± 0.05 p	1.14 ± 0.29 m	51
Mean	5.38 ± 1.11	2.10 ± 0.57	56

(1) Mean values ± standard deviation (n=3). Different letters indicate significant differences between accessions for each site, according to the Tukey HSD test (P<0.05)
(2) Percentage of reduction of TGA comparing raw and peeled potatoes

Supplementary Table 7. Reducing sugars content (% FW) in potato landraces evaluated in two locations

Landraces	Cotopaxi[(1)]				Tungurahua[(1)]				Overall mean[(1)]			
Leona blanca	0.011	±	0.003	a	0.082	±	0.002	g	0.046	±	0.039	a-d
Leona negra	0.017	±	0.002	a	0.062	±	0.003	f	0.039	±	0.025	a-d
Carrizo	0.019	±	0.001	a	0.010	±	0.002	ab	0.015	±	0.005	ab
Mlagrosa	0.028	±	0.037	a	0.026	±	0.000	c	0.027	±	0.023	a-c
Carrizo 2	0.032	±	0.004	a	0.011	±	0.002	ab	0.021	±	0.012	ab
Uvilla	0.035	±	0.002	a	0.051	±	0.002	e	0.043	±	0.009	a-d
Chaucha	0.044	±	0.003	a	0.064	±	0.002	f	0.054	±	0.011	b-e
Bolona	0.045	±	0.002	a	0.089	±	0.002	h	0.067	±	0.024	c-e
Moroponcho	0.051	±	0.000	a	0.038	±	0.001	d	0.045	±	0.007	a-d
Norte Roja	0.072	±	0.002	a	0.170	±	0.005	i	0.121	±	0.054	f
Hualcala	0.170	±	0.115	b	0.029	±	0.001	c	0.099	±	0.106	ef
Sta. Rosa blanca	0.234	±	0.006	bc	0.297	±	0.002	j	0.265	±	0.035	i
Osito	0.290	±	0.002	cd	0.093	±	0.004	h	0.192	±	0.108	gh
Rosada	0.323	±	0.001	cd	0.054	±	0.002	e	0.188	±	0.147	g
Chaucha negra	0.367	±	0.000	de	--				0.367[(2)]	±	0.000	j
Chaucha amarilla	0.439	±	0.003	e	0.064	±	0.003	f	0.251	±	0.206	hi
Chaucha pintada	--				0.006	±	0.002	a	0.006[(2)]	±	0.002	a
Curipamba	--				0.013	±	0.002	b	0.013[(2)]	±	0.002	ab
Leona	--				0.077	±	0.000	g	0.077[(2)]	±	0.000	de
Mean	0.136	±	0.011		0.069	±	0.002		0.102	±	0.043	

(1) Mean values ± standard deviation (n=3). Different letters indicate significant differences between accessions for each site, according to the Tukey HSD test (P<0.05)
(2) Mean based on modified population marginal mean

"-- " No information available.

Supplementary Table 8. Dry matter content (%) in potato landraces evaluated in two locations and the overall mean

Landraces	Cotopaxi				Tungurahua				Overall Mean			
Leona blanca	23.6	±	1.24	a	24.4	±	0.89	a-b	24.0	±	1.05	a
Leona negra	22.9	±	1.22	a-b	24.9	±	0.83	a	23.9	±	1.45	a
Leona	22.8	±	1.14	a-c	23.7	±	0.98	a-c	23.3	±	1.06	a-b
Uvilla	22.8	±	0.34	a-d	22.8	±	0.77	a-f	22.8	±	0.53	a-d
Puña	22.6	±	0.68	a-d	23.1	±	0.43	a-e	22.9	±	0.57	a-c
Chaucha amarilla	22.5	±	1.39	a-i	22.6	±	0.81	c-i	21.0	±	0.86	c-k
Osito	22.5	±	0.74	a-d	21.1	±	1.50	c-i	21.8	±	1.30	b-i
Milagrosa	22.4	±	0.90	a-e	21.8	±	0.80	b-g	22.1	±	0.83	a-h
Hualcala	22.4	±	2.01	a-f	22.6	±	1.10	a-f	22.5	±	1.45	a-f
Tushpa	22.0	±	0.54	a-f	20.8	±	0.76	d-i	21.4	±	0.88	b-j
Curipamba	22.0	±	1.40	a-f	23.2	±	1.59	a-d	22.6	±	1.50	a-e
Chaucha pintada	21.9	±	0.77	b-i	20.0	±	0.87	b-g	21.0	±	1.18	c-k
Cacho blanco	21.8	±	0.73	a-h	20.9	±	1.01	c-i	21.4	±	0.92	b-k
Rosada	21.8	±	1.15	a-h	22.4	±	1.63	a-f	22.1	±	1.30	a-h
Carrizo2	21.8	±	0.85	a-h	21.7	±	0.27	b-g	21.7	±	0.56	b-i
Jubaleña	21.5	±	0.50	a-i	22.0	±	0.50	b-g	21.8	±	0.53	b-i
Carrizo	21.5	±	2.51	a-i	23.0	±	0.94	a-e	22.2	±	1.88	a-g
Moroponcho	21.1	±	1.44	a-i	21.8	±	0.28	b-g	21.5	±	1.00	b-j
Macholulo	21.0	±	0.50	a-i	22.4	±	0.56	a-f	21.7	±	0.88	b-i
Chaucha	20.8	±	0.59	a-g	21.2	±	1.19	f-i	20.9	±	1.27	c-k
Leona negra norte	20.8	±	1.39	a-i	20.8	±	1.01	d-i	20.8	±	1.09	c-k
Quillu	20.6	±	0.54	a-i	21.4	±	0.53	c-h	21.0	±	0.64	c-k
Chaucha roja	20.6	±	0.95	a-i	22.5	±	1.00	g-i	20.0	±	0.74	h-m
Chaucha1	20.5	±	0.50	h-i	19.4	±	0.52	f-i	19.3	±	1.10	k-m
Suscaleña negra	20.1	±	0.40	b-i	20.6	±	0.55	d-i	20.4	±	0.53	f-m
Chaucha blanca	20.0	±	0.50	g-i	22.0	±	0.49	h-i	18.6	±	0.50	lm
Coneja blanca	20.0	±	0.50	b-i	22.0	±	0.98	b-g	21.0	±	1.29	c-k
Sole negra	20.0	±	0.50	b-i	21.8	±	0.77	b-g	20.9	±	1.16	c-k
Bolona	19.7	±	1.21	b-i	23.0	±	1.01	a-e	21.4	±	2.05	b-k
Sta Rosa amarilla	19.7	±	0.59	g-i	21.0	±	0.45	c-h	20.0	±	1.98	h-m
Durazno	19.5	±	0.50	c-i	21.9	±	0.34	b-g	20.7	±	1.36	d-k
Chaucha negra	19.4	±	0.83	a-i	21.6	±	0.87	a-f	21.5	±	1.38	b-j
Calvache	19.4	±	0.54	d-i	20.3	±	0.58	e-i	19.9	±	0.72	i-m
Norte roja	19.0	±	2.45	e-i	20.3	±	1.02	e-i	19.7	±	1.83	i-m
Huagrasinga	19.0	±	0.50	f-i	21.0	±	0.50	c-i	20.0	±	1.18	h-m
Chaucha negra camote	18.6	±	0.69	d-i	18.6	±	0.37	b-g	20.5	±	1.42	e-l
Sta Rosa blanca	18.5	±	1.17	b-i	21.4	±	1.49	c-i	20.3	±	0.85	g-m
Chaucha2	18.5	±	0.51	a-d	20.1	±	0.93	a-f	22.6	±	1.02	a-e
Coneja negra	18.3	±	0.59	i	20.5	±	0.50	d-i	19.4	±	1.29	j-m
Violeta	18.1	±	0.34	i	18.5	±	0.51	i	18.3	±	0.43	m
Mean	20.8	±	0.89		21.6	±	0.80		21.2	±	1.09	

(1) Mean values ± standard deviation (n=3). Different letters indicate significant differences between accessions for each site, according to the Tukey HSD test (P<0.05)

Annex 1. Analysis of variance combined and proportion of total variance for yield per plant (kg), greening and dormancy of potato landraces grown in Cotopaxi, Tungurahua and Carchi.

		Mean square						
Source	**df**	**Yield**	**PTV(%)**	**df**	**Greening**	**PTV(%)**	**Dormancy**	**PTV(%)**
Environment (E)	2	3.87**	30.75	2	0.075**	0.38	1.071**	0.75
Genotype (G)	39	0.22**	34.09	36	0.967**	89.1	7.096**	89.63
GxE	73	0.09**	26.1	69	0.50**	8.84	0.357**	8.64
Error	228	0.01	9.06	214	0.003	1.64	0.013	0.97
Total	344			323				

** Significant at 1%
PTV(%) : Proportion of total variance

Annex 2. Analysis of variance combined and proportion of total variance for enzymatic discoloration (ED) of potato landraces grown in Cotopaxi, Tungurahua and Carchi.

		Mean square			
Source	**df**	**ED1**	**PTV(%)**	**ED2**	**PTV(%)**
Environment (E)	2	0.088**	0.63	2.384**	10.00
Genotype (G)	36	0.489**	63.23	0.706**	53.41
GxE	66	0.143**	33.9	0.251**	34.81
Error	208	0.003	2.24	0.004	1.74
Total	314		100		

** Significant at 1%
PTV(%) : Proportion of total variance

Annex 3. Analysis of variance combined and proportion of total variance for total glycoalkaloid (TGA), reducing sugar (RSC) and dry matter content (DMC) of potato landraces grown in Cotopaxi and Tungurahua.

		Mean square									
		TGA									
Source	**df**	**Raw**	**PTV(%)**	**Peeled**	**PTV(%)**	**df**	**RSC**	**PTV(%)**	**df**	**DMC**	**PTV(%)**
Environment (E)	1	38.972**	3.47	16.880**	11.2	1	0.029**	3.13	1	41.13**	6.12
Genotype(G)	19	46.448**	78.65	3.470**	43.76	18	0.033**	64.14	39	10.43**	60.57
Gx E	19	10.500**	17.78	3.530**	44.52	14	0.020**	30.23	39	2.13**	12.37
Error	78	0.014	0.09	0.01	0.52	66	3.50E-04	2.49	158	0.89	20.93
Total	119					102			239		

** Significant at 1%
PTV(%) : Proportion of total variance

Annex 4. Soil fertilization recommendation of INIAP based on NPK soil content

	Soil content			Recommendation		
	N	**P**	**K**	**N**	**P205**	**K20**
	ppm		Meq/100ml		kg/ha	
Low	<30	<10	<0.19	150-200	300-400	100-150
Medium	31-60	11-20	0.2-0.38	100-150	200-300	60-100
High	>61	>21	>0.39	60-100	100-200	40-60

Chapter 4

Tuber quality characteristics of Ecuadorian potato landraces and farmer preferences

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Tuber quality characteristics of Ecuadorian potato landraces and farmer preferences

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Abstract

Antioxidants, such as polyphenols and carotenoids, are present in potato and reported to have positive effects on human health. High levels of antioxidants have been reported in Andean potatoes. However, for Ecuadorian landraces there is a lack of data on these compounds. The objective of this study was to assess variation for dry matter content (DMC), total polyphenol content (TPC) and total carotenoid content (TCC) in a representative sample of landraces and 2) to determine if farmer preferences for certain landraces are based on characteristics related to nutritional value.

The observed values for DMC, TPC and TCC demonstrated the wide variability. The DMC ranged from 16% to 24%, the TPC from 0.94 to 4.28 mg $100g^{-1}$of dry weight (DW) and the TCC from 35 to 1.225 μg $100g^{-1}$ of fresh weight (FW) and correlated positively with tuber flesh color. The landraces Papa chacra, Chaucha botella, Sabanera and INIAP-Estela were selected for use in breeding to increase the antioxidant content.

The farmer´s main criteria for selecting potato landraces were good taste, tuber yellow flesh color and mealy consistence. These characters have been reported to be associated with some quality traits related with potato taste as DMC, low levels of glycoalkaloids and high content of carotenoids. Farmer's preferences include empirical valuation of potato-quality rather than specific knowledge on nutritional characteristics. Furthermore several farmers selected potato landraces based on the criteria "novelty variety", referring to landraces that are new in the region.

The results of this research suggest that Ecuadorian potato landraces are important sources of health promoting compounds as carotenoids and polyphenols. The landraces and improved varieties with high levels of TPC and TCC as Papa chacra, Chaucha botella, Sabanera and INIAP-Estela could be used within breeding programs seeking to increase antioxidant content in potato. Furthermore, the extent of the use of these potato landraces by farmers and breeders is discussed.

Key words: Antioxidants, polyphenols, carotenoids, potato landrace

Introduction

In the Ecuadorian highlands, potato is the second most important crop after maize, and it is an important staple food for the population. Approximately 300,000 tons of potatoes are produced annually (http://www.faostat.fao.org) and the annual consumption is 32 kg.year^{-1} per capita in urban places (Devaux et al., 2010).

The main sources of potatoes for consumers in urban areas are the improved varieties. Only 20 out of the approximately 350 landraces reported for Ecuador actually reach urban markets (Cuesta et al., 2005a; Unda et al., 2005) and a recent study in areas of local potato production (Carchi, Chimborazo and Loja) showed that landraces are still in the hands of poor and small-scale farmers (Monteros, 2011).

In the Andes farmers grow potatoes varieties that display an extraordinary diversity of taste and texture and come in fascinating array of shapes and colors. These native potatoes have been important in the nutrition and economy of Andean subsistence farmers (http://www.cipotato.org). Several reports have shown that potato landraces contain higher concentrations of specific nutrients than improved varieties (Andre et al., 2007; Burgos et al., 2007; Burgos et al., 2009) and de Haan (2007), suggested that the consumption of diverse potato landraces can make a valuable contribution to enhanced nutrition.

Subsistence farmers in the Ecuadorian highlands traditionally produce commercial potatoes for the fresh market and grow potato landraces for home consumption, these landraces have been selected and conserved over centuries mainly based on quality traits (taste, shape and color), characters that are related with their traditional cooking techniques (Monteros et al., 2010). These potatoes have been the basis of the farmer's diet in rural areas.

The South American potato landraces show a large variation in nutritional content. Andre et al. (2007) reported variation among 74 Andean landraces with respect to iron (from 30 to 160 μg g^{-1} of DW), zinc (12.6 to 28.8 μg g^{-1} of DW), calcium (271 to 1093 μg g^{-1} of DW) and total vitamin C (217.7 to 689.5 μg g^{-1} of DW).

Potato is also considered a good source of antioxidant phytochemicals like carotenoids and polyphenols (Brown, 2005). The positive effect of antioxidants on human health has been reported by several authors (Andre et al., 2006; Arts and Hollman, 2005; Teow et al., 2007; Yang et al., 2001). For this reason there is a continuous search for new compounds with antioxidant activity (Campos et al., 2006; Liu, 2004; Yang et al., 2001).

Nevertheless information on the extent of variation with respect to antioxidant contents within the native Andean potatoes is still scarce (Andre et al., 2007; Bonierbale et al., 2004; Brown, 2008) and does not exist for Ecuadorian potatoes.

The objective of this study was to assess the variability for potato tuber dry matter content, total polyphenol content and total carotenoid content in 23 representative potato landraces and determine if farmers preferences about potato landraces in three representative areas are based on characteristics related to nutritional value.

This information will be very useful for INIAPs potato breeding program to select germplasm with high contents of these compounds for direct use or as progenitors to improve the nutritional value of potato and if farmers preferences about potato landraces in the study areas are related with nutritional characteristics.

Materials and methods

Evaluation of landraces at Santa Catalina Experimental Station

We studied 23 potato landraces collected from farmer's fields in three provinces of Ecuador: Carchi (9 landraces), Chimborazo (3 Landraces) and Loja (11 landraces). These landraces were selected based on the SSR genotypic information conducted on 152 accessions (Monteros, 2011). We also included three Ecuadorian commercial varieties: INIAP-Estela, INIAP-Natividad and Superchola.

A field experiment was carried out in Quito at the Santa Catalina Experimental Station (EESC) of the National Institute for Agricultural Research (INIAP), the environmental conditions are described in Annex 1. A random complete block design with three repetitions was used. The landraces were planted in single row plots of ten plants per repetition with a plant spacing of 0.25 m and a row spacing of 1.0 m.

Chemical fertilization was applied prior to the planting using INIAP`s recommendations based on chemical soil analysis and consisted of 100-250-80 kg ha^{-1} of Nitrogen, Phosphorus and Potassium respectively. To avoid late blight six sprays were done using dimethomorph and cymoxanil in rotation and to control insects (*Premnotripes vorax*, *Lyriomiza huidobrensis* and *Epitrix* spp.) four sprays of propenofos were applied.

Sample preparation

A sample of approximately 2 kg was collected per landrace and per repetition. The tubers were randomly selected from a bulk of 10 plants harvested. These tubers were put in opaque bags, labeled and taken to the Laboratory of Nutrition and Quality in

Santa Catalina Experimental Station, Quito, Ecuador. For polyphenol and carotenoids analysis the whole tubers were ground, freeze-dried and stored at -51^{o}C prior to extraction and analysis.

Dry matter determination

The total dry matter content was determined according to (Bonierbale et al., 2007). Five tubers were chopped (about 500 g total) into small 1-2 cm cubes. They were mixed thoroughly and two sub-samples of 200 g each were taken. The exact weight of each sub-sample was recorded as fresh weight. Next, each sub-sample was placed in an open container in an oven at 80^{o}C for 72 hours or until constant dry weight was reached. Each subsample was weighted immediately after removal from the oven (recorded as dry weight). The dry matter content for each sub-sample was calculated with the following formula: Dry matter % = (dry weight / fresh weight) x 100.

Total polyphenol content

Total polyphenol content was measured according to (Cros et al., 1982) with minor modifications. Polyphenol was extracted with 70% methanol from the freeze dried potato sample, under continuous stirring for 45 minutes, after which the extract was filtered. An aliquot was taken and mixed with distillated water, Folin and Ciocalteu reagent and sodium carbonate at 20% (Singleton et al., 1999). This solution was quantified in the spectrophotometer UV-VIS 2201 (Shimadzu Corp., Kyoto, Japan). The total phenolic content was expressed in g kg^{-1} of gallic acid and reported in Dry Weight (DW). The calibration was done according to (Cros et al., 1982).

Total carotenoid content

Carotenoid analysis was carried out according to (Kimura et al. 2007). First, 3 g of the freeze dried sample was extracted with acetone (Merck KgaA, Darmstadt, Germany) in an Ultra Turrax Teckmar homogenizer (IKA-Werke, Wilmington, NC, USA) for 3 min at 5000 rpm. The extraction was repeated until the residue was colorless. The extracts were transferred to a 500 ml separatory funnel with petroleum ether (Merck, Darmstadt, Germany) and washed 3 – 4 times with water to remove any acetone residue. The resulting saponified extracts were brought to a volume of 50 ml with petroleum ether. The total carotenoid content was calculated using the absorbance measured in a Shimadzu spectrophotometer UV-VIS 2201 (Shimadzu Corp., Kyoto, Japan) at 450 nm and the extinction coefficient for mixtures of carotenoid (2492). The total carotenoid content is expressed in micrograms of carotenoid per 100 gram in fresh weight basis. The calibration was done according to (Scott et al. 1996).

Evaluation of landraces in Carchi, Chimborazo and Loja

Besides the evaluation at the Santa Catalina Experimental Station, we also evaluated the potato tuber dry matter content, total polyphenol and total carotenoid from landraces grown in their provinces of origin (place of collection) for two cycles during 2008 and 2009 (Annex 1). We planted 9 landraces in Carchi (North of Ecuador), 16 in Chimborazo (Center of Ecuador) and 24 in Loja (South of Ecuador) with one replication per landrace.

During the first and second year, local farmers interested in potato landraces provided land-space, except the second year in Carchi where a local agricultural high school was chosen for the evaluation. Samples were collected and sent to the Laboratory of Nutrition and Quality in Santa Catalina Experimental Station for analysis as described for the Santa Catalina trial.

Farmer preferences

Three farmer meetings of one day each were organized in each research area: one in San Gabriel-Carchi (December, 2009), another in Pisicaz-Chimborazo (February, 2010) and one in Tenta-Loja (November, 2009), During these meetings we recorded information regarding the use of local landraces by using participatory tools (Cuesta et al., 2007b) and farmers selected locally collected landraces to take home as seed tubers.

In Carchi, all the farmers that provided the landraces were invited for a one-day meeting. Later in February 2010, 40 farmers were interviewed. One group of farmers (30) from 12 communities had previously worked together within INIAP’s participatory potato breeding program. The second group (10 farmers) was randomly selected from 6 locations. In both cases farmers were from distinct potato production areas in Carchi and had a good knowledge of the potato crop. During the interview we asked farmers about the preferred “potato variety” and the criteria of selection referring either to landraces or improved commercial varieties.

In Chimborazo we invited farmers from six communities. These communities were selected because they were interested in growing potato landraces. During the day of the event 17 native landraces were presented to the farmers for selection. Six bags of 2 kg per accession were displayed in the patio of the communal centre. In total 6 bags per landrace were prepared so every community had the opportunity to select one bag of every landrace if farmers representing the community agreed upon this. A tag with the name of the landrace was put in front of each group of bags. Farmers could register the landraces they wanted and the criteria for selection. Then one farmer per community would put tags on the landraces they selected as a group.

In Loja, we invited farmers from whom we collected potato landraces (Monteros, 2011). We prepared one bag of approximately 4 kg of tubers per landrace (24 in total) and presented them to the farmers in the patio of a local school. A tag with the name of the landrace was put in front of each bag. The farmers could walk around the bags and freely select the landraces they preferred to take home as seed-tubers. They were not restricted in the number of landraces they could take home. We registered how often a landrace was selected by the farmers and also the criteria of selection.

Data analysis

We calculated analyses of variance (one-way ANOVA) for landraces to determine the variation in dry matter content, total polyphenol and total carotenoid grown at EESC. The Shapiro-Wilk test was used to determine normal distribution of the data. The data for total polyphenol and total carotenoid contents were log-transformed and subsequently subjected to analyses of variance. The significance of differences among means was calculated by using a pairwise multiple comparison procedure (Tukey test at $P<0.05$).

We performed Pearson correlation between tuber colors (skin and flesh) to total carotenoid and total polyphenol concentrations. Analyses were carried out using SPSS version 16.0 (SPSS Inc. 2007). Estimates of the variance components ANOVA were used to compute broad-sense heritability (*H*) for each trait it was estimated as the ratio of the genotypic (σ_G^2) to total phenotypic variance, $H = \sigma^2_G/(\sigma^2_G+\sigma^2)$, where, σ^2_G= genotypic variance, σ^2= residual variance (Bos, 1995).

For each region, the relative frequency was calculated per variety/landrace selected and criteria of selection. Data were expressed in percentage.

Results

Variation of traits in potato landraces

The Analysis of variance indicated significant genotypic variation at $P<0.001$ for potato tuber dry matter, total polyphenol and total carotenoid contents. Tukey ranking of landraces and commercial varieties are presented in Table 1.

Dry matter content (DMC)

The DMC among landraces varied from 15.8% for Sabanera to 23.0% for Puña. The Tukey test showed a group of landraces with high DMC (from 21.0% - 23.0%) which included the tetraploids Rosada, Puña, Roja plancha, Negra ojona, Hualcala, Uva, Colorada antigua, Violeta and Suscaleña negra and the diploids Chaucha botella and Papa chacra (Table 1).

The improved variety Superchola was also in this group. The other improved varieties in our study, INIAP-Estela and INIAP-Natividad, showed a DMC of 19.7% and 19.8% respectively. The landraces Carriza, Esperanza, Colorada, Negra and Sabanera had the lowest DMC ranking from 16% to 18% (Table 1). The estimate of broad-sense heritability for DMC was 0.87.

Total polyphenol content (TPC)

The TPC varied from to 4.28 g kg^{-1} DW for Papa chacra to 0.94 g kg^{-1} DW for the improved variety Superchola. According, to the Tukey test the landraces with highest contents (1.90 to 4.28 g kg^{-1}DW) were: Papa chacra, Negra ojona, Sabanera, Morasurco, Suscaleña blanca, Suscaleña negra, Colorada antigua, Chaucha botella, Colorada, Carriza and Puña. The improved variety INIAP-Estela was also in this group (Table 1).

Table 1. Concentrations of Potato Tuber Dry matter (%), Total Polyphenol (g kg^{-1} DW) and Total Carotenoid (μg $100g^{-1}$ FW) in Ecuadorian landraces.

Common name	Code	Ploidy	Skin color[a] Primary color / Secondary color	Flesh color Primary color / Secondary color	Dry Matter[b]		Total Polyphenol[c]		Total Carotenoid[d]	
Puña	FMFHRA-04	4X	RP / Y	C / A	23.07	a	1.90	cdefgh	40.0	gh
Superchola	Improved var.	4X	Pi / Y	Y / A	22.77	a	0.94	i	112.3	abc
Roja plancha	AXC-30	4X	R / WC	Yb / A	22.70	a	1.88	cdefghi	49.3	defgh
Chaucha botella	AXC-15	2X	Pi / O	Y / A	22.51	a	2.10	bcdefgh	122.5	a
Negra ojona	MG-11	4X	B / O	C / A	22.20	ab	3.01	abcd	77.0	abcdefg
Rosada	AXC-29	4X	Y / WC	C / A	22.00	ab	1.42	efghi	100.7	abc
Huancala	AMFY-3	4x	R / WC	C / A	22.00	ab	1.42	fghi	52.0	cdefgh
Papa chacra	MPG-21	2x	Y / P	Yb / A	21.83	ab	4.28	a	114.3	ab
Uva	JS-2	4x	RP / Y	W / A	21.50	ab	1.38	hi	62.3	bcdefgh
Colorada antigua	MPG-42	4x	R / WC	Yb / A	21.43	ab	2.28	abcdefgh	85.3	abcdef
Violeta	AXC-25	4x	Y / WC	W / A	21.30	ab	1.83	cdefghi	77.0	abcdefg
Suscaleña negra	MOPG-8	--	RP / O	C / A	21.10	abc	2.33	abcdefgh	35.3	h
Chaucha roja	MPG-28	4x	B / O	Yb / A	20.57	abcde	1.56	defghi	54.3	cdefgh
Coneja	FMRAFH-02	4x	Y / O	Yb / A	20.30	abcde	1.96	cdefgh	93.3	abc
Parda pastusa	AC-42	3x	Pi / Y	C / A	20.17	abcde	1.43	efghi	46.3	efgh
Mampuera	AXC-2	--	P / Y	C / A	20.07	abcde	1.39	ghi	91.0	abcde
INIAP-Estela	Improved var.	4x	RP / Y	Y / A	19.80	abcde	3.36	abc	92.7	abcd
Morasurco	AXC-9	4x	P / Y	C / P	19.80	abcde	2.99	abcde	70.0	abcdefg
INIAP-Natividad	Improved var.	4x	Y / Y	Y / A	19.67	abcde	1.70	cdefghi	60.7	abcdefgh
Bolona	MOPG-15	4x	Br / WC	Yb / A	19.20	abcde	2.09	bcdefgh	52.7	cdefgh
Suscaleña blanca	ARX-4	--	RP / Y	W / A	19.00	abcde	2.94	abcdefg	36.0	h
Carriza	MPG-20	4x	P / Y	Yb / P	18.03	bcde	2.51	abcdefgh	101.0	abc
Esperanza	ARX-1	--	RP / Y	Yb / A	17.03	cde	2.31	abcdefgh	40.3	gh
Colorada	MOPG-3	4x	RP / Y	Yb / A	16.57	de	2.95	abcdef	68.3	abcdefgh
Negra (Carriza o Cat.)	MOPG-2	4x	P / Y	C / P	16.47	de	1.84	cdefghi	67.0	abcdefgh
Sabanera	AC-34	4x	RP / O	W / A	15.77	e	4.08	ab	47.3	fgh

[a] Code colors (Gomez, 2000). A=Absent, W=White, WC= White-cream, C=Cream, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, B=Blackish. [bcd] Mean for 3 repetitions. Tukey test α=0.05

The group with the lowest content of TPC (0.94 – 1.43 g kg^{-1}DW) included the landraces Parda pastusa, Rosada, Hualcala, Mampuera, Uva and the improved variety Superchola (Table 1). The estimate of broad-sense heritability value for TPC was 0.89.

Total carotenoid content (TCC)

The total carotenoid content showed values from 35.0 μg $100g^{-1}$FW for Suscaleña negra to 122.5 μg $100g^{-1}$ FW for Chaucha botella. The landraces with the highest content of total carotenoid (60.7 - 122.5 μg $100g^{-1}$FW) were: Chaucha botella, Papa chacra, Carriza, Rosada, Coneja blanca, Mampuera, Colorada antigua, Violeta, Negra ojona, Morasurco, Colorada, Superchola, INIAP-Estela, INIAP-Natividad, Negra-carrizo and Uva. The landraces Sabanera, Parda pastusa, Esperanza, Puña, Suscaleña blanca and Negra had a lower TCC varying from 35.3 to 47.3 μg $100g^{-1}$FW (Table 1). The estimate of broad-sense heritability for TCC was 0.91

Correlation analysis

We found a highly significant correlation (at $P<0.01$) between flesh color and carotenoid ($r = 0.467$) content (Figure 1). All other correlations were not significant.

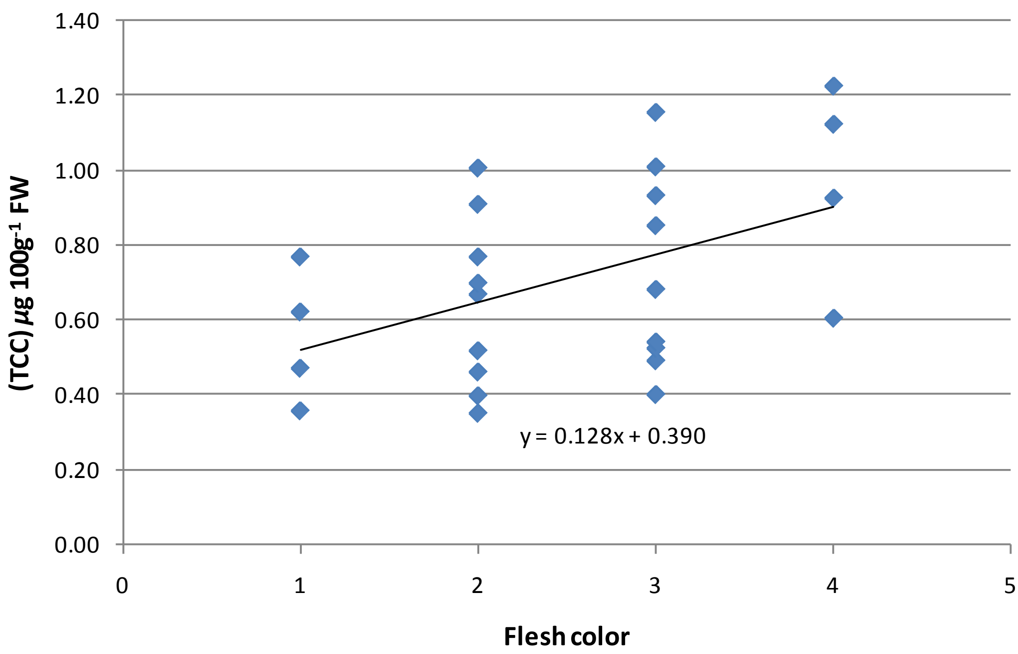

Figure 1. Correlation between total carotenoid content TCC (µg $100g^{-1}$ FW) and tuber flesh color according to the color card (Gómez, 2000) of Ecuadorian potato landraces.

Farmer preferences

The quality criteria used for the selection of potato landraces by farmers are described in Table 2. The most important characteristics found to influence the preference were good taste, yellow flesh color, novelty variety and mealy consistence with 47%, 29%, 22% and 22% of average preference respectively, while the less important characters were mean tuber size and yellow skin color (<6%).

Table 2. Farmers preference criteria about potato landraces in three Ecuadorian areas. Data expressed in percentage.

Characteristics*	Carchi(40)**	Chimborazo (40)**	Loja (21)**	Average
Good taste	31	41	67	47
Yellow flesh	39	5	42	29
Novelty variety(a)	14	12	39	22
Mealy	23	9	33	22
Long shape	36	9	15	20
Big size	24	7	15	16
Pink skin	19	0	21	13
Waxy consistence	10	3	15	10
Round shape	14	0	12	9
Red-purple skin	13	7	0	7
Mean size	19	0	0	6
Yellow skin	9	0	9	6

* Character described in Chapter 2
** Total of participants
(a) Novelty variety= landrace that is new in the region

Carchi:

In this research area forty farmers were interviewed about landrace preference, most of the respondents (39%) selected yellow flesh color as the main criteria of selection of potato landraces. While in second and third place were the characters long tuber shape and good taste with 36% and 31% of preference respectively. The criteria big tuber size, mealy consistence had lower preference (24% and 23%) and less than 19 % of farmers preferred pink skin color, mean tuber size, round tuber shape and “novelty variety” (Table 2).

The information about the preference of landraces in Carchi is shown in Figure 2. The improved variety Superchola was preferred by 80% of the respondents. Among the landraces Rosada was the most preferred by 40% of farmers, Violeta was second (23%).

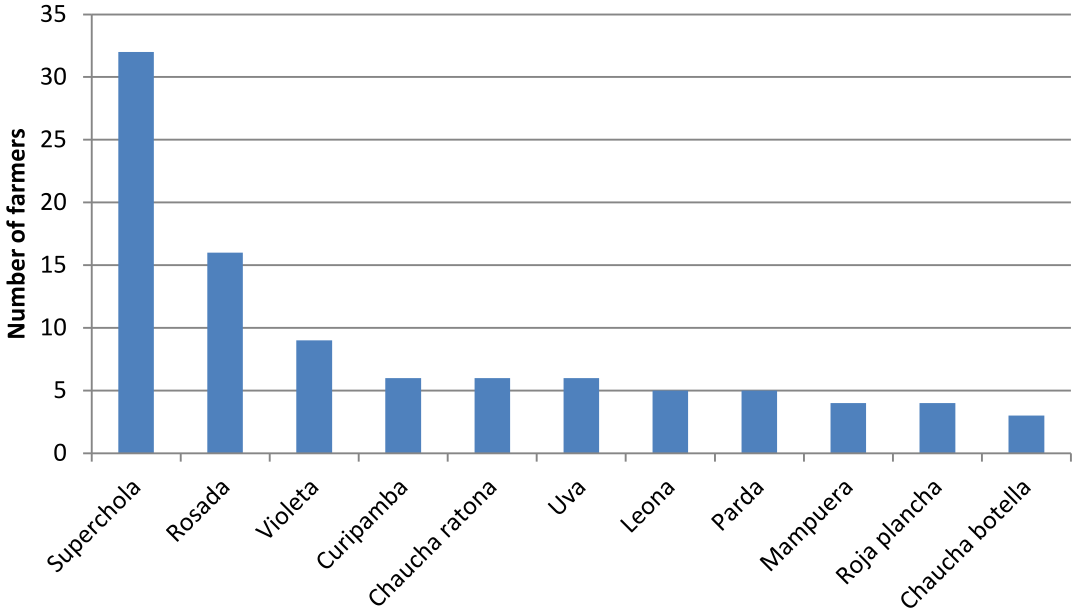

Figure 2. Potato varieties (local landraces or commercial varieties) preferred by farmers in Carchi based on the survey. The number of farmers that selected a variety is show on the y axis.

Our trial in EESC (Table 1) identified Rosada among the landraces with the highest dry matter content 22% and it was also included in the group with highest total carotenoid content (100.7 µg 100g^{-1}FW). The polyphenol content was below the average of the group of landraces we studied (1.42g kg^{-1} DW) while Violeta in the EESC trial was in the first group for DM (21.3%) and also for total carotenoid content (77 µg 100g^{-1}FW). This landrace showed a total polyphenol content of (1.83 g kg^{-1} DW) and was classified in the second group.

Chimborazo:

Forty farmers representing 6 communities attended the workshop in Pisicaz. In this region, 41% of farmers selected potato landraces based on good taste criteria. The character of “novelty variety” was reported for 12% of farmers. The characters mealy consistence, long tuber shape, big size, yellow flesh color, high yield and red purple skin were mentioned by 5% -9% of the farmers. Less preferred were waxy consistence and earliness. The characteristics mean tuber size and yellow skin colors were not mentioned at all (Table 2).

Figure 3, shows the selection of landraces by the communities. The landraces Cacho and Chaucha amarilla were preferred by all communities. The landraces Tulca roja, Uvilla amarilla and Cacho negro were selected by 5 communities and Uvilla, Norteña and Puña were selected by 4 communities.

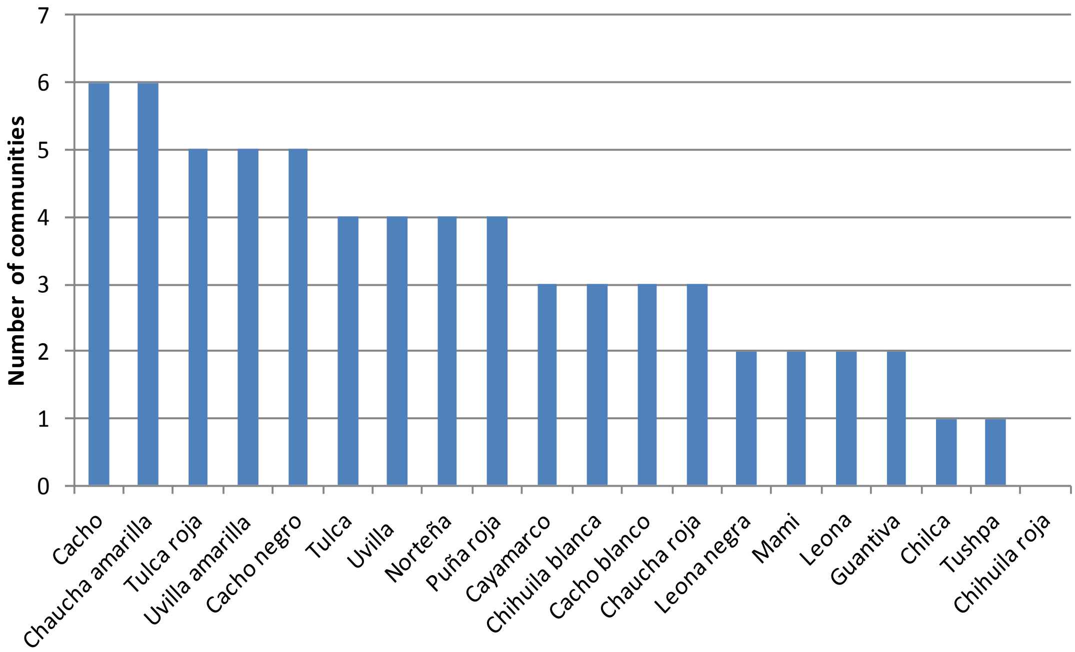

Figure 3. Preference of landraces by farmers representing six communities in Chimborazo. The number of communities that selected the landraces is included in the y axis. Farmers could freely walk through the displayed landraces but the selection was made by consensus of the community members.

The landraces Cacho and Chaucha amarilla had the highest average DMC (24%) among landraces. For TPC, Cacho was in the group of highest TPC (3.94 g kg^{-1} DW), Chaucha amarilla was intermediate (2.77 g kg^{-1} DW), while for TCC was below the average (50 µg $100g^{-1}$ FW) (Table 3).

Loja:

Twenty one farmers attended the workshop in Loja. In this province good taste was the most preferred character by 67% of farmers, while character of “novelty variety” and tuber yellow flesh color were mentioned by 42% and 39% of the respondents respectively. Pink skin color and mealy consistence were preferred by 21% and 33% respectively. Big tuber size, long tuber shape and waxy consistence were preferred by 15% of farmers and the criteria less mentioned were round tuber shape and yellow tuber skin by less than 12% (Table 2).

The landraces Wicupa amarilla and Guata blanca ojona were the most preferred by 43% and 62% of farmers respectively, while the least preferred were Bolona and Papa huinga that were not selected by any farmer (Figure 4). The preferred landraces Guata blanca ojona had intermediate TPC (2.65 g kg^{-1} DW) and TCC (150 g kg^{-1} DW) while Wicupa amarilla was in the group of highest TPC (4.40 g kg^{-1} DW) and TCC (320 µg $100g^{-1}$ FW) (Table 3).

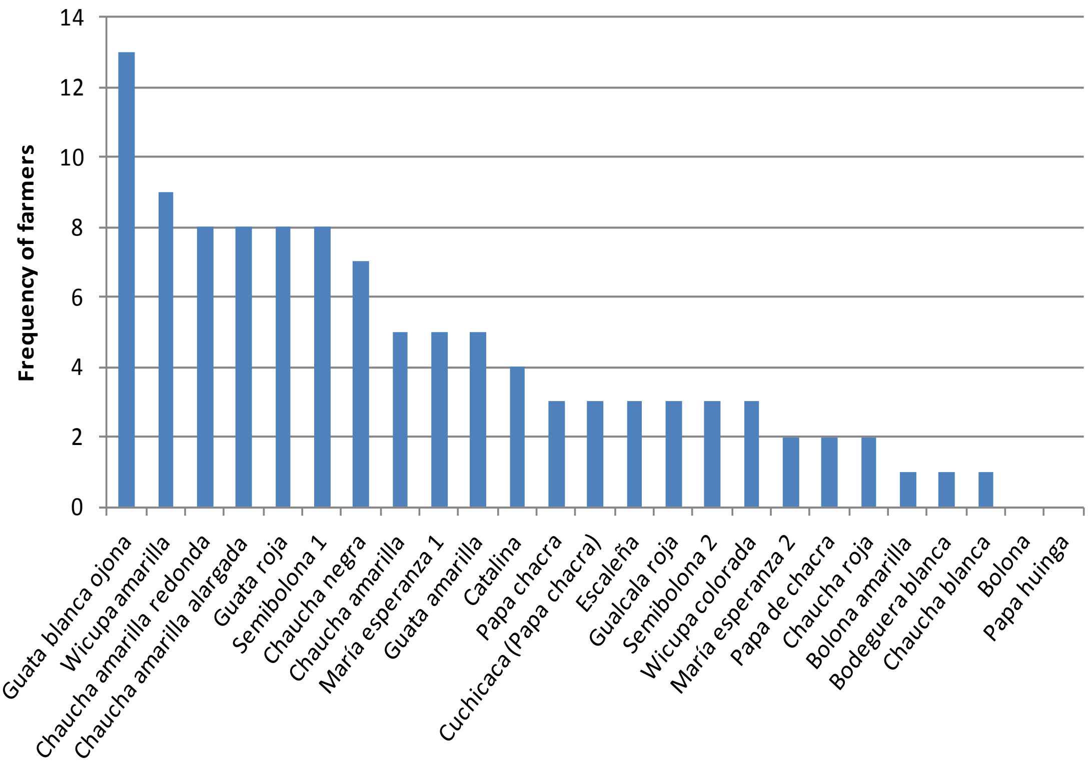

Figure 4. Local landraces preferred by farmers in Loja. The number of farmers who selected landraces is shown on the y axis. Farmers could freely select as many landraces they wanted from the displayed landraces

Table 3. Potato landraces selected by farmers from Carchi, Chimborazo and Loja, morphological characteristics and values for dry matter content (DMC %), total polyphenol content TPC (g kg^{-1} DW) and total carotenoid content TCC (µg $100g^{-1}$ FW).

CARCHI*							
Landrace	**Shape**	**Eye**	**Skin**	**Flesh**	**DMC**	**TPC**	**TCC**
Superchola	Oblong	Shallow	Pi/Y	Y	22.8	0.94	112.3
Rosada	Round	Medium	Y/WC	C	22.0	1.42	100.7
Violeta comun	Oblong	Medium	C/P	C/Y	23.2	3.15	90.0
CHIMBORAZO*							
Landrace	**Shape**	**Eye**	**Skin**	**Flesh**	**DMC**	**TPC**	**TCC**
Cacho	Eliptic	Deep	RP/Y	Y	24.0	3.94	65.0
Chaucha amarilla	Round	Medium	Y/P	O	24.0	2.77	50.0
Tulca roja	Eliptic	Deep	R	O	19.0	3.54	60.0
Uvilla amarilla	Compressed	Deep	Y/P	Y	23.3	4.04	50.0
Cacho negro	Eliptic	Deep	B	Y	20.8	3.47	45.0
Puña	Ovate	Medium	RP/Y	C	22.5	2.18	80.0
LOJA*							
Landrace	**Shape**	**Eye**	**Skin**	**Flesh**	**DMC**	**TPC**	**TCC**
Guata blanca	Round	Deep	Br/R	WC	N/D	2.65	150.0
Wicupa amarilla	Eliptic	Deep	Br/R	C	N/D	4.40	320.0
Ch. amarilla red.	Ovate	Medium	O	Y	22.0	3.04	460.0
Ch. amarilla al.	Eliptic	Medium	Y	Y	20.0	3.65	160.0
Semibolona 1	Round	Medium	Br/R	Y	20.1	2.43	50.0
Papa de chacra	Round	Meidum	R/P	Y	N/D	4.68	120.0
Papa chacra	Round	Medium	Y/P	Yi	23.6	4.70	114.3

[a] Color codes (Gomez, 2000). Primary color/Secondary color: W=White, WC= White-cream, C=Cream, Yi=Yellow intense, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, V= violet, B=Blackish.
Ch. amarilla red= Chaucha amarilla redonda, Ch. amarilla al.= Chaucha amarilla alargada
*Average data from two years of evaluation

Discussion

Nutritional quality of Ecuadorian landraces

Dry matter content

The DMC of the evaluated landraces varied from 15.8% to 23.0%. Applying the scale proposed by (Cacace et al., 1994) more than 61% of the landraces had a high (>20.0%) DMC, 23% had intermediate content (from 18.0% to 19.9%) and 15% had low DMC (<17.9%). This character is a variety characteristic and is influenced by climate, soil and cultural factors as was demonstrated by Stevenson et al., (1964), Love and Pavek (1991), Werner et al., (1998) and Laboski and Kelling (2007) studying diploid and tetraploid potatoes.

The estimate of broad sense heritability was 0.87, which means that most of the variation observed was due genetic differences among landraces. The value is higher than those found by (Ruttencutter et al., 1979), who measure the heritability of breeding clones; they found values up to 0.74 and demonstrate that this character could be accumulated by means of breeding.

The improved varieties INIAP-Natividad and INIAP-Estela had a DMC slightly lower than the values reported by Cuesta et al. (2007c,d); they reported 20% and 22% for these varieties, respectively. The differences are most likely due to environmental factors, this trait is affected by soil and climate as was demonstrated by Cacace et al., (1994) and Laboski and Kelling (2007) evaluating clones and improved varieties.

The variety Superchola is extensively used in the Northern area of Ecuador. It had a DMC similar to that reported by the INIAP (22%-24%) and its DMC is significantly higher than the other two improved varieties.

Based on the DMC most of the Ecuadorian landraces evaluated (70%) were suitable for processing as French fries or chips potatoes. However, in some cases the shape was not ideal, as long or round tubers without deep eyes are preferred (Kirkman, 2007; Van Eck, 2007).

In Table 4 the landraces with the highest contents of DMC, TPC and TCC are presented. The landraces Puña, Roja plancha, Chaucha botella and the improved variety Superchola with the highest DMC could be selected as progenitors for breeding to improve this character. Since most of the variation observed was genetic, we expect fast progress in breeding for this character.

Total polyphenol content

The total polyphenol content (TPC) values were very similar to those found by Lachman et al., (2008) who evaluated some yellow and purple flesh European varieties and found values between 2.46 and 4.81 g kg^{-1} DW. They were also quite similar to those reported by André et al., (2007), who evaluated the antioxidant capacity of 79 potato accessions of the International Potato Center (CIP) that represent more than 60% of the variability in the potato collection. They found a TPC values from 1.12 to 3.77 g kg^{-1}DW. Only two skin and flesh purple accessions had TPC of 5.99 kg^{-1} DW and 12.37 kg^{-1} DW respectively.

The improved varieties showed different contents, INIAP-Estela was one of the top three varieties with the highest TPC (3.36 g kg^{-1}DW) compared to Superchola that had the lowest content (0.94 g kg^{-1}DW). INIAP-Natividad had an intermediate performance with a content of 1.70 g kg^{-1}DW.

The estimated broad sense heritability was 0.89 which means that most of the observed variation was due to genetic differences among the landraces evaluated. Several authors have reported the significant effect of the genetic factor in the variation of the TPC, Hamouz et al., (2006), Lachman et al., (2008) who measured the TPC on European varieties and Andre et al., (2009a), who studied the effect of environment and genotype on polyphenol compounds of thirteen Andean potato varieties.

The landraces with the highest TPC were red-purple, purple or blackish skinned. This relation between skin color and TPC has been previously reported by (Andre et al., 2007). Lewis et al., (1998) and Andre et al., (2007) found higher concentrations of polyphenols in purple- or red-skinned tubers than in their white counterparts. Purple- and red-skinned tubers contained twice the TPC as white-skinned tubers (Ezekiel et al., 2012).

Interestingly, besides their antioxidant attributes in human, acylated anthocyanins present in colored potatoes represent promising natural colorants for the food industry (Andre et al., 2007). Thus, colored potatoes as Papa chacra and Sabanera with high TPC could be a promising source of favorable antioxidant in human nutrition and natural colorant for the industry or for use in breeding (Table 4).

Total carotenoid content

The total carotenoid content (TCC) values were in the same order of magnitude as those reported by Breithaupt and Bamedi (2002) who measured a TCC of 58–175 μg

100g^{-1} FW in yellow fleshed varieties and 38–62 μg 100g^{-1} FW in white fleshed varieties. However, these values are lower than those reported by Brown et al., (2005) studying potato varieties and selections from the USDA/ARS breeding program at Prosser, Washington, USA. They found a range from 35 to 795 μg 100g^{-1} FW. Nesterenko and Sink (2003), evaluating fifteen potato lines from the Michigan State University breeding program in the USA, reported carotenoid levels ranging from 48 to 879 μg 100g^{-1} FW. More recently Burgos et al., (2009b) found the TCC for some of the *Solanum phureja* accessions reaching much higher values (1840 μg 100 g^{-1} FW). So the Ecuadorian landraces are in the lower range.

Most of the variation for TCC in this study was due to genetic differences among varieties as described by Lu et al., (2001), who studied diploid clones or by Nesterenko and Sink (2003) who characterized tetraploid breeding clones. This effect is confirmed by the broad sense heritability of 0.91 which is in close agreement with the value previously reported (H = 0.96) in nine clones from the USDA, Agriculture Research Service Beltsville Potato Breeding Program by Haynes et al., (2010).

The landraces with the highest TCC Chaucha botella and Papa chacra that belongs to *Solanum phureja* group were all highly yellow pigmented (Table 4). The high carotenoid content of Phureja group has already been reported in several studies as well as the strong correlation between carotenoid concentration and yellowness (Brown et al., 1993; Lu et al., 2001) and significantly higher mean levels of total carotenoids were observed in diploid *Solanum phureja* accessions when compared to tetraploid varieties (Brown, 2008).

In this study usually landraces with the highest TCC were correlated positively with the yellow fleshed tubers (Figure 1), while most of the white cream flesh tubers had lowest carotenoid values (Table 1), the strong correlation between carotenoid concentration and yellowness has been previously reported (Brown et al., 1993) and Lu et al., (2001) showed that both total and individual carotenoid contents are positively correlated with tuber yellow intensity.

The orange and yellow color of the tuber flesh is caused by the presence of specific carotenoids mainly zeaxanthin and lutein (Burgos et al., 2009) and recently Wolters et al., (2010) conclude that only genotypes combining presence of the dominant *Chy2* allele with homozygosity for the recessive *Zep* allele that is present mainly in *S .phureja* potatoes produced orange-fleshed tubers that accumulated large amounts of zeaxanthin. This compound is found in significant levels in relatively few dietary components including some maize cultivars and yellow orange pepper varieties (Burgos et al., 2009).

Then the importance of potato landraces especially those from *S. phureja* group that contribute with the *Zep* allele responsible of high levels of zeaxanthin. *Solanum phureja* potatoes may aid in the recommended daily uptake of zeaxanthin, as potatoes constitute a considerable part of the human diet in Ecuador (Chun et al., 2005).

This study suggests that sufficient heritable genetic variation exists for TCC and TPC in Ecuadorian potato landraces, variation that could be exploited through direct use or through crop improvement. Colored skin and yellow fleshed landraces represent an important source of antioxidants beneficial in human health.

Table 4. Summary of landraces with the highest contents of DMC (%), total polyphenol content TPC (g kg^{-1} DW) and total carotenoid content TCC (µg $100g^{-1}$ FW).

Landrace	Skin	Flesh	DMC	Landrace	Skin	Flesh	TPC	Landrace	Skin	Flesh	TCC
Puña	RP/Y	C	23.1	Papa chacra	Y/P	Yi	4.28	Chaucha bl.	Pi/O	Y	122.5
Superchola	P/Y	Y	22.8	Sabanera	RP	W	4.08	Papa chacra	Y/P	Yi	114.3
Roja plancha	R/WC	C	22.7	INIAP-Estela	RP/Y	Y	3.36	Superchola	Pi/Y	Y	112.3
Chaucha bot.	Pi/O	Y	22.5	Negra ojona	B	C	3.01	Carriza	P/Y	Yi	101.0
Negra ojona	B	C	22.2	Morasurco	P/Y	C	2.99	Rosada	Y/WC	C	100.7
Rosada	Y/WC	C	22.0	Colorada	RP/Y	Yi	2.95	Coneja	Y	Yi	93.3
Huancala	R / WC	C	22.0	Suscaleña bl.	RP/Y	W	2.94	INIAP-Estela	RP/Y	Y	92.7
Papa chacra	Y/P	Yi	21.8	Carriza	P / Y	Yb / P	2.51	Mampuera	P/Y	C	91.0

[a] Color codes (Gomez, 2000). Primary color/Secondary color: W=White, WC= White-cream, C=Cream, Yi=Yellow intense, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, V= violet, B=Blackish.
Chaucha bot. = Chaucha botella, Chaucha bl. = Chaucha blanca

Farmers´ preferences for potato landraces

In general, tuber quality traits good taste, tuber yellow flesh color, long tuber shape and mealy consistence were the preferred characters by farmers in all regions. Furthermore the character “novelty variety” was an important criteria for farmers of Chimborazo and Loja.

Good taste was the preferred characteristic in the three locations. In Carchi the landrace Rosada, in Chimborazo Cacho and Chaucha amarilla were selected mainly for their good taste. Good taste is a complex trait that depends on the interaction of several volatile compounds and soluble cellular constituents as describe (Taylor et al., 2007) and that could be affected by reducing sugar content (RSC) and total glycoalkaloid (TGA). Sucrose levels above 1% fresh weight (FW) are reported to give an unacceptably poor taste to boiled potatoes (Storey, 2007) and several studies described that potato glycoalkaloids at elevated levels (>14 mg $100g^{-1}$) make the potato taste bitter (Sinden et al., 1976; Friedman, 1997).

Furthermore the DMC could also affect taste since this character has effect on tuber cooking texture and this trait is a critical component of efficiency in manufacturing potatoes for the processing industry (Taylor et al., 2007).

For some dish preparations certain “types” of potato landraces are commonly used. An example concerns landraces used to obtain boiled potatoes for direct consumption and soups or stews. Boiled potato landraces used for direct consumption should be mealy (high dry matter content). Soups and stews, however, commonly contain “watery” landraces (low dry matter content) (De Haan, 2009; Monteros et al., 2010). It seems likely that potato preference according to taste is greatly influenced by the appropriate cooking technique.

Several dishes require a mix of landraces rather than a single cultivar, the most common example is “cariucho” which is a traditional dish containing fababeans, oca, melloco and mix of mealy and “watery potatoes” (Monteros et al., 2010). In Chimborazo, the landrace Tulca low DMC (19%) and the high DMC landraces Puña (22.5%) or Chaucha amarilla (24%) are commonly used to prepare this traditional dish.

There are dishes that require a particular landrace. An example is the dish called “cuy” (guinea pig with potatoes), a dish commonly served at special occasions in Chimborazo; it should contain a potato that disintegrates after cooking. This makes landraces with mealy texture as Puña (DMC 22.5%) preferred for the dish. In Loja the landrace Wicupa amarilla was selected as good for consumption in soups while Chaucha amarilla redonda (22% DMC) and Chaucha amarilla alargada (20% DMC) were qualified by farmers as the most delicious potatoes (consumed in soups or fried).

Despite the fact that farmers did not have knowledge about the traits involved in good taste, they have been selected potatoes with low levels of TGA and RSC and depending on the usage of potatoes farmers have knowledge about the potato tuber texture which is key quality determinant of cooked potatoes (Taylor et al., 2007), farmers associated mealy texture with high DMC landraces and “watery” potatoes with low DMC. The same relationship has been reported by other studies (Jansky, 2008; De Haan, 2009; Monteros et al., 2010).

A large percentage of farmers preferred red or purple skin potatoes with yellow flesh color; both characters are associated with high levels of anthocyanins and carotenoids that are natural antioxidants which are highly desirable in diet because of their beneficial effects on human health (Brown, 2005).

The few farmers attending the local meeting in Carchi indicated that they currently have little interest in potato landraces. The apparent reason is the current lack of market opportunities. In Carchi, most farmers cultivate improved varieties, which are marketed in the cities of Tulcan and San Gabriel (Yanez and Cuesta, 2006). The surveys showed that the local farmers prefer the commercial improved variety “Superchola” over the landraces (Figure 2), again pointing at the interest in marketable potatoes for income generation. According to Cuesta et al., (2005a) the preference for commercial varieties over local landraces results in loss of landraces.

The interest on recovering less frequent landraces “novelty variety” character also drove the choices in all areas. For example in Loja, landraces considered by farmers to be lost or present in only low frequency, such as Papa de chacra and Papa chacra growing within maize, were selected by some farmers. In the Loja area this kind of potatoes is important as staple food for self-consumption to accompany maize and other local crops.

Despite the fact that tuber eye depth and round tuber shape are important traits for the fresh and processing market as we described in Chapter 2, the first character was not mentioned at all by any farmer and the second trait had low preference. This is most likely due to the fact that most of the landraces cultivated by farmers are not sold in the market (Unda et al., 2005), where round tuber shape and shallow eyes are important requirements of traders and consumers (Chapter 2), most of the potato landraces are for self consumption and depending on the landrace, varieties with deep eyes usually are prepared without peeling as boiled potatoes for direct consumption or combined with other Andean tubers in a traditional dish called “cariucho” (Monteros et al., 2010).

In Chapter 2 the landrace Bolona was the most preferred in the Southern region, in this study was not selected by any farmer, it is because farmers from Loja probably consider this landrace as commercial variety, easy to find in the market that is not a novel potato as result was not selected among the potato landraces.

Farmer’s preferences on potato landraces were related to tuber and processing quality traits. The characters good taste, yellow flesh and mealy consistence were the most preferred, result similar was reported in Chapter 2 about preferences of potatoes for the fresh market. However, regarding to landraces long shape was more preferred than round shape and shallow eyes were not important.

Furthermore, we have shown that farmers´ preferences include empirical valuation of potato-quality rather than specific knowledge on nutritional characteristics of these potatoes. It is necessary to raise awareness on these nutritional qualities with farmers and consumers which could increase consumption and cultivation.

Safeguarding landrace diversity

We observed in Chimborazo and Loja that farmers still have an interest in potato landraces. Women are important curators of potatoes on the farm as men migrate to look for additional income generating activities (Monteros, 2011). Their interest is mainly for self-consumption and is driven by flavour or uses in traditional local dishes.

Our results also showed that local farmers can be important users of genebank materials as observed by Engels and Visser (2003) and Bonierbale et al., (2004) to support local food security. Re-patriation of locally accepted landraces assures the continuity of cultivation of less frequent landraces.

Use in potato breeding

The main objectives of the potato breeding program of Ecuador is to obtain new improved varieties with resistance to late blight and good agronomic characteristics like high yield and early maturity and recently INIAP became interested in the inclusion of quality traits as criterion for selection, especially for the generation of new varieties for the processing market e.g. chips and French fries (Cuesta et al., 2005b).

Ecuadorian potato landraces have been considered as possible source of genes for resistance to biotic and abiotic factors. However, Ecuadorian potato landraces have been underestimated as health-promoting crop (Cuesta et al., 2005).

This research demonstrated the importance of Ecuadorian potato landraces as source of important health promoting compounds like carotenoids and polyphenols that are highly desirable in diet because of their beneficial effects on human health (Andre et al., 2007). Some carotenoids as the zeaxanthin is mainly present in diploid Andean potatoes as *Solanum phureja* and high levels of polyphenols are related to red, purple or blackish skin mainly from *Solanum andigenum* landraces (Ezekiel et al., 2012).

The advantage of the potato landraces evaluated in this study is the large variation observed for the different traits together with the high heritability estimates for DMC (0.87), TPC (0.89) and TCC (0.96). Then the landraces with the highest contents could be used as progenitors to develop new potato varieties with high dry matter, carotenoids and polyphenols content through plant breeding and we expect a fast progress in breeding for those characters.

Therefore for high DMC the landraces Puña, Roja plancha, Chaucha botella and the improved variety Superchola are good options to use in breeding. While, Papa chacra, Sabanera, Negra ojona, Morasurco, Colorada, Suscaleña blanca and the improved variety INIAP-Estela could be selected as progenitors to increase the levels of TPC.

Additionally, the landraces Chaucha botella, Papa chacra, Carriza, Rosada, Coneja, Mampuera and the improved varieties Superchola and INIAP-Estela could be selected as progenitors to develop improved varieties with high TCC. These potatoes with high DMC, TPC and TCC add value to potato consumption and might open new market niches for potato landraces with high antioxidant content.

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Annex 1. Environmental conditions of three locations to measure tuber quality traits in Ecuadorian potato landraces.

		Location 1		Location 2		Location 3	
Province	Pichincha	Carchi		Chimborazo		Loja	
Year	2009	2008	2009	2008	2009	2008	2009
Canton	Quito	San Gabriel	San Gabriel	Colta	San Juan	Saraguro	Saraguro
Location	INIAP-Sta. Catalina	La Delicia	San Gabriel	El Belen	Pisicaz	Tenta	Gañil
Altitude (m)	3,058	2,952	2,908	3,380	3,300	2,650	2,570
Longitude	78°33′15″W	77°43¨35´´W	77°48´34´´W	78°47´22´´W	78°46´30´´W	79°17´12´´W	7°14´11´´W
Latitude	00°22′4″N	0°38´29´´N	0°36´20´´N	1°43´10´´S	1°37´56´´S	3°35´49´´S	3°37´25´´S
Average temp. (°C)	12.0	12.3	12.4	10.5	11.0	13.2	13.5
Rain fall (mm)	900	850	800	470	450	700	650
N (ppm)	60	61	67	59	75	35	32
P (ppm)	16	15	12	14	24	14	11
K (ppm)	0.30	0.39	0.41	0.32	0.36	0.24	0.28

Chapter 5

Quantitative trait loci analysis for tuber shape, eye depth, skin and flesh color in a diploid potato population derived from native Ecuadorian *S. phureja* landraces

Quantitative trait loci analysis for tuber shape, eye depth, skin and flesh color in a diploid potato population derived from native Ecuadorian *S. phureja* landraces

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Abstract

Potato tuber shape, eye depth, skin and flesh color are important quality traits for the fresh and processing market. In the present study we developed a mapping population CHAR-01 from two diploid *S. phureja* parents Chaucha roja (Parent-1) and Chaucha amarilla (Parent-2). The two parents and 175 progeny were genotyped using DArT markers, and we assessed the segregation of tuber shape, eye depth, skin and flesh color in this population. Quantitative Trait Loci (QTLs) affecting these important quality traits were identified using the genetic map developed for this population. The most prominent QTLs for tuber shape and eye depth were detected on chromosome X (Parent-2) and explained 33.7% and 14.6% of the variance, respectively. The loci that control these traits were linked. The most important QTLs for skin and flesh color were on chromosome X (Parent-1, 19.9%) and III (Parent-1, 13.9%) respectively. Additional QTLs with minor effects were also detected.

Novel QTLs were also found in the population, underpinning the importance of the Ecuadorian landraces, for tuber shape and eye depth we identified QTLs *Sh-1*, *Sh-2, Ey-1*, *Ey-2* and *Ey-3*. For skin color two QTLs *Sk-2* and *Sk-3*, *Sk -2* were found, which constitute candidate genes for controlling anthocyanin biosynthesis. New, presently unknown QTLs *FL-1* and *FL-3* involved in zeaxanthin accumulation in the yellow-fleshed potatoes were also identified. These results improve our understanding of the inheritance of traits relevant for variety development in potato and the possibility toward the use by INIAP of new approaches for genomic research and develop of new varieties improving the efficiency and precision of conventional plant breeding trough molecular assisted selection (MAS).

Key words: Native potatoes, *Solanum phureja*, tuber shape, eye depth, skin color, flesh color, quantitative trait loci, DArT marker.

Introduction

Potatoes are the most important crop in the horticultural landscape of many countries (Jiménez et al., 2009). In Ecuador, potato is the primary staple crop and one of the most lucrative market crops cultivated in the highlands. Most of the potato production is for domestic consumption and potato planting and harvesting is possible the whole year round due to the country's location on the equator (Devaux et al., 2010).

From Chapter 2, it became clear that the potato quality demands depend on the actor (farmer, trader or consumer) in the production chain and on the region where the potato was grown or consumed. For Ecuador the main tuber traits important for the fresh market were tuber shape, eye depth, skin, flesh color and taste and we also concluded that breeders should pay more attention to the demands of these different actors in the chain.

Despite good results obtained using conventional breeding, new technologies such as DNA marker technology can increase the success of breeding efforts. Numerous marker technologies have been developed and used in potato breeding. This includes restriction fragment length polymorphism (RFLP)(Botstein et al., 1980), randomly amplified polymorphic DNA (RAPD)(Williams et al., 1990), amplified fragment length polymorphism (AFLP)(Vos et al., 1995), microsatellites or simple sequence repeats (SSR)(Hearne et al., 1992) and single nucleotide polymorphism (SNP)(Soleimani et al., 2003).

Recently, another new marker technology, Diversity Arrays Technology (DArT) has been developed (Jaccoud et al., 2001). In DArT, polymorphism detection is based on measuring the presence versus absence of DNA fragments in genomic representations generated from samples of genomic DNA (Kilian et al., 2005). The use of these tools made it possible to construct linkage maps, which are useful for identifying chromosomal regions that contain genes controlling simple as well as quantitative traits using quantitative trait loci (QTL) analysis (Collard et al., 2005; Mohan et al., 1997). Once molecular markers closely linked to desirable traits are identified, they can be used in marker-assisted selection (MAS) at early stages of plant development (Collard and Mackill, 2008).

In case of potato, molecular linkage maps have been constructed for the 12 chromosomes in several diploid mapping populations (Bonierbale et al., 1988; Brugmans et al., 2002; Gebhardt et al., 1989; Gebhardt et al., 1991; Jacobs et al., 1995; Tanksley et al., 1992; van der Voort et al., 1997; van Eck et al., 1995) and also in tetraploid potato (Meyer et al., 1998). These molecular maps and the DNA markers are the current backbone of genome analysis in cultivated potato and related tuber-bearing *Solanum* species (Gebhardt, 2005b). Markers linked to QTLs can be used to more rapidly incorporate desirable regions into agronomically superior genotypes and recently the genome sequence of potato *S. tuberosum* group Phureja DM1-3 516 R44 (DM) is available that provides a platform for genetic improvement of potato (Potato Genome Sequencing Consortium, 2011).

For tuber shape, a single locus on chromosome X was identified with a dominant allele *Ro* conferring round tuber shape (Van Eck et al., 1994b), other reports mention additional QTLs on chromosome II, V and XI (Bradshaw et al., 2008), II and XI (ŚLiwka et al., 2008) and VII and XII (Sørensen, 2006), clearly showing the complexity of the trait. Eye depth appears to be controlled by a single locus, which is closely linked to the *Ro* locus on chromosome X at a distance of 4 cM (Li et al., 2005).

Pigmentation of the tuber skin is controlled by a locus located on chromosome X (van Eck, 2007) and genetics studies have identified locus *Y/y* on chromosome III conferring different tuber flesh colors (Bonierbale et al., 1988). The *Y* gene has been associated with β–carotene hydroxilase (*Chy*) and additional modifying genes are suggested to be involved in controlling total carotenoid levels (Brown et al., 2006).

Recently Kloosterman et al., (2010) found that *Chy* was as responsible for a major quantitative trait locus for flesh color and by association analysis, the yellow fleshed tubers which accumulate high levels of zeaxanthin epoxidase (*Zep*) were found to be controlled by a combination of the dominant *Chy* allele and homozygous recessive *Zep* allele (Wolters et al., 2010). Furthermore, (Acharjee et al., 2011) using Random Forest regression found that genes *Chy* and *Zep* were significantly associated with potato tuber flesh color.

All of these molecular approaches are widely and successfully used in developed countries. However, there is still little adoption in developing countries because of limited human and financial resources, inadequate high-throughput capacity, poor phenotyping infrastructure and lack of information systems (Ribaut et al., 2010).

In Ecuador there are several activities in progress, including the molecular characterization of the Ecuadorian potato collection, the characterization of *P. infestans* isolates collected from all over the country and the construction of linkage maps. Here we describe the identification of QTLs for shape, skin and flesh color in a diploid population resulting from a cross between two native potato landraces.

The information obtained will be used to set up a MAS potato breeding program for selection of improved varieties using the Ecuadorian biodiversity, with focus on late blight resistance and quality that are required by the different actors of the potato agri-food chain in three Ecuadorian regions.

Materials and methods

Plant material:

Two diploid native landraces of *S. phureja* from the Ecuadorian potato collection were used to develop the mapping population. The female parent (Parent-1) was Chaucha roja (HSO 369) with a red skin, oval tuber shape and deep eyes while the male parent (Parent-2) was Chaucha amarilla (HSO 131) has yellow skin, elliptic tuber shape and shallow eyes. Both landraces have yellow flesh. A total of 200 offspring F1 tubers were obtained; this population will be referred to as CHAR-01.

The population was planted in the Sta. Catalina Experimental Station from National Agricultural Research (INIAP) of Ecuador at 3,058 meters above sea level. The trial had a randomized complete block design with two blocks and single-drill plots of three tubers spaced 40 cm apart. The distance between adjacent drills was 100 cm. Chemical fertilization was applied previous to the planting using the INIAPs recommendation for potato that consists of 100-250-80 kg ha^{-1} of Nitrogen, Phosphorus and Potassium respectively. To avoid pests and diseases, chemical crop protection was carried out, four applications of cymoxanil, four of dimethomorph to control late blight and four sprays of thiametoxam and lambdacihalotrina to avoid insects (*Premnotripes vorax*, *Lyriomiza huidobrensis* and *Epitrix* spp.) were made.

Phenotyping:

At harvest time for each offspring tuber shape, eye depth, skin and flesh color were measured on five tubers of each plot.

Tuber shape was determined according to (Gómez, 2000), who described eight types of tuber shape, which were transformed into numerical scores from 1 to 8, where 1 = compressed, 2= round, 3=ovate, 4=obovate, 5= elliptic, 6=oblong, 7=long-oblong and 8=elongate.

Eye depth was scored using a 1-9 scale, where one means protruding eye and nine means very deep eye (Gómez, 2000).

Tuber skin color, was measured visually according to a color card (Gómez, 2000), from 1–9 scale, where 1= white-cream, 2= yellow, 3=orange, 4=brown, 5=pink, 6=red, 7=red-purple, 8=purple and 9 blackish.

Tuber flesh color, was evaluated visually using the color card (Gómez, 2000), from 1–8, where 1=white, 2=cream, 3=yellow (bright), 4=yellow, 5=yellow (intense), 6=red, 7=purple, 8=violet.

Segregation ratio of phenotypic traits were tested using the Chi-square test with a significance threshold of P=0.05. Estimates of the variance components were used to compute broad-sense heritability (H) for each trait. It was estimated as the ratio of the genotypic (σ^2_g) to total phenotypic variance, $H = \sigma^2_g / (\sigma^2_g + \sigma^2_e/r)$, where, σ^2_g= genotypic variance, σ^2_e= error variance and r is the number of replications (Bos, 1995).

DNA extraction and marker analysis:

The DNA was extracted from each offspring using the tuber sprouts at INIAP Biotechnology lab, according to the protocol described (http://www.diversityarrays.com). DNA was packed and shipped to Diversity Arrays Technology Pty Ltd. (DArT technology), Canberra, Australia. The analysis was performed by DArT technology. A DArT array (Jaccoud et al., 2001) containing 1426 markers was used. Marker information for 175 individuals, included the parents, was received from DArT technology, 25 samples were not analyzed because of poor DNA quality.

Construction of the linkage map:

The mapping population consisted of the parents and a subset of 175 individuals of the CHAR-01 population. Linkage analysis was performed in JoinMap ver. 4 (Van Ooijen, 2006) with parameters set for CP (cross pollinator) derived progeny and Haldane´s mapping function.

The grouping parameters used was a recombination frequency threshold smaller than 0.25. Loci were placed into linkage groups (LG) using a minimum LOD score of 3. Linkage groups were identified as representing (part of) specific chromosomes based on the position of known DArT markers using previously published potato map (http://www.potatogenome.net). Maps were visualized using the software package MapChart 2.1 (Voorrips, 2002). Maps were constructed for each of the parents separately.

QTL analysis:

The QTL analysis was conducted using MapQTL 6.0 software (Van Ooijen, 2009). The two parental maps were used separately for the analysis. Interval mapping (IM) was applied to reveal QTL regions for tuber shape, eye depth, skin and flesh color in the offspring population using the established linkage map and the observed phenotypic traits.

In order to determine a genome wide significance threshold for the LOD score, the 1,000-times permutation test at the 0.05 significance level was calculated for each trait and parent maps. A QTL was considered significant when it had a LOD score higher than the genome-wide threshold. LOD peaks were used to estimate the position of the QTLs on the map. A nonparametric single marker-based Kruskal-Wallis analysis was conducted to confirm the significance of QTLs detected by interval mapping and to detect additional potential QTL when they were examined individually. For the Kruskal-Wallis test, an association was indicated when the mean values of the marker classes were significantly different at $P<0.01$.

Results

Phenotypic characterization of the CHAR-01 population:

In order to identify the variation of the external tuber quality traits of CHAR-01 population a tuber sample of each offspring per replicate was evaluated for each morphological character. All the phenotypic traits evaluated in the CHAR-01 population deviated from normality.

The full range of tuber shape was observed from grade 1 (compressed) to grade 8 (elongate). Most of the offspring (51) had a round tuber shape (Figure 2a). Tuber eye depth had a variation from shallow (grade 3) to very deep (grade 9). Most of the individuals had shallow or deep eyes, 82 and 74 genotypes respectively, with 19 individuals with very deep eyes (Figure 2b). Tuber skin color varied from white-cream (score 1) with 27 individuals to red-purple (score 7) with 10 individuals. Most of the offspring (98) had yellow color (Figure 2c). Tuber flesh color had a variation from white (score 1) to intense yellow (score 5). Most of the clones (58) had a bright yellow color (Figure 2d). The estimated broad sense heritabilities calculated were 0.86, 0.91, 0.74 and 0.94 for tuber shape, eye depth, skin color and flesh color respectively.

DArT markers:

In the CHAR-01 population 733 polymorphic DArT markers were identified, 388 for the parent-1 (P1) and 134 for the parent-2 (P2). In addition, we found 211 bridge markers. In total 599 markers for P1 and 345 for P2 were used for the analysis (Table 1).

Linkage map construction:

The linkage map was generated for each parent based on a population of 175 individuals. The parent-1 map covered a total map distance of 388.6 centimorgans (cM), while the parent-2 map covered a total map distance of 281.9 cM (Table 1).

Based on the position of known DArT markers in the DM potato genome sequence (Potato Genome Sequencing Consortium, 2011) the linkage groups determined by JoinMap ver. 4 (Van Ooijen, 2006), were assigned to the potato chromosomes. A total of 266 redundant markers (with the same scoring patterns) were identified 247 for P1 and 19 for P2 (Table 1). These markers were excluded from the analysis.

For parent-1, twenty-one linkage groups (LGs) were identified; the mean distance between two consecutive loci was 1.26 cM. The number of markers per chromosome ranged from 3 for chromosome XII to 71 for chromosome VII. There were no markers on chromosome IV. The average number of markers per chromosome was 26. We excluded 247 markers because, according to JoinMap analysis, they were perfectly identical, with a similarity of 1.00, consequently they will map at exactly the same position (Van Ooijen, 2006). Furthermore, the analysis could not assign 43 markers to any linkage group (Table 1).

For parent-2, nineteen LGs were identified; the mean distance between two consecutive loci was 0.93 cM. The range of markers per chromosome was 3 for chromosome IV and 70 for chromosome VII. The average number of markers per chromosome was 25, there were no markers on chromosome VIII and we excluded 19 markers located in identical positions and 23 markers were not assigned to any group (Table 1). Despite the presence of markers on the chromosome III, IV and XII, it was not possible to construct separate linkage groups for these chromosomes using the JoinMap analysis.

Table 1. Summary information about of CHAR-01 linkage map

	Parent-1		Parent-2	
Chromosome	Number of markers	Length (cM)	Number of markers	Length (cM)
I	21	17.8	47	75.0
II	17	0.8	5	14.6
III	41	34.6	15	[a]
IV	0	--	3	[a]
V	26	49.4	20	42.3
VI	23	33.5	32	48.1
VII	71	53.6	70	48.6
VIII	4	16.0	0	--
IX	14	25.6	22	6.0
X	39	52.3	33	21.9
XI	50	70.9	50	25.3
XII	3	34.3	6	[a]
Total	**309**	**388.6**	**303**	**281.9**
Excluded *	247		19	
Ungrouped**	43		23	
TOTAL	599		345	

[a] Join Map analysis could not calculate the chromosome map
* Markers in identical positions (Redundant markers)
** These markers were not assigned to any linkage group

QTL analysis:

To identify the position of genomic regions involved in shape, skin color, flesh color, eye depth. QTL analysis was performed using the parental linkage maps (P1 and P2). QTLs were consistently identified for tuber shape, eye depth, skin and flesh color by Interval mapping and Kruskal-Wallis for P1 on chromosomes I, III, VI, IX and X and for parent-2 on chromosomes I, V, VI and X (Figure 1, Table 2). Additional associations for tuber shape, eye depth and skin color on P1 and skin color on P2 were identified by Kruskal Wallis analysis (Table 2).

Discussion

Our results showed that most of the traits evaluated were controlled by a few major genes and some of the QTLs previously identified in other *Solanum* populations for tuber shape, eye depth, skin and flesh color were also identified in the CHAR-01 population. In addition some new QTLs were detected.

DArT map

For diploid potatoes, several linkage maps have been constructed using different mapping populations and marker types (Bonierbale et al., 1988; Brugmans et al., 2002; Gebhardt et al., 1989; Jacobs et al., 1995; Tanksley et al., 1992; van der Voort et al., 1997; van Eck et al., 1995). However, our research reported in this chapter describes one of the first maps of diploid potato constructed using DArT markers.

Śliwka et al., (2012a) and (2012b) published the mapping of a major resistance gene *Rpi-rzc1* against *P. infestans* originating from *Solanum ruiz-ceballosii* and a late blight resistance gene on chromosome VII in a population coming from *S. michoacanum* using DArT markers. Another map containing, amongst others, DArT markers was created for the *S. tuberosum* group Phureja DM1-3 516 R44 (DM) was published recently (Potato Genome Sequencing Consortium, 2011).

The *S. phureja* diploid map of DM consists of 2,530 markers, including 1,827 DArT markers, 316 Simple Sequence Repeat markers and 387 Single Nucleotide Polymorphisms. For the genotyping of the CHAR-01 population 1,426 DArT markers were used, of these 562 markers were in common with DM. For the mapping of the CHAR-01 population 733 polymorphic DArT markers were used, 388 for the parent-1, 134 for the parent-2 and 211 as bridge markers.

In the mapping process, DArT markers were classified as redundant when they showed identical scores among the progeny, leading to clustering at one genetic position. Since DArT markers are obtained by cloning random fragments of genomics representations (Wenzl et al., 2006), some degree of redundancy is expected (Rodríguez-Suárez et al., 2012).

In CHAR-01 population considerable redundancy among DArT markers was recorded, as consequence 266 markers were removed from the analysis. High level of marker redundancy has been previously reported using DArT markers in banana (Risterucci et al., 2009), oat (Oliver et al., 2011), lilium (Shahin et al., 2011), apple (Schouten et al., 2011) and wild barley (Rodríguez-Suárez et al., 2012).

In our study DArT markers tended to cluster in various regions, with little or no coverage in other regions as result DArT coverage was not uniform across the genome of the CHAR-01 population. For example some chromosomes as VII, X and XI in both parents had good coverage with DArT markers, whereas the chromosomes IV, VIII and XII had a few markers and in some cases there were no recombination among these markers. This low level of polymorphism affected the resolution of our map; chromosome IV was not identified in either of the parents and for the parent-2 the chromosomes III, VIII and XII were also not identifiable. Such clustering of DArT markers may be caused by an absence of recombination between the markers due to tight genetic linkage or high DNA sequence similarity.

Although the overall quality and resolution of the CHAR-01 linkage map obtained in this study (388 cM for P1 and 282 cM for P2) was low, the coverage was not uniform across the potato genome and one chromosome was not identified on P1 and four on P2, the chromosome X where QTLs for tuber shape, eye depth and skin color have been reported (Li et al., 2005; van Eck, 2007; Van Eck et al., 1994b), had good DArT marker coverage. An alternative to improve the resolution of map based on DArT, other markers could be included such as SSR markers with known position on the genome.

Tuber shape and eye depth:

The shape of the tuber is one of the most eye-catching traits of the potato crop (Van Eck et al., 1994a). The tuber shape which is most favoured depends on the actor in the potato food chain. In Ecuador most of the consumers prefer round or long shapes depending on the region (Chapter 2). To minimize waste, varieties with long tubers are preferred for French fries and varieties with round tubers are ideal for crisps (Van Eck et al., 1994a, Kirkman, 2007). Eye depth is also an important component of tuber quality as it adds to the cost of peeling and affects the general appearance (Li et al., 2005).

In our study, general tuber shape and eye depth showed a large variation, from compressed to elongate and from shallow to very deep, respectively (Figure 2). These distributions suggest a polygenic inheritance. However, at the diploid level some studies have concluded that the inheritance is monogenic and regulated by the *Ro* locus for tuber shape (Van Eck et al., 1994a) and *Eyd* locus for eye depth (Li et al., 2005).

To analyze if tuber shape follows a Mendelian model of segregation, the eight classes identified were reduced to three (round, oval and long) as was done in other populations studied (De Jong and Burns, 1993; Li et al., 2005). Based on this classification the segregation of tuber shape observed was 58:83:34 for round, oval and long, which fits a 1:2:1 monogenic ratio (X^2= 0.148; P< 0.01). As both parents in CHAR-01 were oval shape, round shape must be dominant over long, which fits the model proposed by (De Jong and Burns, 1993; Van Eck et al., 1994b), that round shape (*Ro_*) is dominant over long (*ro ro*).

Tuber eye depth had a segregation of 82:74:19 (shallow, deep and very deep). Excluding the very deep types (19), the relation was 1:1 for shallow and deep types (X^2=0.41 P<0.001), which suggests that either the female or male parent are heterozygous while the other was homozygous at that locus (*Eyd_* x *eyd eyd*), as one of the parents had shallow eyes and the other deep. In our study either the deep or shallow may be dominant. For the presence of very deep eye types in the CHAR-01 population there are two possible explanations. First, the existence of one or more modifying factors as Li et al., (2005) suggested for the presence of intermediate depth eye types in a genetic mapping diploid population studying the genetics of tuber eye depth. Second, in the scoring used for tuber eye depth in our study, the very deep types were more close to the deep type; in this case the relation 1:1 for shallow and deep eyes still persist.

In previous studies using hybrid mapping populations consisting of *S. phureja*, *S. vernei* and *S. tuberosum,* QTLs for tuber shape and eye depth were identified on chromosome X, they are encoded by two major loci *Ro ro* and *Eyd eyd* located close to each other (Van Eck et al., 1994a; Li et al., 2005).

In the CHAR-01 population we detected consistently QTLs for tuber shape and eye depth in chromosome I and X. The QTLs with the major effect for tuber shape *Sh-3* and for eye depth *Ey-4* and *Ey-5* were located in chromosome X (Parent-2). The percentage of total phenotypic variance explained by these QTLs was 33.7%, 10.5% and 14.6% respectively.

For tuber eye depth our results are comparable with the values reported by Śliwka et al., (2008) when studied diploid hybrid population 98-21 with values of phenotyping variation ranging between 10.3% and 14.7%. However, for tuber shape the percentage of phenotypic variation in our study was higher than those found by Śliwka et al., (2008) study that reported a value of 2.7%.

The QTLs *Sh-3* and *Ey-4* located on chromosome X probably are similar to the *Ro ro* and *Eyd eyd* loci reported by van Eck et al., (1994b). The mapping results in the CHAR-01 population demonstrated that *Sh-3* and *Ey-4* are closely linked. In our study both loci are 4 cM apart, similar to the result of Li et al., (2005).

However, additional QTLs for tuber shape and eye depth were identified on chromosome I, *Sh-1*, *Sh-2* and *Ey-1*, *Ey-2* (P1 and P2) and *Ey-3* (P2) with smaller effects than the QTLs identified on chromosome X. Results of the mapping analysis shows that *Sh-1*, *Ey-1* and *Sh-2*, *Ey-3* are linked. The presence of these QTLs has not been reported previously. This is probably due of the genetic background of the CHAR-01 population as QTL effects may differ in different genetic backgrounds due interactions with other loci or epistasis (Holland, 2001; Liao et al., 2001).

Tuber skin color

The skin potato tuber color results from differences in the accumulation of red, purple or no anthocyanin pigments (Jung et al., 2009). In diploid potato three classical loci *I*, *R*, and *P* are known to be involved in coloration of potato tuber skin (Dodds and Long, 1955, 1956). The potato *R* locus on chromosome II, is required for the production of red anthocyanins, while the *P* locus that maps to chromosome XI is required for the synthesis of purple pigments such as petunidin based anthocyanins and purple delphinidin-based pigments and a third locus, *I* on chromosome X, is required for the synthesis of red or purple anthocyanins in tuber skin (Van Eck et al., 1994b; De Jong et al., 2004; Jung et al., 2009).

The CHAR-01 population showed a large variation for skin color, from white-cream to red-purple, the QTL analysis of the CHAR-01 population for tuber skin color identified a major QTL *Sk-1* located in chromosome X, it accounted for 19.9% of the total phenotypic variation, a result that is comparable to previous reports (De Jong et al., 2004; Van Eck, 2007).

The QTL *Sk-1* probably is the *I* locus required for the synthesis of red or purple anthocyanins in tuber skin that correspond to *Petunia* locus *an2* encoding R2R3MYB transcription factor of the anthocyanin pathway (De Jong et al., 2004, Jung et al., 2009). De Jong et al., (2004) established that *an2* mapped close to the telomere of lower arm of chromosome X, a result confirmed by the *an2* position in the DM potato genome, where *an2* is located between 51.551 Mb and 51.552 Mb on chromosome X, close to *Sk-1* identified in our study. Therefore we confirm *an2* as candidate gene for *I* locus.

The absence of QTLs on chromosome II and XI (locus *R* and *P*) may be explained by the very limited resolution of our genetic map on chromosome II, whereas the *P* locus probably was not present in our population since the CHAR-01 and the progeny were not purple skinned.

Two additional QTLs *Sk-2* (P1) and *Sk-3* (P2) with minor effects were detected on chromosome IX and V, both QTLs that have not been reported previously. The QTLs *Sk-2* and *Sk-3* probably are involved in anthocyanin biosynthesis in the skin tuber. The research of Spelt et al., (2000) and De Jong et al., (2004) support this hypothesis. They mention that on chromosome V there are at least two anthocyanin biosynthesis genes, chalcone isomerase (*chi*) and chalcone synthase (*chs*) and in chromosome IX the bHLH gene homologous of petunia anthocyanin is located.

The sequence of DM confirms the location of the genes *chi*, *chs B* and *chs 2* on chromosome V at positions between 42.671 and 44.099 Mb, and this is likely to correspond to *Sk-3*. This region of chromosome V constitutes an important section for traits related to anthocyanin biosynthetic pathway where several candidate genes were located. Furthermore, the published sequence of the potato (DM) genome, confirms the location of the bHLH gene in chromosome IX in position between 47.305Mb and 47.309Mb that probably corresponds to *Sk-2.*

Additionally, the QTLs *Sk-1* and *Ey-2* were located in the same region on chromosome X (P1). There is no previous report about this relationship. However, the linkage between the loci for tuber skin color and tuber shape have been demonstrated by De Jong and Rowe (1972) and confirmed by De Jong (1987) and since loci for tuber eye depth and shape are linked (Li et al., 2005). Thus, the loci for skin color and eye depth might be linked. This relation between *Sk*-1 and *Ey-2* was identified only for P1 because the *I* locus responsible for the red anthocyanin biosynthesis was present only on this parent.

Tuber flesh color

The flesh color of potato tubers is due to the accumulation of two different classes of pigment anthocyanins and carotenoids (Brown, 1993). Tuber yellow flesh color depends on carotenoids such as lutein and zeaxanthin (Lu et al., 2001). Genetics studies have identified locus *Y/y* on chromosome III conferring different tuber flesh colors (Bonierbale et al., 1988) and recently Wolters et al., (2010) investigated the genetic and molecular biology of orange flesh color in potato, they hypothesized that only genotypes combining presence of the dominant beta-carotene hydroxylase (*Chy*) allele with homozygosity for the recessive zeaxanthin epoxidase (*Zep*) allele produced orange-fleshed tubers that accumulated large amounts of zeaxanthin.

Tuber flesh color had a continuous variation from white-cream to intense yellow in the CHAR-01 population, the segregation observed was 34:58:49:34 fits the 1:2:2:1 ratio (X^2= 5.54 P<0.001). This relation does not correspond to the one locus Mendelian model and suggest that there is more than one gene involved. This result could be explained by the expression of additional color factors that are involved in the genetic background of the population (*S. phureja*) or the presence of modifying genes that are affecting the different degrees of yellowness as ŚLiwka et al., (2008) suggested when studied diploid hybrid population 98-21.

In the CHAR-01 population, one of the QTLs with the major effect *FL-2* was located on chromosome III, which is similar to the position reported by Bonierbale et al., (1988). However, it was only detected in P1, as for P2 the analysis did not calculate a map for chromosome III.

In our study the QTL *FL-2* explained 13.9% of the total phenotypic variation; this value is higher than those previously reported. Śliwka et al., (2008) in population 98-21 for tuber flesh color identified a minor putative QTL in chromosome III that explained 3.7% of the total variation.

The QTL *FL-2* probably is associated with β–carotene hydroxilase (*Chy*), which has been mapped at the same position as the *Y* locus (Thorup et al., 2000) and in several studies *Chy* has been reported as the main candidate gene for controlling tuber flesh color (Brown et al., 2006; Kloosterman et al., 2010; Wolters et al., 2010). Furthermore, measuring the association between a transcriptomics data set and flesh color using Random Forest regression it was found that in the top 50 of associated genes by their variable importance *Chy* ranked first (Acharjee et al., 2011).

Recently with the publication of the DM genome sequence, the position of *Chy* in chromosome III was confirmed, this gene is located between 20.358 Mb and 20.361 Mb that mapped in a close position with *FL-2* reported in our study.

Two additional QTLs *FL-1* and *FL-3* were located on chromosome I and VI in both parents respectively. The presence of these QTLs has not been previously reported. These may be explained by modifying genes that are involved in the different grades of yellowness of the tuber flesh (Bonierbale et al., 1988; Schick, 1956; van Eck, 2007).

The *FL-1* probably correspond to the carotenoid cleavage dioxygenase gen (*CCD*) that according to Zhou et al.,(2011) research *Chy*, *Zep* and *CCD* are the main genes involved in the carotenoid metabolic pathway. The DM potato genome mapped the *CCD* in chromosome I in a close position with *FL-1*. Thus, *Chy*, *Zep* and *CCD* are candidate genes for tuber flesh color where the synergistic effect of elevated expression of *Chy* as well as suppressed expression of *Zep* and *CCD* is responsible for zeaxanthin accumulation in the yellow-fleshed potatoes (Zhou et al., 2011).

The presence of *FL-3* in chromosome VI is agree with the DM potato genome that mapped the *Chy* candidate gene for controlling tuber flesh color in the interval

(34.166Mb - 34.168Mb) in chromosome VI, that is near the location of *FL-3* identified in our study.

The QTL *FL-1* on chromosome I, are located in the same region as the QTLs *Sh-1* and *Ey-1*. There are no previous reports about a functional relationship between these loci. However, D´hoop et al., (2008), studying quality traits in potato using association mapping, report loci for tuber flesh color on several chromosomes, including chromosome I.

Our study identified in CHAR-01 population novel QTLs that have not been reported previously, for tuber shape and eye depth QTLs *Sh-1*, *Sh-2, Ey-1*, *Ey-2* and *Ey-3* identified on chromosome I. For skin color two QTLs *Sk-2* and *Sk-3* were detected on chromosome IX and V respectively, *Sk -2* probably correspond a (*chi*) or (*chs*) genes, while *Sk-3* is related to *bHLH* gene, which constitute candidate genes for controlling anthocyanin biosynthesis.

For tuber flesh color the QTLs *FL-1* and *FL-3* were located on chromosome I and VI. *Fl-1* probably correspond to (*CCD*) gen and *Fl-3* possibly corresponde to (*Chy*) gen, both candidate genes for controlling tuber flesh color.

Furthermore there were also QTLs that are consistent with other studies using mapping populations with different backgrounds e.g. QTLs for tuber shape, eye depth, and tuber skin color on chromosome X (Van Eck et al., 1994a; Li et al. 2005) or QTLs for tuber flesh color on chromosome III (Bonierbale et al., 1988).

Implications for potato Breeding

Potato breeding in INIAP traditionally consisted of making crosses between pairs of parents with complementary characteristics, followed by several selection cycles (Cuesta et al., 2005b). Despite continued improvement of potato by conventional breeding, new technologies such as biotechnology could maximize the probability of success (Collard and Mackill, 2008).

Marker-assisted selection (MAS) is one of the most efficient applications of biotechnology that may greatly increase the efficiency and effectiveness in plant breeding compared to conventional breeding methods (Collard et al., 2005). In our study QTLs for tuber shape, eye depth, skin and flesh color were identified, the DArT markers linked with the QTLs found in our study might be used in the breeding program, to combine these traits in one superior variety with the characteristics demanded by the fresh and processing market (Chapter 2).

The advantage of the QTLs identified in the CHAR-01 population for use in a MAS program is that most of them had large effects e.g. QTL *Sh-3* explained 33.7% of the total phenotypic variation and QTL *Sh-1* explained 19.8% of the total phenotypic variation. Furthermore, QTLs *FL-1*, *Sh-1* and *Ey-1* were located in the same region of chromosome I as well QTLs *Sh-3* and *Ey-4* mapped in similar positions in chromosome X.

These results suggest that DArT markers located close to the QTLs for tuber shape, eye depth, skin and flesh color could be incorporated into a MAS breeding scheme in order to obtain the required potato phenotypes. Furthermore, from Chapter 2, it has become clear that the main external quality traits for the fresh and processing market are related to tuber shape and eye depth.

Based on these requirements of the fresh and processing market in the first phase of the breeding scheme, MAS for tuber shape and eye depth should be applied. The objective is to select round tubers for the fresh market and chips industry and long tubers for the processing market as French fries. In both cases tubers with shallow eyes is required.

Therefore, markers associated with *Sh-3* and *Ey-4* in chromosome X, and markers linked to *Sh-1* and *Ey-1* in chromosome I constitute good alternatives. An advantage of DArT markers is that they can readily be sequenced and converted into a single locus marker for applications in MAS (Hai Thi Hong et al., 2010; Shahin et al., 2011).

The obtained results improve our understanding of the inheritance of quality traits for variety development in potato and will provide a resource for molecular marker development and the genetic characterization of other traits of importance for potato in Ecuador and opens up the possibility toward the use by INIAP of new approaches for genomic research and develop of new varieties improving the efficiency and precision of conventional plant breeding trough MAS.

The availability of the DM potato genome sequence was important for the construction of the genetic map based on CHAR-01 population, as well the identification of candidate genes related to important tuber quality traits associated with DArT markers.

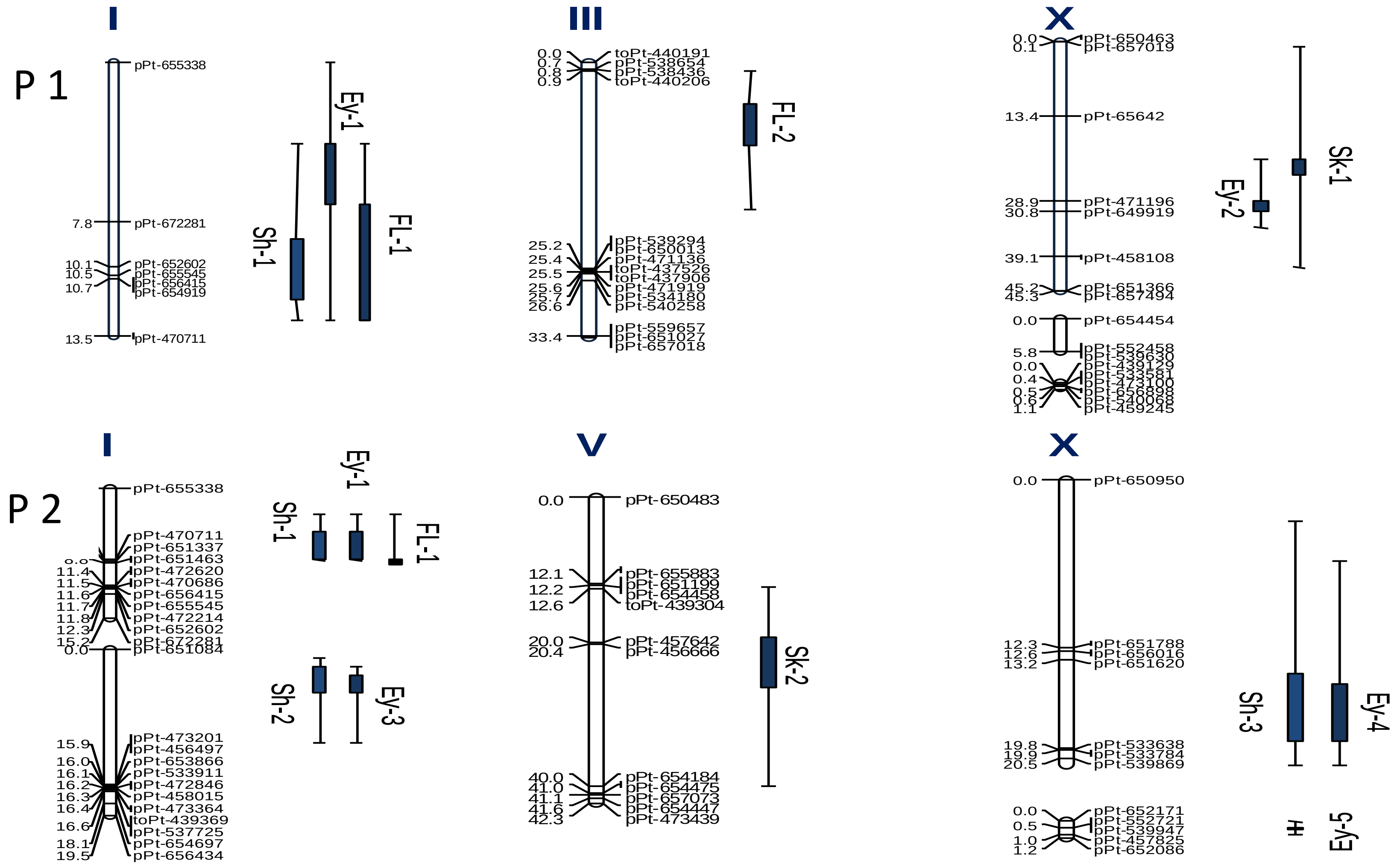

Figure 1. QTLs identified for tuber shape, eye depth, skin and flesh color in potato. Only the chromosomes containing a QTL are shown for the two parents (P1 and P2) of the CHAR-01 population; Sh=Tuber shape, Ey= Eye depth, Sk= Skin color, FL=Flesh color

Qutantitative trait loci analysis

Table 2. Quantitative trait loci associated with tuber shape, eye depth, skin and flesh color by Interval mapping and Kruskall-Wallis analysis in CHAR-01 potato population.

						Interval Mapping					Kruskal-Wallis	
Parent	Trait	QTL	Chromosome	Linkage	Position	DArT Marker Interval		LOD	LOD	%Var	DArT Marker	*P*value
1	Shape	Sh -1	1	21	8.86	capPt-672281	pPt-652602	8.4	2.2	19.8	capPt-672281	0.0001
		Sh -1	1	21	11.69	pPt-654919	pPt-470711	8.4	2.2	19.8	pPt-654919	0.0001
		-	10	8	5.83	N/A	N/A	N/A	N/A	N/A	pPt-539630	0.001
		-	10	23	0.37	N/A	N/A	N/A	N/A	N/A	tpPt-439478	0.01
1	Eye depth	Ey-1	1	21	4.00	pPt-655338	capPt-672281	5.1	2.3	12.5	capPt-672281	0.0001
		-	1	19	1.56	N/A	N/A	N/A	N/A	N/A	pPt-537438	0.0005
		Ey-2	10	7	29.87	pPt-471196	pPt-649919	3.1	2.3	7.8	pPt-471196	0.0005
		-	10	8	5.82	N/A	N/A	N/A	N/A	N/A	pPt-552458	0.0005
1	Skin color	Sk-1	10	7	23.41	pPt-656420	pPt-649919	8.4	2.3	19.9	pPt-649919	0.0001
		Sk-2	9	24	2.07	pPt-456925	pPt-456925	2.4	2.3	6.2	pPt-456925	0.0001
		-	10	23	0.00	N/A	N/A	N/A	N/A	N/A	toPt-439129	0.0005
1	Flesh color	FL-1	1	21	7.00	pPt-655338	capPt-672281	5.7	2.3	13.9	capPt-672281	0.0001
		FL-2	3	13	4.92	toPt-440206	pPt-539294	5.7	2.3	13.9	toPt-440206	0.0001
		FL-3	6	30	2.04	pPt-653319	pPt-651356	2.6	2.3	6.5	pPt-653319	0.005
2	Shape	Sh-1	1	2	8.39	pPt-470711	pPt-470711	6.7	2.2	16.2	pPt-470711	0.0001
		Sh-2	1	19	2.00	pPt-651084	pPt-473201	2.3	2.2	5.8	pPt-651084	0.005
		Sh-3	10	3	15.18	pPt-651620	pPt-533638	15.6	2.2	33.7	pPt-651620	0.0001
2	Eye depth	Ey-1	1	2	5.00	pPt-655338	pPt-651337	3.6	2.1	9.1	pPt-655338	0.0001
		Ey-3	1	19	5.00	pPt-651084	pPt-473201	3.7	2.1	9.2	pPt-651084	0.0005
		Ey-4	10	3	19.18	pPt-651620	pPt-533638	4.2	2.1	10.5	pPt-533638	0.0001
		Ey-5	10	4	0.52	pPt-654281	pPt-457825	6.0	2.1	14.6	pPt-457825	0.0001
2	Skin color	Sk-3	5	20	22.36	pPt-456666	pPt-456666	2.3	2.1	5.8	pPt-456666	0.001
		-	10	22	0.09	N/A	N/A	N/A	N/A	N/A	pPt-459245	0.001
2	Flesh color	FL-1	1	2	8.39	pPt-470711	pPt-470711	4.1	2.1	10.2	pPt-470711	0.0001
		FL-3	6	8	7.00	pPt-653319	pPt-533617	2.9	2.1	6.8	pPt-533617	0.005

A QTL name consists of the code of a trait and a serial number. N/A = Not available. For each QTL the chromosome number, linkage group, the LOD value and the percentage of phenotypic variation accounted for (% var) are presented. The QTLs detected only by Kruskal-Wallis are indicated as “-“.

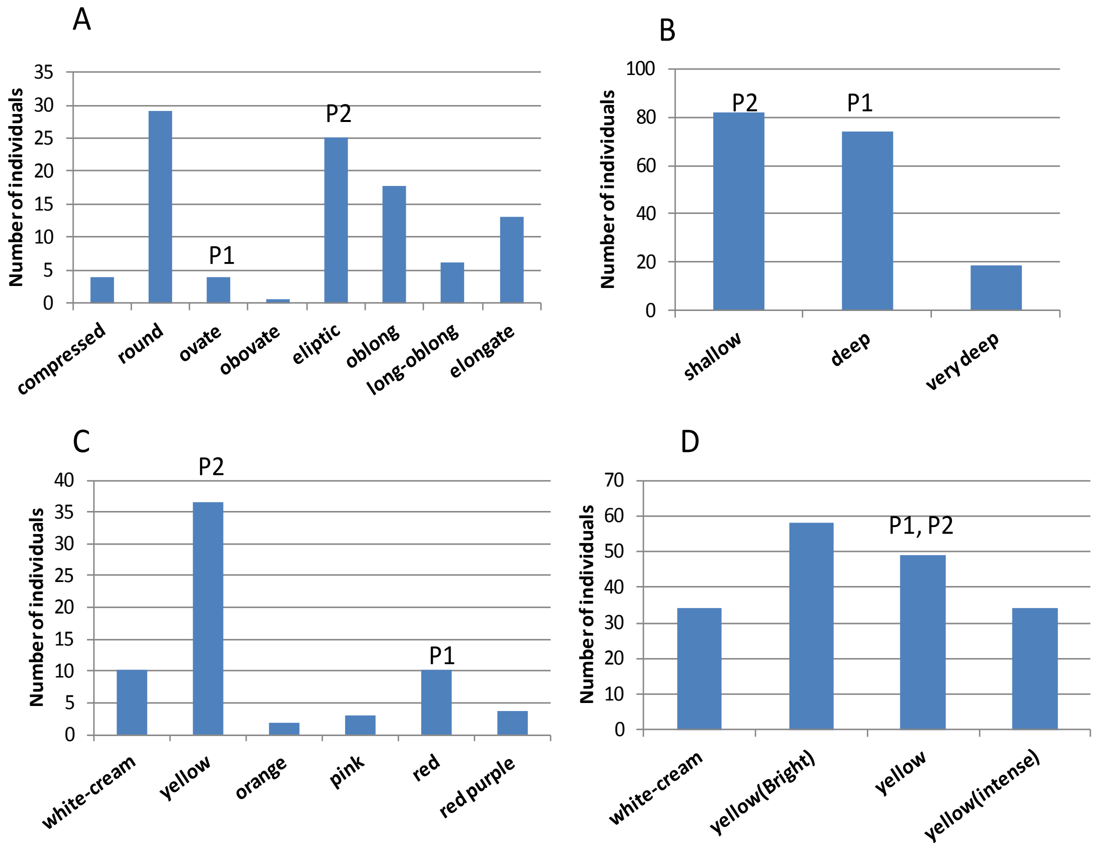

Figure 2. Distribution of the frequencies of tuber shape (A), eye depth (B), skin (C) and flesh color (D) in the CHAR-01 population. The scale of assessment depends on the trait, see Materials and methods.

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Chapter 6

General Discussion

General Discussion

Tuber quality is a subjective and dynamic concept, defined as the sum of favorable characteristics that satisfy the requirements of the different actors in the potato chain. Demands on tuber quality are dependent on the targeted market, such as fresh or processing market.

Breeding for quality to get the ideal potato required for the fresh or processing market is often a complex task and difficult to achieve because of the large number of traits involved and the quantitative nature by which they are inherited, where the resulting phenotype is often based on the interactions among a large number of genes acting together in metabolic pathways (Werij, 2011).

Furthermore, in some cases the selection for one trait has a negative effect on another, e.g. high polyphenol content is a desired character since it is associated with antioxidant capacity of potato. However, this compound also affects enzymatic discoloration as phenolic compounds are oxidized by the enzyme polyphenol oxidase resulting in dark pigments (Friedman, 1997), which is a negative characteristic for the food processing and retail industry (Werij et al., 2007). Therefore, the development of one improved variety that combines all the desired characteristics is a mission difficult to accomplish. As an alternative a set of varieties, all dedicated to a specific application, could be developed.

Fortunately, the genetics of some important quality traits are known. Genes involved have been mapped on the potato genome (Potato Genome Sequencing Consortium, 2011) and the genome sequence of potato is accessible on line (http://www.potatogenome.net), information that will support potato breeders to more fully exploit the genetic potential of potato (Visser et al., 2009).

This thesis defines the "ideotype" of potato for the fresh market required by the main actors in the potato value chain (farmers, traders and consumers) for three Ecuadorian highland regions. Furthermore, in a representative group of potato landraces the variation for the main quality traits was analyzed (Chapter 3, 4) and using DArT markers quantitative trait loci (QTLs) were identified for tuber shape, eye depth, skin and flesh color in a segregating population derived from two *S. phureja* landraces (Chapter 5). Based on all this information, the possibilities for breeding for quality traits to get the ideal potato for the Ecuadorian fresh market based on the genetic variation available in Ecuadorian landraces are discussed.

The potential of the Ecuadorian potato landraces for use in breeding for quality

1. Breeding for the fresh market

Chapter 2 established the preference of farmers, traders and consumers in three Ecuadorian regions. The agronomic traits were quite similar for the three areas with the exception of high production that was not considered in the Southern area; in this region earliness was more important. Furthermore round tuber shape, yellow flesh color and good taste were preferred in all places. However, differences for tuber eye depth, skin color and consistence were found between regions. In Table 1 a description of the ideotype identified in Chapter 2 is presented for the North-Center and the South of Ecuador.

Based on this information and despite the fact that the traditional varieties cultivated have the quality and processing characteristics required, new improved varieties need to be produced because the agronomic attributes of the present day cultivars are not acceptable since all are late blight susceptible, low yielding and have a long life cycle. While the new improved varieties released by INIAP have the agronomic characteristics, they do not suit the quality characteristics of the ideal potato identified for each region (Chapter 2). Therefore, it is necessary to develop a new improved variety with the characteristics of the ideotype for the North-Center and South region (Table 1).

Based on the results of Chapter 3, a summary of the landraces with the best characteristics for the fresh market are presented in (Table 2), the outstanding landraces were Uvilla, Milagrosa and Jubaleña with similar attributes according to the ideotype identified for the North-Center region (Table 1). However, it is necessary to improve some traits that were not present in these landraces, e.g. tuber shape of Milagrosa is not round and the yield of Uvilla is lower than that of other commercial varieties.

Furthermore the diploid landraces Chaucha pintada and Chaucha amarilla and the tetraploid Leona blanca showed the characteristics required for the Southern region. Nevertheless it is necessary to improve tuber shape in these landraces since all have an oblong tuber shape (Table 2).

Tuber shape is genetically controlled by a single locus *Ro/ro* where round (*Ro_*) is dominant over long (*roro*) (Van Eck et al., 1994a). Thus the landraces with round shape such as Uvilla, Puña, Rosada or Bolona with the *Ro* allele should be included in the breeding scheme as progenitors to improve this character in future varieties.

Furthermore in Chapter 5 we identified three QTLs (*Sh-1, Sh-2* and *Sh-3*) associated with tuber shape located on chromosome I and X. These markers could be useful in selecting genotypes with lower dosage of long shape alleles.

The landraces Rosada and Puña had also the quality characteristics demanded in the North-Center and South region respectively (Table 1), but the tuber flesh color was not ideal, it was cream (Table 2).

Table 1. Ideotype of potato identified in three Ecuadorian regions based on the preferences of farmers, traders and consumers.

North-Center	South
Agronomic traits	
Late blight resistance	Late blight resistance
Marketable potato	Marketable potato
High production	Earliness
Tuber quality traits	
Round shape	Round shape
Shallow eyes	Medium eyes
Red/pink skin	Yellow skin
Yellow flesh	Yellow flesh
Big/mean size	Big size
Tuber processing traits	
Good taste	Good taste
Mealy consistence	Waxy consistence
Fast cooking	For "locro" soup

In the breeding scheme it is also necessary to include progenitors with high total carotenoid content (TCC), a trait that is related to yellow flesh color (Burgos et al., 2009, Haynes et al., 1994). Yellow-fleshed potatoes are generally characterized by higher contents of lutein, violaxanthin and total carotenoids (Nesterenko and Sink, 2003) and genetics studies have identified locus *Y/y* on chromosome III conferring different tuber flesh colors (Bonierbale et al., 1988).

The diploid landraces Chaucha botella and Papa chacra, the tetraploid Rosada and the improved varieties Superchola and INIAP-Estela are important sources of genes for high TCC (yellow flesh color) according to the results of Chapter 4 (Table 4). Moreover, we could use the QTLs associated to yellow flesh color (*FL-1, FL-2* and *FL-2*) identified in Chapter 5 for selecting genotypes with this character in a molecular assisted selection program (MAS).

The variation of the different quality traits observed in potato landraces (Chapter 3), offer a great opportunity to get the ideotype required for each Ecuadorian region (Table 1) through traditional breeding or using MAS with the QTLs identified in Chapter 5. Since most of the observed variation was genetic and most of the quality traits showed high heritability we expect fast progress in breeding for those characters.

Table 2. Potato landraces selected for high yield kg plant^{-1}, tuber shape, eye depth, skin color, flesh color, greening (days after harvest), dormancy (days after harvest), dry matter content (DMC %), total glycoalkaloid content (TGA mg 100g^{-1}) and reducing sugar content (RSC %) for the fresh market.

2n	Landrace	Shape	Eye depth	Skin(a) Color	Flesh(a) color	Yield	Greening	Dormancy	DMC	TGA	RSC
4x	Uvilla	Round	Shallow	Y/R	Yb	0.26	56.8	82.4	22.8	10.96	0.043
2x	Chaucha p.	L-oblong	Medium	Y	Yb	0.74	93.3	18.4	21.0	2.72	--
4x	Milagrosa	Oblong	Shallow	Pi	Y	0.88	71.6	103.4	22.1	9.88	0.027
4x	Bolona	Round	Medium	WC/Pi	Yb	0.41	94.9	37.3	21.4	4.64	0.024
4x	Carrizo	Oblong	Deep	P	C	0.55	88.7	16.3	22.2	2.82	0.015
2x	Chaucha am.	Oblong	Medium	O	Yi	0.70	66.1	8.3	21.0	5.18	0.251
4x	Jubaleña	Oblong	Shallow	R/P	Y	0.52	59.1	59.0	21.8	--	--
4x	Leona	Oblong	Medium	WC/Pi	C/P	0.61	93.3	17.9	23.3	2.35	0.077
4x	Leona blanca	Oblong	Shallow	Y	Yb	0.45	51.3	89.4	24.0	10.19	0.046
4x	Leona negra	Oblong	Shallow	P/R	WC	0.32	--	--	23.9	5.50	0.039
4x	Puña	Round	Shallow	R/P	C	0.30	73.1	76.2	22.9	--	--
4x	Rosada	Round	Shallow	Pi	C	0.50	--	--	22.1	7.13	0.188
2x	Sta. Rosa am	L-oblong	Deep	Y	Yi	0.67	39.7	15.6	20.0	--	--
2x	Sta. Rosa bl.	Eliptic	Medium	Y	Yb	0.45	28.8	31.9	20.3	7.66	0.265

[a] Color codes (Gomez, 2000). Primary color/Secondary color: W=White, WC= White-cream, C=Cream, Yi=Yellow intense, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, V= violet, B=Blackish. Chaucha p.= Chaucha pintada, Chacuha am.= Chaucha amarilla, Sta. Rosa am.= Sta. Rosa amarilla, Sta. Rosa bl.= Santa Rosa blanca, L-oblong= Long oblong.

2. Breeding for the processing market

In Ecuador currently the number of industries and potato products are increasing with enhancing demand of specific varieties for processing. At present no variety has been developed for processing purpose locally despite the fact that demand for potatoes with processing characteristics is gradually increasing (Devaux et al., 2010).

Our study in Chapter 3 identified several tetraploid landraces that match with the industry standards for processing as French fries regarding to dry matter content (DMC), reducing sugar content (RSC), enzymatic discoloration (ED) and morphological characteristics as described by Kirkman, (2007). In Table 3 a summary of landraces with the best characteristics are presented, outstanding the landraces Leona blanca and Leona negra while, at the diploid level landraces Chaucha amarilla and Chaucha pintada had many of the characteristics demanded by the processing industry with the exception of tuber eye depth and yield.

These landraces had medium depth of eyes, which makes it necessary to improve this character which is genetically controlled by major locus (*Eyd*) that is dominant to shallow (*eyd*). Landraces or improved varieties with shallow eyes should be included as progenitors into the breeding scheme to improve this character.

In Chapter 5 we found several QTLs associated to tuber eye depth (*Ey-1, Ey-2, Ey-3, Ey-4 and Ey-5*) located on chromosome I and X. Using MAS we could select genotypes with low dosage of deep eyes alleles.

Moreover, for processing as crisps the landraces, Puña, Milagrosa, Uvilla and Rosada, had the required characteristics for crisps potatoes (Table 3) according to the industry requirements (Kirkman, 2007). However, for ED some landraces, especially the colored ones, had high ED scores, which is a negative characteristic for use in the industry (Werij et al., 2007). Therefore, white-cream and yellow skinned potato landraces should be preferred.

Based on our results potato landraces are an important source of genes to develop improved varieties with the characteristics demanded by the processing industry and since most of the variation observed was genetic (Chapter 3), we expect a fast progress in breeding for these characters and we could use the QTLs identified in a MAS program. However, to improve agronomic traits as tuber yield it is necessary to include in the breeding scheme other genotypes with this characteristic.

Table 3. Potato landraces selected for high yield kg plant^{-1}, tuber shape, eye depth, dry matter (DMC %), total glycoalkaloid content (TGA mg 100g^{-1}), enzymatic discoloration (ED) at 30 and 180 min and reducing sugar content (RSC %) for the processing market.

2n	Landrace	Shape	Eye depth	Skin color(a)	Flesh color(a)	Yield	TGA	ED1-ED2	DMC	RSC
4x	Leona blanca	Oblong	Shallow	Y	Yb	0.45	10.19	2.0-4.1	24.0	0.046
4x	Leona negra	Oblong	Shallow	P/R	WC	0.32	5.50	--	23.9	0.039
4x	Leona	Oblong	Medium	WC	C/P	0.61	2.35	2.0-4.4	23.3	0.077
4x	Puña	Round	Shallow	RP	C	0.30	--	2.0-3.2	22.9	--
4x	Curipamba	Oblong	Medium	R/WC	C	0.43	3.31	1.3-2.8	22.8	0.013
4x	Uvilla	Round	Shallow	Y/R	Yb	0.26	10.96	1.7-3.3	22.8	0.043
4x	Hualcala	Oblong	Medium	R	C/P	0.73	2.91	1.7-4.0	22.5	0.099
4x	Milagrosa	Oblong	Shallow	Pi	Y	0.88	9.88	3.2-6.8	22.1	0.027
4x	Rosada	Round	Shallow	Pi	C	0.50	7.13	--	22.1	0.188
4x	Jubaleña	Oblong	Shallow	RP/Y	Y	0.52	--	2.0-5.4	21.8	--
4x	Carrizo2	Oblong	Medium	P/C	C/P	0.56	4.24	2.0-4.0	21.7	0.021
4x	Macholulo	L-oblong	Shallow	P	C	0.49	--	1.8-4.3	21.7	--
2x	Chaucha am.	Oblong	Medium	O	Yi	0.70	5.18	1.3-2.3	21.0	0.251
2x	Chaucha p.	L-oblong	Medium	Y	Yb	0.74	2.72	3.0-5.3	21.0	--
4x	Leona ne. n.	Oblong	Shallow	P/C	C/P	0.69	3.00	--	20.8	--

[a] Color codes (Gomez, 2000). Primary color/Secondary color: W=White, WC= White-cream, C=Cream, Yi=Yellow intense, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, V= violet, B=Blackish. Chaucha am.= Chaucha amarilla, Chaucha p. = Chaucha pintada, Leona ne.n.= Leona negra norte, L-oblong= Long oblong.

3. Breeding to improve antioxidant content

This thesis provides useful information concerning the potential of the Ecuadorian potato landraces to contribute to the dietary antioxidant intake.

Considerable variation was identified within Ecuadorian potato landraces for TPC and TCC, in Table 4 a summary of the landraces with the highest TPC and TCC is shown, the landraces with the highest contents were Papa chacra, Chaucha botella and the improved variety INIAP-Estela. Moreover, the landrace Sabanera and the improved variety Superchola were outstanding with high TPC and TCC respectively.

The red-purple and blackish skin potatoes showed the highest levels (Table 4), which was comparable with the results from previous studies in Andean potatoes from the CIP collection (Andre et al., 2007). These landraces are important sources of anthocyanins which is a natural colorant and antioxidant (Brown et al., 2005) that could also be used for developing functional foods /nutraceuticals or may also serve as natural colorant in food industry since the cost of production of potatoes is relatively low as compared to other horticultural crops (Ezekiel et al., 2012).

A recent study (Wolters et al., 2010) has shown that genes responsible for zeaxanthin content, a carotenoid responsible for the yellow-orange color, is present mainly in *S. phureja* landraces. This carotenoid could aid in the recommended daily uptake of zeaxanthin, since high levels of this compound are found in relatively few dietary products (Breithaupt and Schlatterer, 2005).

The landraces Chaucha botella and Papa chacra, both belonging to the *S. phureja* group, had the highest TCC (Table 4). These landraces represent an important germplasm source for enhancing the carotenoid content and the intensity of yellow-flesh trait in tetraploid potatoes, a trait that was the most preferred for the different actors (Chapter 2) and for farmers regarding to potato landraces (Chapter 4).

Furthermore, the diploid and tetraploid landraces with high TPC Papa chacra and Sabanera and the improved variety INIAP-Estela could be exploited through direct use or through crop improvement to develop varieties with high levels of these antioxidants at diploid or tetraploid level or may serve as novel sources of natural colorants and also a powerful source of potato antioxidant micronutrients.

These diploid landraces could be combined with wild species with resistance to late blight such as *S. paucissectum* and *S. acroglosum* (Villamon et al., 2005) for the development of diploid potato genotypes with high carotenoid content and good agronomic characteristics for specialty markets or for combining with a bridge species producing 2n gametes to get tetraploid potatoes (Hutten, 1994; Jansky and Peloquin, 2006).

If people knew that colored potatoes have higher levels of antioxidants than white – cream potatoes (Ezekiel et al., 2012) and the deeper the color, the greater the content (Haynes et al., 1994), it might increase potato consumption. Thus it is necessary to educate people about the potential benefit of colored potatoes. Then improved varieties as INIAP-Estela (purple skin and yellow flesh) with high TCC and TPC (Table 4) would have more chance of adoption and some landraces as Papa chacra and Sabanera could have opportunity to be sold in specialty markets.

This research demonstrates that significant genetic diversity exists for the quality traits in potato landraces, the contents are in agreement with the industry standards to produce French fries or crisp (Table 4) and some Ecuadorian potato landraces are an important source for useful alleles for quality traits for the fresh market to obtain the ideotype identified for the North-Center and Southern region (Table 1) as well to increase antioxidant content for direct use or as potential progenitors for breeding to enhance these traits.

Table 4. Potato landraces selected for high contents of dry matter (DMC %), total polyphenol content TPC (g kg^{-1} DW) and total carotenoid content TCC (µg $100g^{-1}$ FW).

2n	Landrace	Shape	Eye depth	Skin(a) color	Flesh(a) color	DMC	TPC	TCC
2X	Chaucha botella	Obovate	Deep	Pi/y	Y	22.5	2.1	122.5
2X	Papa chacra	Round	Medium	Y/P	Yi	21.8	4.3	114.3
4X	Superchola	Oblong	Shallow	Pi/y	Y	22.8	0.9	112.3
4X	Carriza	Oblong	Medium	P/Y	Yi	18.0	2.5	101.0
4X	Rosada	Round	Medium	Y/WC	C	22.0	1.4	100.7
4X	Coneja	Compress	Deep	Y	Yi	20.3	2.0	93.3
4X	INIAP-Estela	Round	Medium	RP/Y	Y	19.8	3.4	92.7
4X	Mampuera	Oblong	Deep	P/Y	C	20.1	1.4	91.0
4X	Morasurco	Oblong	Deep	P/Y	C	19.8	3.0	70.0
4X	Colorada	Eliptic	Deep	RP/Y	Yi	16.7	3.0	68.3
4X	Roja plancha	Round	Deep	R/WC	C	22.7	1.9	49.3
4X	Sabanera	Round	Medium	RP	W	16.0	4.1	47.3
4X	Puña	Ovate	Medium	RP/Y	C	23.1	1.9	40.0
--	Suscaleña blanca	Oblong	Medium	RP/Y	W	19.0	2.9	36.0
4X	Negra ojona	Round	Deep	B	C	n/d	3.0	--

[a] Color codes (Gomez, 2000). Primary color/Secondary color: W=White, WC= White-cream, C=Cream, Yi=Yellow intense, Y=yellow, Yb= Yellow bright, O=Orange, Pi=Pink, Br=brown, R=Red, P=Purple, RP=Red-purple, V= violet, B=Blackish.

Molecular markers

Recently, the potato genome sequence was published (Potato Genome Sequencing Consortium, 2011) opening up new possibilities for potato breeders to identify desirable allelic variants of genes underlying traits of interest for breeding. Linking up genetic maps, through physical maps to the genome sequence or the comparison of the primer sequence for our markers associated with QTLs identified could give us the region controlling the trait of interest. Furthermore, the identification of genes in the area between two flanking markers of our QTLs could result in new possible candidate genes (Werij, 2011).

For our study we developed a molecular map using DArT markers based on the CHAR-01 population that was derived from a cross between two diploid *S. phureja* parents. Several QTLs for tuber shape, eye depth, skin and flesh color were identified, most of them confirming previous research (Van Eck et al., 1994a, van Eck et al., 1994b, Li et al., 2005). We also identified QTLs that have not been reported previously, for example for tuber shape and eye depth, we found QTLs for these trait on chromosome I. Other authors using populations with different genetic backgrounds identified QTLs for tuber shape on chromosome, X (Van Eck et al., 1994a), II, V and XI (Bradshaw et al., 2008), II and XI (ŚLiwka et al., 2008).

Despite the advantages mentioned for DArT markers, in our study using this technology DArT markers tended to cluster in various regions, with little or no coverage in other regions as a result of which the coverage was not uniform across the potato genome. The same drawback was reported in oat (Tinker et al., 2009), tomato (Hai Thi Hong et al., 2010) and apple (Schouten et al., 2011). This affected the resolution of our map and several chromosomes were not identified. To enhance the resolution of a genetic map based on DArT markers, other markers should be included, such as SSR markers with known position on the genome. The use of DArT markers combined with SSR markers has been reported in linkage maps of crops like barley (Hearnden et al., 2007), durum wheat (Mantovani et al., 2008), tomato (Hai Thi Hong et al., 2010) and banana (Hippolyte et al., 2010).

In Ecuador our map is the first genetic map developed for a crop and opens up the possibility to study other traits of interest in the CHAR-01 population. Also, it may be possible to perform similar genetic studies in other crops to identify QTLs controlling traits of importance for possible use of Molecular assisted selection (MAS). To date, MAS in potato has been applied to select for potato virus X, Y, root cyst nematode, potato wart and late blight resistance (De Koeyer et al., 2010; Gebhardt et al., 2006; Ortega and Lopez-Vizcon, 2012). However, until now the selection of new improved varieties in Ecuador has been based on phenotype rather than genotype.

The advantage of the QTLs identified in the CHAR-01 population is that most of them had large effects and they were identified in a population that comes from two Ecuadorian potato landraces with a *S. phureja* background. However, marker validation in other genetic backgrounds still is necessary prior to use in a MAS program (Collard and Mackill, 2008). Furthermore, DArT markers could be transformed into a PCR marker and used in MAS (Hai Thi Hong et al., 2010).

The present study revealed genomic regions in chromosome I and X responsible for up to 34% of the total phenotypic variation associated with tuber shape and eye depth. While in chromosome V an important region was identified where several candidate genes related to anthocyanin biosynthetic pathway are located.

The practical use of the information obtained in this thesis for the potato-breeding program of INIAP is through the introduction of molecular marker technology to support traditional breeding. The QTLs identified in the CHAR-01 population (Chapter 5) can be included in a MAS program to improve the selection efficiency for the quality traits associated.

INIAP should evaluate the possibility to use MAS for the development of new potato varieties with resistance to disease and pest attacks, and tolerance to environmental stresses. A first step can be made by using published molecular markers associated with these characters e.g. for PVY resistance we could use the SCAR marker RYSC3 described by (Kasai et al., 2000) and marker STM0003 described by (Song et al., 2005) for cyst nematode the markers RGpa5, SPUD1636 reported by (Bryan et al., 2002) and the markers RGPa5-vrnHC described by (Sattarzadeh et al., 2006).

The use of molecular markers linked to genes controlling important traits should enable INIAP to move from conventional phenotypic selection to genotypic selection for major genes and also for quantitative traits with a much higher chance of success for new varieties. This PhD project has taken the first steps on that route.

Factors that have influenced the acceptance of new varieties

Breeding for resistance to late blight and high yield have been the main priorities of INIAP´s potato breeding program in the last years. A lot of efforts have been made and several improved varieties have been released with these characteristics. However, most of these varieties have not been accepted by the actors in the chain and as a result they are not as widely spread as INIAP hoped for. Several factors affected the acceptance of new varieties, which can be summarized as:

1) The improved varieties released did not meet all the requirements of the actors in the chain
2) The new improved varieties released have to compete with old varieties with strong consumer preference.

1) The improved varieties released did not meet all the requirements of the actors in the chain

In the last years INIAP has included only farmers' criteria in the selection of new varieties (Cuesta et al., 2007a). Some reports (Andrade and Cuesta, 1997; Cavatassi et al., 2009; Danial et al., 2007) have suggested that consumers' preferences for the ideal potato are transmitted to farmers through traders, so it would be sufficient to meet the criteria of farmers and consumers and in this way, establish the characteristics of the ideal potato demanded for the actors in the chain.

Participatory plant breeding (PPB) approaches have been applied for the selection of advanced breeding clones and improved varieties (Danial et al., 2007). This methodology identified the farmers criteria about potato crop at planting, flowering and harvest time and defined the "ideotype" for each Ecuadorian region (Cuesta et al., 2007a) from a farmers point of view.

With farmers participation in the selection procedure using PPB methodology, INIAP expected that the adoption and diffusion of the new released potato varieties among farmers would be successful (Cuesta et al., 2007a). However, despite the good performance and acceptance of the new varieties among farmers, they were not accepted by traders and consumers; one of the main reasons was that the quality traits did not match with their preferences.

The most recent example is the improved variety INIAP-Estela released in 2007, which was selected using PPB methodology and meeting all the farmers requirements (Cuesta et al., 2007c). But, although farmers expressed great satisfaction with this variety, it was not preferred by traders and as a result farmers decided not to continue growing of this variety. The main reason was that the purple skin color and the mean depth of the eyes were not appropriate for the market.

2) The new improved varieties released have to compete with old varieties that have a strong consumer preference.

The new potato varieties released by the potato breeding program of INIAP have to compete with varieties that have been cultivated for many years, such as Superchola, INIAP-Gabriela, INIAP-Cecilia and Bolona, which are all varieties that have a strong consumer preference with a well defined set of attributes that make it difficult to change the consumer preference. However, most of these varieties do not meet the agronomic requirements since they are late blight susceptible, low yielding, late maturing and have high costs of production and according to our results (Chapter 2) most of the actors in the chain were interested in new varieties.

This situation could facilitate the replacement of the old varieties for genotypes with better agronomic characteristics and similar quality characteristics. The most recent example is the replacement of INIAP-Gabriela (released in 1982) for INIAP-Fripapa (released in 1995) in Chimborazo Province (center region), mainly because of its low yield and susceptibility to late blight (Yanez and Cuesta, 2006). In the near future the variety Unica (Colombian origin) could out-compete Superchola in the Northern region and in the South the native variety Bolona could be replaced by a new variety with better agronomic characteristics.

Thus the potato breeding program of INIAP, to increase the possibilities of success of their improved varieties, should develop varieties that approach the “ideotype” defined by the different actors in the chain and for each Ecuadorian region (North-Center and South). Such varieties could have a chance of success and might replace old varieties in the short run.

Prospects of breeding for quality at INIAP-Ecuador

The goal of plant breeding is to assemble more desirable combinations of genes to obtain the ideal potato (Collard and Mackill, 2008). The efficiency of the breeding and selection process can be assessed in many different ways including the ultimate success of the varieties released and the frequency with which new varieties are produced (Asíns, 2002).

For the processing market the required characteristics regarding to morphological characters, DMC, RSC and ED have been defined by the industry (Kirkman, 2007; Van Eck et al., 1994b). Actually these characteristics are not available in the majority of the improved Ecuadorian potato varieties and as consequence most of the potatoes used for the French fries are imported from Belgium, The Netherlands and United States (Devaux et al., 2010) and the Colombian variety Capiro is preferred for crisps potatoes (Cavatassi et al., 2009). In the near future INIAP has a major challenge for the development of a new improved variety for the processing industry.

For the fresh market in Ecuador the situation is more complex, the potato “ideotype” is affected by tradition, customs, food habits, the geographical region and the preference of the main actors involved in the potato value chain. Besides, the traditional improved varieties cultivated for several years have a strong influence on the preference in each region as was demonstrated in Chapter 2. INIAP´s main breeding methods to obtain new improved varieties have been through traditional breeding making crosses between pairs of parents with complementary characteristics, followed by several selection cycles and selection of clones from the International Potato Center (CIP) (Cuesta et al., 2005b) and in this system the selection is based on general appearance and agronomic performance.

Including molecular technology in the conventional breeding program of INIAP has been limited by the absence of trained human resources, lack of funding and the lack of appropriate infrastructure. However, in the last years (with Governmental support) INIAP has improved the infrastructure for molecular marker analysis and some researchers have been trained in molecular technologies. Currently, the use of molecular markers including SSR, AFLP, SNP can be performed in the INIAP biotechnology laboratory. However, the cost of genotyping is in some cases a bottleneck. A low-cost alternative for genotyping large a quantity of samples is the use of service specialized laboratories. For example to outsource the detection and screening of DArT markers to Diversity array technology Pty Ltd (DArT P/L) (http://www.diversityarrays.com), or Triticarte (http://www.triticarte.com) are good options.

Despite the fact that introductions from CIP are a fast and cheap method to select potatoes with the characteristics required usually the genotypes from CIP do not have good performance under Ecuadorian highland conditions and do not have the quality characteristics required. Several advanced clones from CIP with resistance to different pathogens as the A and B population have been tested under Ecuadorian conditions during the last 20 years. As a result several clones were selected for good agronomic characteristics (high yield, resistance to late blight) and only a few were selected by farmers and were released as improved varieties like e.g. INIAP-Fripapa (Thiele, 2008).

We found that CIP clones with better performance usually did not have the tuber quality and processing characteristics demanded by farmers, traders and consumers, since these characteristics are influenced by the region and the traditional varieties cultivated (Chapter 2). Thus it is difficult to find a genotype from CIP that suits all the quality requirements of Ecuadorian people. Although CIP wants to see their new genotypes grown as widely as possible, breeding for local conditions in Ecuador is necessary.

Despite the fact that INIAP and local Ecuadorian potato breeding is necessary the International Potato Center (CIP) plays an important role in supporting national breeding programs providing progenitors with good agronomic characteristics. CIP also should support the established networks of breeding programs in Latin America e.g. Red Latin papa **(**http://www.cipotato.org/redlatinpapa**)** through training, technical assistance, interchange of information and maintaining collaborative projects with national programs.

Since 1989 in Ecuador there is a regional office of CIP located in Santa Catalina Research Station of INIAP. Despite they have adequate infrastructure the main constraint is the limited number of researchers as result they are focus mainly on late blight and seed potato research. As consequence the collaborative breeding activities have been trough CIP Lima office. However, in the last years this collaboration has been reduced. Then, is necessary to strengthen the collaborative activities with CIP and to take advantage of the infrastructure of CIP-Quito to develop more research activities, e.g. breeding.

Traditional breeding has been the main method used by INIAP to get new improved varieties. But, due to the large number of traits required to get the ideal potato and the polygenic nature of most of these characters, the probability of success is low.

However, the large genotypic variation that exists for the quality traits identified in Chapter 3 and 4, together with the fact that the contribution of the genotype to the variance was significantly higher than that of the G x E interaction for most of the quality traits means that the selection response will be greater and we will expect great progress in breeding for those characters. In Chapter 3 and 4 several landraces were selected as possible progenitors to be included in the breeding scheme. These results are summarized in Table 3 and 4.

Furthermore, using molecular marker technology as MAS might support the development of new potato varieties with required characteristics. In Chapter 5 we identified QTLs with large effects for tuber shape, eye depth, skin and flesh color that could be included in the breeding scheme. Nevertheless, for some other traits like yield, carotenoid content and for some agronomic characteristics as resistance to late blight the inclusion of other potato genotypes with better characteristics is necessary to get the “ideotype” required. Advanced progenitors from CIP and breeding clones or improved varieties from INIAP may be alternatives to include in the breeding scheme.

Proposal of breeding for quality at INIAP-Ecuador

Finally based on the information obtained in this thesis an overview of how the potato breeding for the fresh and processing market could look like is presented in Figure 1, it combines traditional breeding at diploid and tetraploid level combined with the use of molecular marker technology.

The potato breeding scheme consist of three phases: pre-breeding activities, selection phase under INIAP-Experimental Station conditions and selection in regional trials.

1. Pre-breeding

The landraces selected as progenitors in Chapter 3 and 4 have different ploidy level, therefore breeding at the diploid and tetraploid level is possible to perform.

1.1. Diploid level

Most of the potato breeding in INIAP has been done at the tetraploid level; several disadvantages associated with diploid level have been identified, as low yield and self incompatibility (Hutten, 1994). However, two major advantages have been reported, direct transfer from the wild and cultivated diploid *Solanum* species to *Solanum tuberosum* and disomic inheritance of characters (Hougas and Peloquin 1958).

Therefore in the breeding scheme of INIAP the *Solanum phureja* landraces selected in Chapter 3 and 4 could be combined with wild species to include resistance to late blight and we would expect vigorous interspecific F1 hybrids as describe (Hougas and Peloquin 1960).

Based on the results of this thesis we recommend as progenitors the diploid landraces selected in Chapter 3 Chaucha pintada and Chaucha amarilla and in Chapter 4 Papa chacra and Chaucha botella, to incorporate resistance to late blight we could use wild species e.g. *S. paucissectum* and *S. acroglosum* diploid species with resistance to late blight (Villamon et al., 2005). Experimental crosses will be made to evaluate general combining abilities. Good combining breeding parents will be crossed and the F1 progenies will be obtained.

The F1 progenies will be sown in a nursery and transplanted later into small pots and field. The clones obtained with good agronomic characteristics (e.g. vigorous development, short stolons) will be selected as progenitors to cross with a bridge specie (*Solanum phureja)* as male parent producing 2n gametes to obtain a tetraploid potato through 4x - 2x hibridrization as describe (Hutten, 1994), the landrace “chaucha amarilla” could be used for this purpose.

Alternatively the best diploid clones selected from F1 progenies could pass to the next selection phases on Station and in Regions for the development of diploid varieties for specific markets.

1.2 Tetraploid level

Breeding at tetraploid level is the common method used by INIAP to obtain improved varieties. Traditionally, INIAP has selected parents with complementary characteristics based on improved varieties and advanced clones (Cuesta et al., 2005b). However, based on the results of Chapter 2 and the industry requirements we suggest including parents from complementary groups of germplasm to exploit heterosis effect (Mendoza and Haynes, 1974) to improve agronomic and quality characteristics.

The potato landraces Leona blanca, Uvilla, Milagrosa, Sabanera, Jubaleña and Bolona from Andigena group with the best quality characteristics (Table 3 and 4) could be selected as progenitors. These landraces should be combined with improved varieties as INIAP-Estela, Superchola and INIAP-Natividad which are hybrid varieties (Tuberosum x Andigena) with good agronomic characteristics and quality. Furthermore to include late blight resistance, high yield and earliness advanced breeding clones from INIAP or CIP could be incorporated. Additionally if we want to improve some specific attribute we could include some of the landraces selected for specific traits described in Table 3 and 4.

In order to design the crossing block, general combining ability of the parents will be evaluated. The tetraploid clones (4x - 2x hibridrization) obtained from the pre-breeding at the diploid level will be crossed with good combining progenitors selected at tetraploid level. The F1 progenies will be planted in a nursery and transplanted into small pots and field for selection. The superior clones selected from F1 progenies could be included in a molecular assisted selection (MAS) program (Collard and Mackill, 2008).

Molecular assisted selection

Based on the requirements of the fresh and processing market we propose to apply MAS (Collard and Mackill, 2008) for tuber shape and eye depth to select round tubers for the fresh market and crisps industry and long tubers for the processing market as French fries.

We propose to use the markers pPt-651620 and pPt 533638 associated with *Sh-3* and *Ey-4* locus identified in chromosome X and markers capPt-672281 and pPt 655338 linked to *Sh-1* and *Ey-1* locus found in chromosome I (Chapter 5).

Furthermore, since QTL for tuber yellow flesh color *FL-1* was located in the same region of *Sh-1* and *Ey-1* locus, tuber yellow flesh color one of the most preferred attribute described in Chapter 2 and 4 will be also included in the selection procedure. The advantage of DArT markers is that they can be transferred into a PCR marker (Hai Thi Hong et al., 2010).

In the future we suggest to include MAS for pathogen resistance e.g. cyst nematode using the markers RGpa5, SPUD1636 reported by (Bryan et al., 2002) and the markers RGPa5-vrnHC described by (Sattarzadeh et al., 2006). Furthermore, using the information of the published potato genome (Potato Genome Sequencing Consortium, 2011) new markers for important traits could be identified. However, the validation of these molecular markers in our germplasm is needed previous their use in MAS (Langridge and Chalmers, 2005).

In the last years abiotic stresses such as drought and cold have become limiting for the potato production in Ecuador (Cuesta, 2010). These factors may affect plant growth as well productivity (Evers et al., 2012). Then in the short time breeding for abitoic stresses will be also a priority of the INIAP breeding program and the use of molecular marker technology could be an alternative to increase the efficiency of selection. For drought tolerance several SNP markers associated with QTLs involved in this trait has been identified under in vitro conditions (Anithakumari et al., 2011).

2. Selection under INIAP- Santa Catalina Research Station conditions

The best clones selected from the previous phase will enter the screening trials at INIAP- Santa Catalina Research Station.

In this location several cycles of selection will be performed to choose the best clones with good agronomic characteristics and quality. The details of the management and selection procedure of the clones are described in (Cuesta, 2008).

The best clones selected regarding to agronomic characteristics will be evaluated for tuber quality and processing characteristics, DMC, RSC, TGA, ED and antioxidant contents. In Chapter 3 and 4 we demonstrate that the variation of these traits was mainly genetic effect. Then we could select the best clones based on genotype variation.

3. Regional trials

The selected clones from the previous phase will be compared with several of the recommended clones and commercial varieties in yield trials in several locations with replicates during at least three years to measure the adaptation and stability under different environments. Each year clones will be dropped from the trials when they show no improvement over the recommended ones.

According to their external and internal quality characteristics the clones could be selected for the processing or for the fresh market trials according with the required ideotype (Chapter 2) or the industry standards (Kirkman, 2007).

For the fresh market, participatory plant breeding approaches (Danial et al., 2007) including farmers, traders and consumers preference criteria will be used to support the selection of new varieties for the North-Center and South region, is important to include traditional varieties in the trials in order to the different actors could compare them with the advanced clones. This could facilitate the adoption and acceptability of these new germplasm as describe (Ashby et al., 2009).

While for the processing market the clones with the characteristics required for the industry will be evaluated for adaptation and quality for processing as crisps and French fries. Since there is not a local variety with the characteristics required for the processing we expect a fast adoption by the industry and farmers of the new improved potatoes.

The seed potato availability could affect the distribution and adoption of the new varieties for this reason previous the release of the new potatoes is necessary to produce in appropriate quantities seed potato of high quality (certified seed) to assure the seed supply to farmers. Actually the minimum required at the moment of release is ten tons per variety (Cuesta et al., 2010). However, this quantity is lower if we want a large distribution of these varieties. Then we propose to increase the amount required and if necessary include specialized seed multipliers farmers that have been trained by INIAP to produce additional seed, but information about potential demand is necessary.

At the end based on the performance of the clones in the different trials and the preference of the different actors (farmers, traders and consumers) or the processing industry new varieties with the characteristics required could be released.

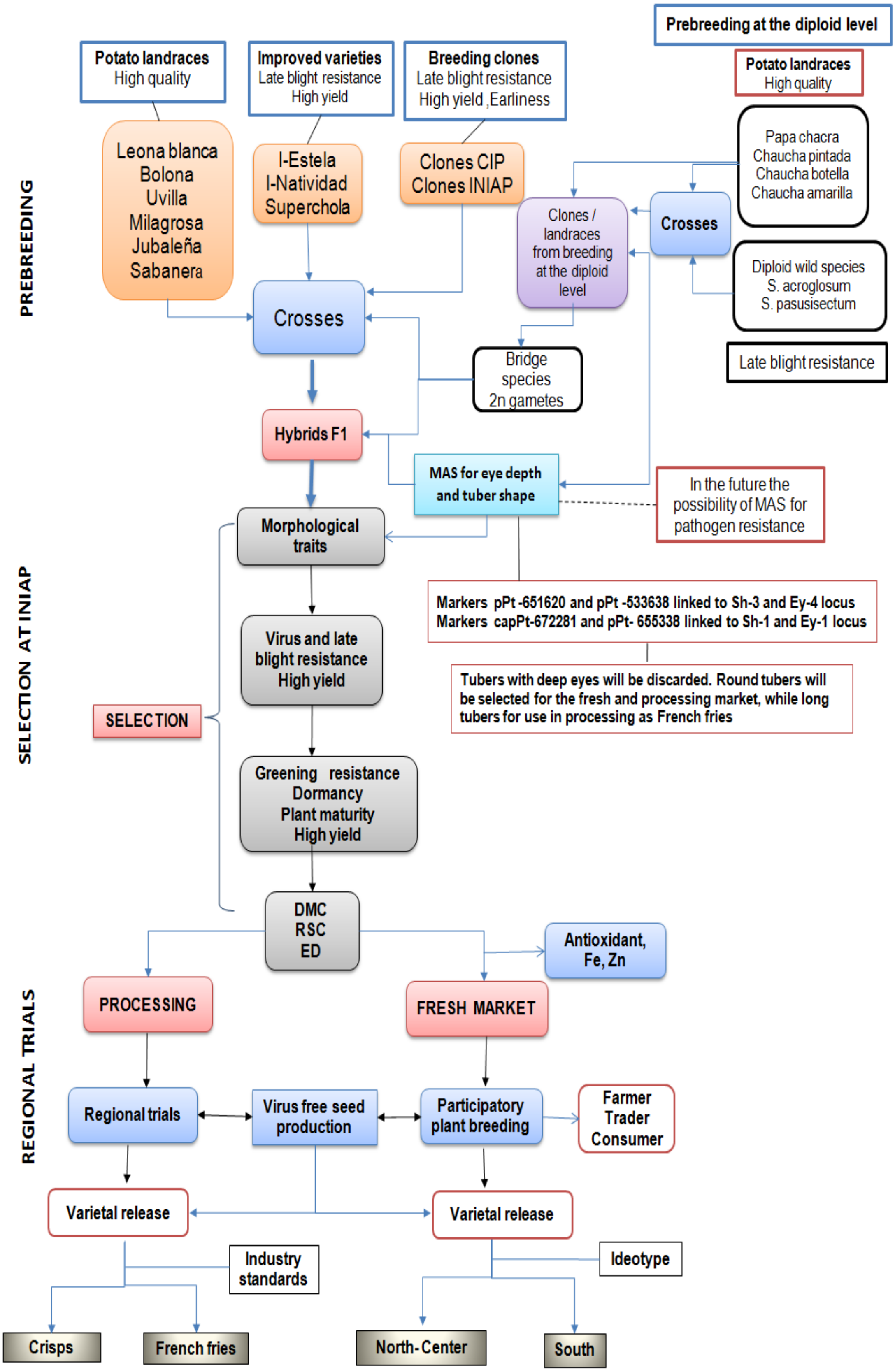

Figure 1. Schematic overview of potato breeding scheme for the development of improved varieties for the fresh and processing market based on Ecuadorian potato landraces

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Summary

The quality in potato is defined as the sum of favorable characteristics of the tuber. A complex set of external and internal quality traits are required for fresh and processing potatoes. External quality traits include tuber shape, eye depth, skin and flesh color but also dormancy and greening are important. Internal quality traits include the content of dry matter (DMC), reducing sugars (RSC), glycoalkaloids (TGA), enzymatic discoloration (ED) and nutritional quality.

In this thesis we identified the potato "ideotype" required for the Ecuadorian fresh market and studied the variation for the main quality traits for the fresh and processing market in a representative group of Ecuadorian potato landraces. Furthermore, Diversity Array Technology (DArT) markers were used to identify Quantitative Trait Loci (QTLs) for important traits as tuber shape, eye depth, skin characteristics and flesh color in a mapping population CHAR-01 based on *S. phureja* landraces.

The results from this thesis will be used in the INIAP potato breeding program to obtain the "optimized" potato required for each Ecuadorian region, which is a difficult task to perform through traditional breeding. However, using the variation available among potato landraces which we have identified and the inclusion of advanced breeding clones from INIAP and the International Potato Center (CIP), together with molecular marker technology, the development of new improved varieties with the desired quality traits will be feasible.

In Chapter 2, we identified the potato "ideotype" for each Ecuadorian region based on preference criteria of the three main actors in the potato value chain, farmers, traders and consumers. Differences among regions and chain actors for potato preferences were found. In general, farmers in all areas were concerned about the characteristics related to agronomic aspects; consumers were interested in tuber quality and processing characteristics while traders were interested in marketability of potatoes and healthy tubers.

The key quality traits for farmers were late blight resistance, tuber yellow flesh color and round shape. For traders tuber yellow flesh color, good taste and marketable potatoes were important, while for consumers, good taste, tuber yellow flesh color and mealy consistence were the most important traits.

The preferred ideotype in the Northern and Center area of Ecuador were quite similar: round tuber shape, red or pink skin color, shallow eyes, big or mean size, mealy consistence and fast cooking while in the Southern area the ideotype should have

yellow skin color, mean depth of eyes, big size, suitable of “locro” soup and soft consistence. In all cases the ideal potato should be resistant to late blight, be high yielding and early maturing. Furthermore, good taste, yellow flesh and suitability for several cooking applications were preferred.

Tuber quality and processing characteristics in each region were related to varieties traditionally cultivated in these regions, in the North Superchola, in the Center, INIAP-Gabriela, INIAP-Cecilia and in the South Bolona. The ideotype of potato in Ecuador was affected by the preferences of the actors in the chain and was influenced by the region of the country. Therefore potato breeding program of Ecuador to obtain new varieties should focus in the ideotype defined for the North-Center and South region.

In Chapter 3, we studied the variation of the main quality traits in a representative group of potato landraces from the Ecuadorian potato collection in three different environments. For all traits a large variation was observed. The interaction effect genotype x environment (GxE) was significant for most parameters, but was smaller than genotypic effect, except for total glycoalkaloid content for peeled potatoes.

For characteristics such as greening and dormancy the estimates of the broad sense heritability were high (H>0.76), therefore the selection response for the development of new potato varieties will be greater. However, some traits were affected by the environment such as total glycoalkaloid content for peeled potatoes and yield (H < 0.34). Total glycoalkaloid content in all potato landraces was lower than the upper limit considered safe for consumption. Besides this, most potato landraces suited the characteristics of dry matter and reducing sugar content demanded by the processing industry, while the white cream and yellow skinned potatoes showed low enzymatic discoloration compared with colored tubers.

We identified several potato landraces as possible progenitors for use in breeding e.g. Leona blanca, Leona negra, Leona negra norte, Milagrosa, Uvilla, Chaucha amarilla and Chaucha pintada were outstanding, with best characteristics for processing, while Uvilla, Leona blanca, Milagrosa, Puña, Jubaleña, Chaucha amarilla, Chaucha pintada and Bolona seemed best for use in the fresh market.

This study provides useful information concerning the potential of the potato landraces to contribute to get the ideal potato for the fresh and processing market through direct use or through crop improvement for quality.

In Chapter 4, we studied the variability for potato tuber dry matter content, total polyphenol content (TPC) and total carotenoid content (TCC) in 23 representative potato landraces and determined if farmers preferences about potato landraces in three representative areas are based on characteristics related to nutritional value.

A large variation for dry matter and antioxidant content was observed, most of the variation was due genotype (*H* > 0.87). The antioxidant content was similar or lower compared to previous studies on improved or Andean potato landraces. Then the landraces with the highest contents could be used to select progenitors to develop new potato varieties with high dry matter, carotenoids and polyphenols content through plant breeding and we expect a fast progress in breeding for those characters.

For high DMC the landraces Puña, Roja plancha, Chaucha botella and the improved variety Superchola are good options to use in breeding. While, Papa chacra, Sabanera, Negra ojona, Morasurco, Colorada, Suscaleña blanca and the improved variety INIAP-Estela could be selected as progenitors to increase the levels of TPC.

Additionally, the landraces Chaucha botella, Papa chacra, Carriza, Rosada, Coneja, Mampuera and the improved varieties Superchola and INIAP-Estela could be selected as progenitors to develop improved varieties with high TCC.

Therefore some Ecuadorian potato landraces are important source for useful alleles for quality traits to increase antioxidant content for direct use or as potential progenitors for breeding to enhance these traits.

Additionally, farmer´s main criteria of selection of potato landraces were good taste, tuber yellow flesh color and mealy consistence. These characters have been reported associated with some quality traits as DMC, low levels of glycoalkaloids and high content of carotenoids. Then farmer's preferences include empirical valuation of potato-quality rather than specific knowledge on nutritional characteristics of these potatoes. Furthermore, several farmers selected potato landraces based on the criteria that they are new in the region.

In Chapter 5, we developed a mapping population CHAR-01 based on *S. phureja* parents contrasting in quality traits. We assessed the segregation of tuber shape, eye depth, skin and flesh color in this population. DArT markers were used for genotyping.

The DArT markers tended to cluster in various regions of the genome, with little or no coverage in other regions, as a result the DArT marker coverage was not uniform across the genome. QTLs affecting these important quality traits were identified using the genetic map developed. The most prominent QTLs for tuber shape and eye depth were detected on chromosome X and explained 33.7% and 14.6% of the variance, respectively. The loci that control these traits were linked. The most important QTLs for skin and flesh color were also on chromosome X, explaining 19.9% of the variance and on chromosome III, explaining 13.9% of the variation. Additional QTLs with minor effects were also detected.

Our study identified novel QTLs that have not been reported previously, for tuber shape and eye depth QTLs *Sh-1*, *Sh-2, Ey-1*, *Ey-2* and *Ey-3* identified on chromosome I. For skin color two QTLs *Sk-2* and *Sk-3* were detected on chromosome IX and V respectively, *Sk -2* probably correspond a (*chi*) or (*chs*) genes, while *Sk-3* is related to *bHLH* gene, which constitute candidate genes for controlling anthocyanin biosynthesis.

New, presently unknown QTLs *FL-1* and *FL-3* involved in tuber yellow flesh color were also found. Comparing the location of these new QTLs with the genome sequence of potato *S. tuberosum* group Phureja DM1-3 516 R44 (DM), which was recently published suggest that they are related to the carotenoid cleavage dioxygenase gen (*CCD*) and β–carotene hydroxilase (*Chy*) respectively, that are involved in zeaxanthin accumulation in the yellow-fleshed potatoes.

Furthermore there were also QTLs that are consistent with other studies using mapping populations with different backgrounds e.g. QTLs for tuber shape, eye depth, and tuber skin color identified on chromosome X or QTLs for tuber flesh color detected on chromosome III.

The obtained results improve our understanding on the inheritance of quality traits for variety development and will provide a source for molecular marker development and the genetic characterization of other traits of importance for potato in Ecuador. This than will allow the possibility toward the use by INIAP of new approaches for genomic research and develop of new varieties improving the efficiency and precision of conventional plant breeding trough molecular assisted selection (MAS).

In Chapter 6, results from the findings of this thesis are discussed in a broader perspective. The possibility of use selected landraces in breeding to obtain the required ideotype for the fresh market, processing market and to enhance antioxidant content is analyzed, as well the probability of use the molecular markers identified in CHAR-01 population in a MAS program for the development of the required varieties are discussed. The factors that have influenced the acceptance of new varieties are considered and a proposal of breeding for the fresh and processing market is presented, it consists in breeding at the diploid and tetraploid level combined with use of molecular markers.

Samenvatting

De kwaliteit van de aardappel wordt bepaald door de som van de gunstige eigenschappen van de knol. Een complexe set van externe en interne kwaliteits eigenschappen zijn nodig voor de verse markt en voor de verwerkende industrie. Externe kwaliteitskenmerken zijn knolvorm, oog diepte, de huid- en vleeskleur, maar ook kiemrust en vergroening zijn belangrijk. Interne kwaliteits eigenschappen zijn onder andere het gehalte aan droge stof, reducerende suikers, glyco-alkaloïden, enzymatische verkleuring en nutritionele kwaliteit.

In dit proefschrift hebben we het "ideotype" voor de aardappel die nodig is voor de Ecuadoriaanse verse markt en verwerkende industrie bepaalt en de variatie in de belangrijkste kwaliteitskenmerken in een representatieve groep van Ecuadoriaanse aardappel landrassen bestudeerd. Verder werden Diversity Array Technology (DART) merkers gebruikt om kwantitatieve loci (QTLs) voor belangrijke eigenschappen als knolvorm, oog diepte, schil kenmerken en vleeskleur te vinden in de CHAR-01 mapping populatie die gemaakt was op basis van *S. phureja* landrassen.

De resultaten uit dit onderzoek worden gebruikt in het INIAP aardappel veredelings programma dat gericht is op het via traditionele veredeling verkrijgen van de "geoptimaliseerde" aardappel voor elke regio in Ecuador, hetgeen een moeilijke taak is. Echter, met behulp van de geselecteerde landrassen en het gebruik van veredelde lijnenafkomstig van INIAP en het International Potato Center (CIP), samen met moleculaire merker technologie, zal de ontwikkeling van nieuwe, verbeterde rassen met de gewenste kwaliteit eigenschappen haalbaar worden.

In hoofdstuk 2, identificeerden we het aardappel "ideotype" voor elke Ecuadoriaanse regio op basis van voorkeuren van de drie belangrijkste actoren in de aardappel keten; boeren, handelaren en consumenten. Er zijn verschillen tussen regio's en de ketenactoren gevonden m.b.t. hun voorkeuren. In zijn algemeenheid hechten de landbouwers in alle betrokken gebieden de meeste waarde aan de agronomische eigenschappen, de consumenten waren vooral geïnteresseerd in knol kwaliteit en verwerkingskenmerken, terwijl handelaren vooral geïnteresseerd waren in verhandelbaarheid en de gezondheid van de aardappelen.

De belangrijkste kwaliteitskenmerken voor de boeren waren phytophthora resistentie, knollen met een gele vleeskleur en een ronde vorm. Voor de handelaren was dit ook de gele knolvleeskleur, en daarnaast een goede smaak en verhandelbaarheid, terwijl voor de consument, een goede smaak, gele vleeskleur en melige consistentie de belangrijkste kenmerken waren.

Hetideotype in Noordelijk en Centraal Ecuador waren zeer vergelijkbaar: ronde knolvorm, rood of roze schilkleur, ondiepe ogen, groot of gemiddelde grootte, melig consistentie en snel koken terwijl in het zuidelijke gebied hetideotypeen gele schilkleur moet hebben, gemiddelde oogdiepte, groot formaat, geschikt voor "locro" soep en een zachte consistentie. In alle gevallen moet de ideale aardappel bestand zijn tegen de aardappelziekte (phytophthora), een hoge opbrengst geven en vroegrijp zijn. Verder hebben een goede smaak, geel vruchtvlees en de geschiktheid voor diverse bereidingsmethoden de voorkeur.

Knolkwaliteit en gewenstebereidingskenmerken waren in elke regio gerelateerd aan variëteiten die daar van oudsher geteeld werden. In het noorden was dat het ras Superchola, in het centrum, de rassen INIAP-Gabriela en INIAP-Cecilia en in het Zuiden het ras Bolona. Aangezien het ideotype voor de aardappel in Ecuador werd beïnvloed door de voorkeuren van de actoren in de keten en de regio van het land moet daar in het veredelings programma rekening mee worden gehouden.

In Hoofdstuk 3 hebben we de variatie in de belangrijkste kwaliteitskenmerken van een representatieve groep van aardappel landrassen uit de Ecuadoriaanse collectie bestudeerd in drie verschillende milieu's. Voor alle kenmerken werd een grote variatie waargenomen. Het interactie-effect genotype x milieu (GXE) was significant voor de meeste parameters maar was kleiner dan het genotypische effect, behalve voor totale glycoalkaloïde inhoud van geschilde aardappelen.

Voor kenmerken zoals vergroening en kiemrust waren de schattingen van de erfelijkheid hoog ($H > 0.76$), daarom zal de te verwachten selectie respons bij de ontwikkeling van nieuwe aardappelrassen groot zijn. Er waren echter ook een aantal eigenschappen die sterk door de omgeving beïnvloed werden, zoals het totale glycoalkaloïdegehalte van geschilde aardappelen en de opbrengst ($H <0.34$). Het totaal glycoalkaloïde gehalte bleef in alle landrassen echter onder de bovengrens die als veilig voor consumptie wordt beschouwd. Daarnaast hadden de meeste landrassen gehaltes aan droge stof en reducerende suikers die geëist worden door de verwerkende industrie, terwijl de aardappelen met een crème witte of gele schil geringe enzymatische verkleuring vertoonden in vergelijking met gekleurde knollen.

We hebben verschillende aardappel landrassen geïdentificeerd die als startmateriaal kunnen dienen in het veredelingsproces. Dit betreft o.a. Leona blanca, Leona negra, Leonanegranorte, Milagrosa, Uvilla, Chaucha amarilla en Chaucha pintada die uitstekend geschikt zijn voor de verwerkende industrie, en Uvilla, Leona blanca, Milagrosa, Puna, Jubaleña, Chaucha amarilla, Chaucha pintada en Bolona die eigenschappen hebben die ze geschikt maken voor de verse markt.

Dit onderzoek heeft nuttige informatie opgeleverd over de mogelijke bijdragevan aardappel landrassen aan de ideale aardappel voor de 'vers' markt en de verwerkende industrie. Dit kan zijn via direct gebruik of door een bijdrage aan de verbetering van de kwaliteit van aardappelrassen via veredeling.

In hoofdstuk 4 bestudeerden we het droge stof gehalte, totaal polyfenolen gehalte en totaal carotenoïden gehalte in een groep van 23 representatieve landrassen. Daarnaast hebben we vastgesteld of de voorkeuren van boeren voor bepaalde landrassen samenhingen met kenmerken die gerelateerd waren aan voedingswaarde.

Er werd een grote variatie voor droge stof en antioxidant gehalte gevonden, die voor het grootste deel genetisch was (H> 0.87). Het gehalte aan antioxidanten was vergelijkbaar of lager in vergelijking met eerdere studies aan rassen en landrassen uit de Andes. Landrassen met de hoogste gehaltes kunnen gebruikt worden in de veredeling gericht op de ontwikkeling van nieuwe rassen met een hoog droge stof, carotenoïden en polyfenolen.

Voor een hoog droge stof gehaltezijn de landrassen Puna, Roja plancha, Chaucha botella en het ras Superchola goede opties. Om het totaal gehalte aan polyphenolente verhogen kunnen de landrassen Papa chacra, Sabanera, Negra ojona, Morasurco, Colorada, Suscaleña blanca en het ras INIAP-Estela worden gebruikt en voor verhoging van het totaal gehalte aan carotenoïden zijn de landrassen Chaucha botella, Papa chacra, Carriza, Rosada, Coneja, Mampuera en de rassen Superchola en INIAP-Estela geschikt. Daarom zijn een aantal Ecuadoriaanse landrassen een belangrijke bron van nuttige allelen voor verbetering van kwaliteits eigenschappen gericht op het verhogen van het gehalte aan antioxidanten; hetzij door direct gebruik of als potentiële donor in het veredelings proces.

Daarnaast waren de belangrijkste criteria die de boeren gebruikten voor de selectie van aardappel landrassen een goede smaak, gele vleeskleuren een melige consistentie. Deze kenmerken worden in verband gebracht met eigenschappen als droge stof gehalte, lage niveaus van glyco-alkaloïden en een hoog gehalte aan carotenoïden. Klaarblijkelijkzijn de voorkeuren van boeren gebaseerd op empirische waarnemingen van aardappel-kwaliteit in plaats van op specifieke kennis over de voedingswaarde van deze aardappelen. Verder selecteerden verschillende boeren aardappel landrassen omdat ze nieuw waren in de regio.

In hoofdstuk 5 hebben we demapping populatie CHAR-01 gemaakt. Deze is gebaseerd op *S. phureja* ouders die contrasteerden in kwaliteits kenmerken. Wij hebben de segregatie van knolvorm, oog diepte, de schil- en de vleeskleur in deze populatie bepaald. DArT markers zijn gebruikt voor de genotypering.

De DarT merkers hadden de neiging te clusteren in verschillende regio's van het genoom, met weinig of geen dekking in andere regio's. Als gevolg daarvan was de dekking van het genoom met DArT merkers niet uniform. QTLsvoor de belangrijke kwaliteitskenmerken werden geïdentificeerd met behulp van de ontwikkelde genetische kaart. De meest prominente QTLs voor knolvorm en oogdiepte werden gevonden op chromosoom X en verklaren respectievelijk 33.7% en 14.6% van de variantie. De loci die deze eigenschappen bepalen waren gekoppeld. De belangrijkste QTLs voor schil-en vleeskleur lageneveneens op chromosoom X, met een verklaarde variantie van 19,9% en op chromosoom III, met een verklaarde variantie van 13.9%. Er werden ook extra QTLs met kleine effecten waargenomen op andere chromosomen.

Onze studie identificeerdeQTLs die niet eerder gerapporteerd zijn. Voor knolvorm en oogdiepte werden QTLs (*Sh-1*, *Sh-2*, *Ey-1*, *Ey-2* en *Ey-3*) geïdentificeerd op chromosoom I. Voor schilkleur werden twee QTLs (*Sk- 2* en *Sk-3*) gevonden op respectievelijk chromosoom IX en V, Sk -2 komt waarschijnlijk overeenkomen met (*chi*) of (*chs*) genen, terwijl *Sk-3* waarschijnlijk betrekking heeft op het bHLH gen, dat een kandidaatgenis voor het regelen van anthocyaan biosynthese.

Nieuwe, tot nu toe niet bekendeQTLs (*FL-1* en *FL-3*) diebetrokken zijn bij de productie van de gele vleeskleur van de knolzijn ook gevonden. De vergelijking van de locatie van deze nieuwe QTLs met de genoomsequentie van aardappel (*S. tuberosum* groep phureja DM1-3 516 R44 (DM)) die onlangs werd gepubliceerd,suggereert dat ze gerelateerd zijn aan het carotenoïd cleavage dioxygenase gen (CCD) en het β-caroteen hydroxilase (*Chy*) gen die beide betrokken zijn bij zeaxanthine accumulatie in de geelvlezige aardappelen.

Verder waren er ook QTLs die consistent zijn met andere studies waarbij mapping populaties met verschillende achtergronden gebruikt zijn, zoals de QTLs voor knolvorm, oog diepte en knol schilkleur op chromosoom X en de QTLs voor knol vleeskleur op chromosoom III.

De verkregen resultaten hebben ons inzicht in de genetische basis van kwaliteit eigenschappen verbeterd en kunnen gebruikt worden voor moleculaire merker ontwikkeling en de genetische karakterisering van andere kenmerken die van belang zijn voor de aardappel in Ecuador. Dit zal het voor INIAP mogelijk maken om de nieuwe mogelijkheden die genomische onderzoek biedt te gebruiken bijde ontwikkeling van nieuwe rassen en voor de verbetering van de efficiëntie en precisie van conventionele plantenveredeling via merkergestuurde selectie (MAS).

In Hoofdstuk 6 worden de resultaten van de bevindingen uit dit proefschrift in een breder perspectief besproken. De mogelijkheden voor het gebruik van geselecteerde landrassen in de veredelinggericht op hetverkrijgen van het vereiste ideotype voor de verse markt, voor de verwerkende industrie en voor het verbeteren van de gehaltes aan antioxidanten wordt geanalyseerd, evenals de kansen die het gebruik van de in de CHAR-01 populatie geïdentificeerde merkers in een MAS-programma voor de ontwikkeling van de nieuwerassenbiedt. De factoren die van invloed zijn geweest de acceptatie van nieuwe rassen zijn geanalyseerd en er is een voorstel om het gebruik van aanwezige wilde en gecultiveerde aardappels (germplasm) te verbeteren gepresenteerd. Tot slot zijn de vooruitzichten van de veredeling opaardappelkwaliteit door INIAP-Ecuador geanalyseerd en een voorstel voor veredeling ten behoeve van de verse markt en verwerkende industrie gepresenteerd.

Resumen

La calidad en papa se define como la suma de características favorables del tubérculo; un grupo complejo de características externas e internas se requieren para el mercado en fresco y procesado. Las características externas constituyen la forma, profundidad de ojos, color de piel y pulpa del tubérculo. Además la dormancia y el verdeamiento son importantes. Las características internas incluyen el contenido de materia seca, azúcares reductores, glicoalcaloides, descoloración enzimática y la calidad nutritiva.

En esta tesis identificamos el “ideotipo” de papa requerido para el mercado en fresco Ecuatoriano y estudiamos la variación de los principales caracteres de calidad en un grupo representativo de variedades nativas de papa. Además usando marcadores DArT se identificaron caracteres cuantitativos (QTLs) para aspectos importantes como forma, profundidad de ojos y color de la pulpa del tubérculo en una población de mapeo denominada CHAR-01 proveniente de variedades *S. phureja*.

Los resultados de esta tesis serán usados por el programa de mejoramiento genético del INIAP para obtener la papa “ideal” requerida por cada región del país, tarea complicada de llevar a cabo a través del mejoramiento convencional, pero con el uso de la diversidad disponible en las variedades nativas seleccionadas y la inclusión de clones avanzados del programa de mejoramiento del INIAP y del Centro Internacional de la papa (CIP) combinado con el uso de marcadores moleculares será posible la obtención de variedades mejoradas con las características de calidad deseadas.

En el **Capítulo 2** nosotros identificamos el “ideotipo” de papa para cada región del Ecuador basados en los criterios de preferencia de agricultores, comerciantes y consumidores. Diferencias entre regiones y actores para las preferencias de papa fueron identificadas. En términos generales en todas las áreas las preferencias de los agricultores estuvieron relacionadas con las características agronómicas, consumidores en características de calidad del tubérculo y de procesamiento, mientras que los comerciantes estuvieron interesado en que las papas sean comerciables y en la sanidad de los tubérculos. Los caracteres claves para los agricultores fueron resistencia al tizón tardío, pulpa color amarillo del tubérculo y de forma redonda. Para los comerciales, los caracteres pulpa amarilla, buen sabor y tubérculos comerciales fueron importantes.

El “ideotipo” de papa en el Norte y Centro de Ecuador fue similar, tubérculo redondo, de color rojo o rosado con ojos superficiales, de tamaño entre medio a grande, consistencia arenosa y rápida cocción, mientras que en el Sur el ideotipo deberá tener tubérculo de piel amarilla, profundidad de ojos medios, tamaño grande con consistencia suave y ser adecuado para preparar “locro”. Además la papa ideal para

todas las regiones deberá incluir resistencia al tizón tardío, alto rendimiento y precocidad, además de forma redonda del tubérculo, buen sabor, color amarillo de la pulpa y que sea apta para varias formas de preparación.

Las variedades tradicionales que han sido cultivadas por años influyeron en las preferencias de los diferentes actores, en la zona Norte de Ecuador la variedad Superchola fue preferida; en el Centro INIAP-Cecila o INIAP-Gabriela y en el Sur la variedad nativa Bolona. Por lo tanto el programa de mejoramiento del Ecuador para obtener nuevas variedades debería enfocarse en el ideotipo identificado para la región Norte-Centro y Sur.

En el **Capítulo 3** estudiamos la variación de los principales caracteres de calidad en un grupo representativo de variedades de la colección Ecuatoriana de papa Para todos los caracteres se observó gran variación en donde el efecto genotipo x ambiente (GxE) fue significativo para la mayoría de caracteres, pero este fue menor que el efecto del genotipo, excepto para el contenido total de glicoalcaloides de papas peladas.

Para los caracteres verdeamiento y dormancia los estimados de heredabilidad en el sentido amplio fueron altos ($H > 0.76$), por lo que la respuesta a la selección dentro del será mayor. Sin embargo, algunos caracteres como contenido total de glicoalcaloides para papas peladas y rendimiento fueron afectados por el ambiente ($H < 0.34$). El contenido total de glicoalcaloides en todas las variedades nativas fue menor que el limite considerado seguro para el consumo. Además, los contenidos de materia seca y azúcares reductores de la mayoría de variedades nativas estuvieron dentro de los valores requeridos por la industria de procesamiento, mientras que las variedades con piel blanco-crema o amarillo mostraron reducida descoloración comparadas con las papas coloreadas.

Nosotros identificamos varias papas nativas como posibles progenitores e.g. Leona blanca, Leona negra, Leona negra norte, Milagrosa, Uvilla, Chaucha amarilla y Chaucha pintada las cuales mostraron las mejores características para procesamiento, mientras que Uvilla, Leona blanca, Milagrosa, Puña, Jubaleña, Chaucha amarilla, Chaucha pintada y Bolona presentaron características para el consumo en fresco.

Este estudio provee con importante información sobre el potencial de las variedades nativas para obtener la variedad ideal de papa para el mercado en fresco y procesamiento a través de uso directo o en mejoramiento para calidad.

En el **Capítulo 4** nosotros estudiamos la variación del contenido de materia seca del tubérculo, el contenido de polifenoles y carotenoides totales en 23 variedades nativas representativas y determinamos en tres zonas si las preferencias de los agricultores acerca de las variedades nativas está relacionada con el su valor nutritivo.

Se identificó gran variación para el contenido de materia seca y antioxidantes, la mayor variación observada fue debido al genotipo (H > 0.87). El contenido de antioxidantes fue similar o menor comparado con estudios previos. Por lo tanto las variedades nativas con los mayores contenidos podrían ser usadas como progenitores para desarrollar nuevas variedades con altos contenidos de materia seca, carotenoides y polifenoles y esperamos un rápido progreso en mejoramiento para esos caracteres.

Para alto contenido de materia seca, las variedades, Puña, Roja plancha, Chaucha botella y la variedad mejorada Superchola son buenas opciones para usar en mejoramiento. Mientras que las variedades Papa chacra, Sabanera, Negra ojona, Morasurco, Colorada, Suscaleña blanca y la variedad mejorada INIAP-Estela podrían ser seleccionadas para incrementar el contenido de polifenoles. Adicionalmente, las variedades nativas Chaucha botella, Papa chacra, Carriza, Rosada, Coneja, Mampuera y las variedades mejoradas Superchola e INIAP-Estela podrían ser seleccionadas como progenitores para desarrollar variedades con altos contenidos de carotenoides. Por lo tanto Las variedades nativas Ecuatorianas son importante fuente de genes para incrementar los contenidos de antioxidantes a través de su uso directo o como progenitores en un programa de mejoramiento genético.

Los principales criterios de selección de los agricultores en relación a las papas nativas fueron buen sabor, color amarillo de la pulpa y consistencia arenosa. Estos caracteres han sido asociados con el contenido de materia seca, bajos niveles de glicoalcaloides, azúcares reductores y altos contenidos de carotenoides. Por lo cual las preferencias de los agricultores incluyen evaluaciones empíricas de la calidad del tubérculo, más que un conocimiento específico de los caracteres nutricionales de las papas. Además el carácter de “novedosa” fue importante para la selección de las variedades nativas.

En el **Capítulo 5**, nosotros desarrollamos una población de mapeo CHAR-01 proveniente de progenitores *S. phureja* contrastantes en caracteres de calidad. Nosotros evaluamos la segregación de la forma del tubérculo, la profundidad de los ojos, el color de la piel y el tubérculo. Marcadores DArT fueron utilizados para el genotipaje. Los marcadores DArT tuvieron una tendencia de agruparse en algunas regiones del genoma con poca o ninguna cobertura en otras, como resultado, la cobertura no fue uniforme. Se identificaron loci para caracteres cuantitativos (QTLs) que afectan la expresión de estos caracteres. Los más importantes QTLs para forma del tubérculo y profundidad de ojos fueron detectados en el cromosoma X (Progenitor-2) este explicó el 33.7% y 14.6% de la variación respectivamente. Los loci que controlan estos caracteres estuvieron ligados. Los más importantes QTLs para color de la piel y pulpa fueron ubicados en el cromosoma X (Progenitor-1, 19%), III (Progenitor-1, 13.9%) respectivamente. QTLs adicionales con efectos menores también se identificaron.

Nuestro estudio identificó nuevos QTLs que no han sido reportados, para forma del tubérculo y profundidad de los ojos QTLs *Sh-1*, *Sh-2, Ey-1*, *Ey-2* y *Ey-3* en el cromosoma I. Para color de la piel dos QTLs *Sk-2* and *Sk-3* fueron detectados en el cromosoma IX y V respectivamente, *Sk -2* probablemente corresponde a (*chi*) o (*chs*) genes, mientras *Sk-3* es relacionado al gen bHLH, los cuales constituyen genes candidatos para controlar la biosíntesis de antocianinas.

Nuevos QTLs desconocidos *FL-1* y *FL-3* involucrados en el color amarillo de la pulpa del tubérculo fueron identificados en la población. Comparando la ubicación de estos nuevos QTLs con la secuencia del genoma de la papa *S. tuberosum* grupo Phureja DM-13 516R44 (DM), estos probablemente están relacionados con el gen cleavage carotenoide dioxygenasa (CCD) y β–caroteno hydroxilase (*Chy*) respectivamente, los cuales están relacionados con la acumulación de la zeaxantina. También se identificaron QTLs que son consistentes con otros estudios, por ejemplo QTLs para forma del tubérculo, profundidad de ojos y color de piel fueron identificados en el cromosoma X o QTLs para color de la pulpa detectados en el cromosoma III.

Los resultados obtenidos mejoran nuestro entendimiento de la herencia de los caracteres de calidad para el desarrollo de variedades y provee importante información para el uso de marcadores moleculares y la caracterización de otros caracteres. Además permitirá el uso de nuevas tecnologías para investigación genómica y el desarrollo de nuevas variedades, utilizando el mejoramiento convencional con el apoyo de la selección asistida (MAS).

En el **Capítulo 6**, los resultados encontrados en esta tesis son discutidos en una perspectiva amplia. La posibilidad de utilizar las variedades nativas seleccionas en mejoramiento para obtener el ideotipo requerido para el mercado en fresco, procesamiento y para mejorar el contenido de anitoxidantes es analizado, así como la probabilidad de usar los marcadores identificados en la población CHAR-01, dentro de un programa MAS es discutido. Los factores que han influido la aceptación de las nuevas variedades son analizados y una propuesta de mejoramiento para el mejoramiento en fresco y procesamiento es presentada la cual consiste en el mejoramiento convencional a nivel diploide y tetraploide combinado con el uso de marcadores moleculares.

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After finishing my MSc studies at Wageningen University in 2003, the possibility to return for a PhD program was very remote. However, with the support of NUFFIC and my employer in Ecuador INIAP, this possibility becomes a reality and in 2007, I began this experience that contributed to my personal and professional development.

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About the author

Xavier Cuesta was born on the 4th of May 1969 in Quito Ecuador. After finishing high school at Colegio Gonzaga, he started his BSc in Agronomy and Plant Breeding in 1986 in Central University of Quito.

In 1992 he started working on The National Agricultural Research Institute of Ecuador (INIAP) at Plant Protection Department, where he developed the BSc thesis related to yellow rust resistance in wheat, he graduated in 1994, later start working as plant breeder in wheat and barley. From 1995 to present is working in the potato breeding program of INIAP.

In 2001 he obtained a scholarship from the Ecuadorian Government to study MSc in Wageningen University at the Laboratory of Plant Breeding. In 2003 he finished his MSc, the topic of work was Comparative analysis of plant maturity of potato under long and short-day growth conditions.

He has been involved in potato breeding for durable resistance against late blight, drought tolerance, participatory plant breeding and in the last years has been responsible of the potato breeding in INIAP, and he is the author of at least seven improved potato varieties released in the last years.

In 2007 he started his PhD thesis on potato quality traits based on Ecuadorian potato landraces at the Laboratory of Plant Breeding, Wageningen University and Research Center (WUR).

He is currently working as potato breeder in the National Agriculture Research Institute (INIAP) of Ecuador. After his defense for the doctorate, he will return to INIAP to continue working on potato research.

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Education Statement of the Graduate School Experimental Plant Sciences

Issued to : Xavier Cuesta Subía
Date: 10th June 2013
Group: Plant Breeding, Wageningen University & Research Centre

1) Start-up phase	*date*
► **First presentation of your project**	
Molecular characterization of quality traits in Ecuadorian native potatoes	Jun 2007
► **Writing or rewriting a project proposal**	
Molecular characterization of quality traits in Ecuadorian native potatoes	Jun-Jul 2007
► **Writing a review or book chapter**	
list title if applicable	
► **MSc courses**	
► **Laboratory use of isotopes**	
Subtotal Start-up Phase	*7,5 credits**
2) Scientific Exposure	*date*
► **EPS PhD student days**	
EPS PhD student day Utrecht	Jun 01, 2010
EPS PhD student day Wageningen	May 20, 2011
► **EPS theme symposia**	
► **NWO Lunteren days and other National Platforms**	
► **Seminars (series), workshops and symposia**	
Louise Vet, Entomology / NIOO: 'Insect-plant interactions in a multitrophic world'	May 11, 2010
Just Vlak, Virology: 'Baculovirus infections of insects: No guts no glory'.	May 11, 2010
► **Seminar plus**	
► **International symposia and congresses**	
Project meeting: 'Providing new opportunities for small holders potato farmers', CIP, Peru	Jan 10-11, 2008
Project meeting Latin-American Network of Innovation on Breeding and Potato spread out, CIP, Peru	Jan 15-18, 2008
Potato Science for the Poor Challenges for the New Milennium Conference, Cuzco, Peru	Mar 25-28, 2008
Potato Congress, Quito, Ecuador	Jun 18-20, 2008
Patata 2008, Vitoria Gasteiz, Spain	Oct 05-10, 2008
Potato congress, Carchi, Ecuador	Nov 13-15, 2008
Latin American Potato Congress (ALAP), Mar del Plata, Argentina	Nov 30-Dec 06, 2008
I International Congress on Native Potatoes	Mar 16-20, 2010
Workshop on evaluations and analysis in potato plant breeding	Mar 22-26, 2010
► **Presentations**	
Oral: CIP-Lima, Peru	Jan 10-11, 2008
Poster: Cuzco-Peru	Mar 25-28, 2008
Oral: Potato Congress Quito, Ecuador	Jun 18-20, 2008
Oral: Patata 2008, Vitoria Gasteiz, Spain	Oct 05-10, 2008
Poster: Latin American Potato Congress (ALAP), Mar del Plata, Argentina	Nov 30-Dec 06, 2008
Oral: I International Congress of Native Potatoes Quito-Ecuador	March 16-20, 2010
Oral: Workshop on evaluations and analysis in potato plant breeding	Mar 22-26, 2010
► **IAB interview**	
► **Excursions**	
Subtotal Scientific Exposure	*18,9 credits**
3) In-Depth Studies	*date*
► **EPS courses or other PhD courses**	
Molecular markers in plant breeding (Quito- Ecuador) INIAP-Nuffic and Wageningen University	Apr 16-May 11, 2007
Modern breeding techniques (Gent Univiersity)	Aug 14-23, 2007
► **Journal club**	
Potato breeding - INIAP-Ecuador	2009-2010
► **Individual research training**	
Molecular Techiques Catholic University Quito Ecuador	Oct 21-24, 2008
Estability analysis INTA Balcarce Argentina	Nov 27-29, 2008
Subtotal In-Depth Studies	*11,5 credits**
4) Personal development	*date*
► **Skill training courses**	
Information literacy, introduction End Note	Jun 2010
Refresh course post harvest management in perishable crops (INIAP-NUFFIC-WUR)	Oct 18-29, 2010
► **Organisation of PhD students day, course or conference**	
International year of potato in Ecuador	May 2008
I International native potatoes congress	March 16 - 20, 2010
Workshop on evaluations and analysis on potato plant breeding	March 22 -26 , 2010
Refresh course post harvest management in perishable crops	October 18-29, 2010
► **Membership of Board, Committee or PhD council**	
Subtotal Personal Development	*6,6 credits**
TOTAL NUMBER OF CREDIT POINTS*	**44.5**

Herewith the Graduate School declares that the PhD candidate has complied with the educational requirements set by the Educational Committee of EPS which comprises of a minimum total of 30 ECTS credits

** A credit represents a normative study load of 28 hours of study.*

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PROPOSITIONS

1. The ideal potato for the Ecuadorian fresh market is a theoretical concept that can be turned into reality through precision breeding. (This thesis)

2. The use of Ecuadorian potato landraces in breeding for tuber quality is not enough to get the ideal potato. (This thesis)

3. Breeding with landraces should never be restricted by patents.

4. Hunger in developing countries is a question of distribution rather than production.

5. A new green revolution is only necessary when the current model of economic development is continued.

6. Carrying out a PhD thesis research is a long race that with the right attitude, perseverance and passion can be completed and even enjoyed.

7. Living in a foreign country is an enriching experience that makes you appreciate your own country more.

Propositions belonging to the thesis, entitled

"Potato quality traits: variation and genetics in Ecuadorian potato landraces"

Xavier Cuesta Subia
Wageningen, 10th June 2013