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Large-Scale Evaluation of Potato Improved Varieties, Genetic Stocks and Landraces for Drought Tolerance

R. Cabello · F. De Mendiburu · M. Bonierbale · P. Monneveux · W. Roca · E. Chujoy

Abstract Potato production worldwide is strongly affected by water stress, either because of insufficient rainfall or due to inadequate irrigation. Improving drought tolerance is consequently becoming a priority for potato breeders, particularly in the perspective of climate change. In the present study, a set of 918 accessions from CIP world potato collection was evaluated under field conditions with full irrigation and deficit irrigation, on the desertic coast of Peru. The set included improved varieties, genetic stocks and landraces. The subset of landraces comprised accessions from the species *Solanum ajanhuiri* Juz. & Bukasov, *Solanum curtilobum* Juz. & Bukasov, *Solanum juzepczukii* Bukasov and *Solanum tuberosum* L. *S. tuberosum* L. included non Andean accessions of the ssp. *Chilotanum* as well as accessions belonging to the Andean cultivar groups Andigenum, Chaucha, Goniocalyx, Phureja and Stenotomum. Under both drought and irrigated treatments, significant differences were found for tuber yield, tuber number and tuber weight among subsets, cultivar groups and accessions. On average, improved varieties and advanced bred lines yielded more under both deficit and well-irrigated conditions than did landraces, while variation for drought susceptibility was greater in landraces and genetic stocks than in improved varieties. Within the subset of landraces, the species *Solanum juzepczukii* Bukasov exhibited the lowest average values and highest variation for drought susceptibility. A high proportion of accessions combining low drought susceptibility and high irrigated yield were found in Andean landraces, and particularly in the species *Solanum curtilobum* Juz. & Bukasov in the *S. tuberosum* L. cultivar groups Stenotomum, Andigenum and Chaucha. The differences observed among species and cultivar groups were not directly related to their eco-geographic distribution. The polyploid species and cultivars groups appeared more drought tolerant than the diploid ones. The study evidenced the interest of Andean landraces as potential sources of drought tolerance in potato breeding programs.

Resumen La producción de papa en el mundo es fuertemente afectada por el estrés hídrico debido a la falta de precipitación o a irrigación inadecuada. Mejorar la tolerancia a sequía es, por lo tanto, una meta prioritaria para los mejoradores de papa, particularmente en la perspectiva del cambio climático. En el presente estudio, un total de 918 accesiones de papa del Banco de Germoplasma del CIP fue evaluado bajo riego completo y riego limitado, en las condiciones desérticas de la costa del Perú. La colección incluyó variedades mejoradas, genotipos de pre-mejoramiento y cultivares locales. El subconjunto de cultivares locales comprendió accesiones de las especies *Solanum ajanhuiri* Juz. & Bukasov, *Solanum curtilobum* Juz. & Bukasov, *Solanum juzepczukii* Bukasov and *Solanum tuberosum* L. *S. tuberosum* L. incluyo accessiones no andinas de la ssp. *chilotanum* y accessiones de los grupos de cultivares andinos *andigenum*, *chaucha*, *goniocalyx*, *phureja y stenotomum*. En condiciones de riego y de sequia se encontraron diferencias significativas para rendimiento, número y peso de tubérculos entre subconjuntos, grupos de cultivares y accesiones. En general, las variedades mejoradas tuvieron mayor

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rendimiento bajo condiciones de sequía y de riego, mientras la variación para susceptibilidad a sequía fue más amplia en cultivares locales que en genotipos de pre-mejoramiento y variedades mejoradas. En el grupo de cultivares locales, la especie *Solanum juzepczukii* Bukasov presentó mas amplia variación y menores valores medias para susceptibilidad a sequía. Una alta proporción de accesiones combinando bajo índice de susceptibilidad a sequía y alto rendimiento bajo riego fue encontrada en cultivares locales andinos, particularmente en la especie *Solanum curtilobum* Juz. & Bukasov y en los grupos de cultivares de *S. tuberosum stenotomum*, *andigenum y chaucha*. Las diferencias observadas entre especies y grupos de cultivares no dependieron de su distribución geográfica. Las especies y los grupos de cultivares poliploides monstraron mejor tolerancia a sequia que los diploides. El estudio puso en evidencia el interés de los cultivares locales andinos como fuentes potenciales de tolerancia a sequia en los programas de mejoramiento de papa.

Keywords Drought · Potato · Landraces · Improved varieties · Genetic stocks

Introduction

Potato, the world's fourth most important food crop, with an annual production of 330 million tons (FAO 2010), regularly undergoes drought stress in most of its growing regions. Drought occurs due to erratic rainfall, especially in tropical and subtropical regions where potato is mainly cultivated under rainfed conditions, or to inadequate irrigation techniques. Drought affects potato growth and production by limiting the amount of productive foliage (Jefferies 1993), decreasing the rate of photosynthesis per unit of leaf area (Ta et al. 2003) and reducing harvest index (Deblonde et al. 1999). It also influences tuber quality (Ta et al. 2003). By exacerbating drought events throughout the world, climate change is expected to strongly impact potato production. Yield losses in the world due to drought are expected to range between 18 % and 32 % in the next 30 years (Hijmans 2003). The response of potato to water stress is well documented (van Loon 1986). All stages of crop development are sensitive to drought stress, but the magnitude of the response highly depends on the timing of water limitation (Spitters and Schapendonk 1990). For example, insufficient water supply in the period between emergence and the beginning of tuber bulking leads to reduced growth rate of foliage, incomplete ground cover and reduced intercepted radiation (Tourneux et al. 2003).

The modern varieties of *S. tuberosum* L. are considered as susceptible to drought stress (Weisz et al. 1994). This is likely to be due to the relatively narrow genetic base of this group, where more than 80 % of the genes of modern varieties come from varieties developed and grown at the beginning of the 20th century (Contreras 2008). To improve potato yield in less optimum climatic conditions and adapt potato to drastic changes in climatic conditions, it is consequently important to explore the capacity of the available germplasm (improved varieties, genetic stocks and landraces) to provide useful traits and genes for facing these challenges. Of particular interest are the Andean potato landraces, extremely diverse and cultivated in a large range of agro-ecological conditions (Ritter et al. 2008). Andean potatoes include the species *Solanum ajanhuiri* Juz. and Bukasov, *Solanum curtilobum* Juz. and Bukasov, *Solanum juzepczukii* Bukasov, and the cultivar groups Andigenum, Chaucha, Goniocalyx, Phureja and Stenotomum within *S. tuberosum* ssp. *andigenum* (Spooner et al. 2007; Ovchinnikova et al. 2011). Due to their evolution and cultivation in the cold and dry Andean Altiplano, the Andean potatoes are supposed to be more drought tolerant than the non Andean *S. tuberosum* potatoes (Ritter et al. 2008). Information on drought tolerance of Andean native potatoes is however scarce. Vasquez-Robinet et al. (2008) reported that within *S. tuberosum* L., photosynthesis is less affected by drought in the Andigenum group than in modern varieties. Little is known, however, about the level of tolerance of the other Andean potatoes.

The objectives of the present study were to analyze the variation for drought tolerance in a large set of improved varieties, genetic stocks and landraces and identify drought tolerant cultivar groups and accessions.

Materials and Methods

Plant Material

A set of 918 potato accessions provided by CIP (Centro Internacional de la Papa) genebank has been used in this study. This set, previously used for diversity studies, was genotyped with micro-satellite markers (Ghislain et al. 2004). It is composed of 226 improved varieties, 74 genetic stocks and 618 landraces.

The subset of improved varieties included foreign varieties and advanced breeding clones extracted from the Late Blight Resistant (LBR) and Lowland Tropic Virus Resistant (LTVR) populations developed at CIP (Bonierbale et al. 2003). Two segregating diploid population (BCT and PD) genetic stocks used in the study were extracted from populations developed at CIP to improve late blight resistance and nutritional characteristics, respectively. The BCT backcross population was developed by Bonierbale et al. (1994). Briefly, an interspecific progeny was developed by crossing a dihaploid *S. tuberosum* clone (USW-2230) as female with an individual of the accession PI473331 of the wild species *Solanum berthaultii* Hawkes. One individual from the F1 progeny (M200-30) was then backcrossed with the *S. tuberosum* parent clone HH1-9 to generate the backcross progeny (Bonierbale et al. 1994). The diploid population PD progenies were produced from a cross between a native cultivated potato belonging to the Phureja cultivar group (with quantitative resistance to potato late blight) and the *S. tuberosum* dihaploid PS-3 highly susceptible to potato late blight (Ghislain et al. 2001).

The 618 landraces accessions belonged, following the taxonomy of cultivated potatoes proposed by Spooner et al. (2007) and Ovchinnikova et al. (2011), to the four species *Solanum ajanhuiri* Juz. & Bukasov (15), *S. curtilobum* Juz. & Bukasov (15), *S. juzepczukii* Bukasov (22) and *S. tuberosum* L. (566). In the present study, we distinguished, within *S. tuberosum* L., different cultivars groups. According to Spooner et al. (2007) cultivar groups are taxonomic categories used by the International Code of Nomenclature of Cultivated Plants to associate cultivated plants with traits that are of use to agriculturists. Based on origin, ploidy and previous classifications, in particular Huamán and Spooner (2002), we considered the cultivar groups Andigenum (261), Chaucha (113), Goniocalyx (45), Phureja (81), Stenotomum (43) and non Andean *S. tuberosum* (23), this last one referred by Ovchinnikova et al. (2011) as Chilotanum group. L. The three species *S. ajanhuiri*, *S. curtilobum*, *S. juzepczukii* and the five *S. tuberosum* cultivar groups were considered as eight different groups in the statistical analysis. Three materials (‘Revolucion’, ‘Achirana’ and ‘Compis’) were included as controls for comparison across trials and years. ‘Revolucion’ is an improved variety, well adapted to the arid conditions of the Peruvian Central Coast of Peru, but susceptible to drought. ‘Achirana’ is a drought tolerant improved variety, grown in several countries worldwide. ‘Compis’ is an Andigenum landrace, well adapted to the dry highlands of Peru.

The set was evaluated throughout 5 years, from 2004 to 2008, in CIP’s La Molina experiment station, located in the coast of Peru, at latitude −12.0778°, longitude −76.9110° and 240 m above sea level. La Molina climate is characterized by the absence of rainfall, high relative humidity (between 71.3 and 92.0 %) and low vapor deficit pressure (from 38 10^{-6} MPa in August to 58 10^{-6} MPa in November). Annual average minimum and maximum temperatures were 14.9 °C and 18.0 °C, respectively. Monthly maximum temperature ranged from 17.1 °C in August to 19.1 °C in November. Accumulated solar radiation increased toward the end of the cropping season and ranged from 1,671 to 4,808 $\mathrm{W m^{-2}}$. Weather inter-annual variation was very low.

The soil is an Entisol, containing 46 % sand, 32 % silt and 22 % clay. Bulk density ranged from 1.3 to 1.2 and field capacity from 24 % to 21 % moisture by weight down the soil profile to 100 cm. Soil organic matter content was 3.1 % and pH was 7.1. Electrical conductivity (EC) and cation exchange capacity were 2.7 DS/m and 10.7 meq 100 g^{-1}, respectively.

Different accessions were evaluated each year with the exception of the controls, cultivated in all years. Planting was done the first week of August, and harvest the last week of November. Germplasm of the three subsets was evaluated in three different trials, due to their different plant type and earliness. Thirty plants per clone, in three replications, in one row and 10 plants per replication were arranged in the field, following an alpha design in a RCBD. Fertilization and weed and pest control were the same for each group and year.

Irrigation frequency and volume were estimated to allow significant differences between treatments and accessions. In the irrigated treatment, water was applied to the crop every 10 days. In the drought treatment, furrow irrigation was stopped 35 days after planting in the case of improved varieties and 42 days after planting in the case of the genetic stocks and landraces, to take into consideration the quicker early growth of the improved germplasm. The total quantity of water received by the crop over the 5 years varied between 375 and 414 mm for the irrigated treatment and 128 and 175 mm in the drought treatment. Soil water potential was measured every day in each treatment using granular matrix sensors (Watermark model 900 M-Monitor, the Irrometer Company, Riverside-California, USA), placed at 30 and 45 cm depth in three sites. Data were recorded every day at 2:00 p.m. with a data logger. Four weeks after stopping irrigation, soil water potential in the fully irrigated treatment ranged from 0.022 to 0.063 MP and exceeded by 0.2 MPa the drought treatment.

Measurements

Improved varieties that had a much shorter growing cycle were harvested 90 days after planting, while genetic stocks and landraces were harvested 120 days after planting. For each plot were measured tuber yield (g $\mathrm{plant^{-1}}$), tuber number (per plant) and average tuber weight (g). Tubers were collected and dried for the determination of tuber dry matter (%). For each accession, a Drought Susceptibility Index (DSI) was calculated as $\mathrm{DSI} = (1 - \mathrm{Yd}/\mathrm{Yw})/\mathrm{D}$, where Yd=mean yield of the accession under drought, Yw=mean yield of the same accession under well-watered conditions, and D=environmental stress intensity (Fischer and Maurer 1978).

Experimental data were subject to ANOVA using SAS-Proc Mixed version 9.1 for WINDOWS in order to adjust the year effect on the accessions.

Results

Variance analysis (Table 1) revealed significant accession and treatment effects for tuber yield, tuber number, average tuber weight, and tuber dry matter. Year and subset effects were not significant. The interaction between treatments and accessions was highly significant. The interaction between subsets and treatments was also significant, except for tuber

Table 1 Variance analysis for tuber yield, tuber number, tuber weight and tuber dry matter in the whole collection

Source of variation	Degrees of freedom	Tuber yield	Tuber number	Tuber weight	Tuber dry matter
Year	8	360365 ns	180.56 ns	6430.83 ns	67.91 ns
Subset (year)	3	45767 ns	92.90 ns	959.59 ns	48.89 ns
Accession	914	316254[a]	409.85[a]	1823.59[a]	40.53[a]
Treatment	1	5894973[a]	993.50[a]	18534[b]	247.12[b]
Treatment[b]Accession	914	61999[a]	59.68[a]	312.16[a]	9.34[a]
Subset[b] Treatment (year)	3	307440[a]	11.17 ns	2308.65[a]	16.52[b]
Year[b] Treatment	8	84197 ns	20.00 ns	1720.20 ns	26.24 ns

[a]significant at 0.01

[b]significant at 0.05 and *ns* no significant

number. The interaction between years and treatments was not significant.

Average tuber yield under irrigated conditions was 813.7, 392.1 and 475.9 g in improved varieties, genetic stocks and landraces, respectively (Table 2). Under drought conditions, tuber yield decreased to 420.2, 223.0, and 299.7 g in improved varieties, genetic stocks and landraces, respectively. Highly significant correlations were noted between tuber yield under irrigated and drought conditions ($r=0.782$, $P<0.001$; $r=0.426$, $P<0.001$; and $r=0.742$, $P<0.001$) in improved varieties, genetic stocks and landraces, respectively. Within each subset, year effects were low or not significant. Accession and treatment effects were highly significant. The interaction between treatment and accession was significant, except for tuber number in the subset of genetic stocks.

Table 2 Variance analysis for tuber yield, tuber number, tuber size and tuber dry matter in the different subsets comprising the whole collection (improved varieties, genetic stocks and landraces)

Source	Degrees of freedom	Tuber yield (g)	Tuber number	Tuber weight (g)	Tuber dry matter (%)
Improved varieties					
Mean values (irrigated conditions)		813.7	15.4	60.1	20.3
Mean values (drought conditions)		420.2	11.9	39.3	23.0
Year	4	429948 ns	24.08 ns	6028.42 ns	138.82 ns
R(year)	10	462385[a]	38.37[a]	2242.57[a]	25.70[a]
Accession	225	403636[a]	221.27[a]	2578.18[a]	20.00[a]
Treatment	1	5276411[a]	322.41[b]	15519[a]	273.58[b]
Treatment[b] Accession	225	88818[a]	26.65[a]	346.19[a]	5.51[a]
Year[b] Treatment	4	98636[b]	17.02 ns	727.15[b]	18.20[a]
Genetic stocks					
Mean values (irrigated conditions)		392.1	11.6	44.6	18.0
Mean values (drought conditions)		223.0	9.2	32.9	20.8
Year	1	431182 ns	5.42 ns	5134.58[b]	0.77 ns
R(year)	4	44333[a]	54.17[a]	720.12[a]	48.73[a]
Accession	75	114059[a]	105.31[a]	2760.17[a]	29.83[a]
Treatment	1	3393898[a]	620.33[a]	16990[a]	875.15[a]
Treatment[b] Accession	75	47234[a]	14.63 ns	384.27[a]	7.06[a]
Year[b] Treatment	1	22110 ns	6.78 ns	25.38 ns	47.49 ns
Landraces					
Mean values (irrigated conditions)		475.9	18.0	30.6	19.9
Mean values (drought conditions)		299.7	14.5	23.0	21.7
Year	4	173191 ns	644.37[b]	8040.20 ns	42.00 ns
R(year)	11	471177[a]	126.14[a]	1608.32[a]	25.60[a]
Accession	620	306391[a]	511.27[a]	1426.81[a]	48.94[a]
Treatment	1	3765890[a]	1526.95[a]	6474.93[a]	351.79[a]
Treatment[b] Accession	618	53568[a]	76.70[a]	290.11[a]	10.94[a]
Year[b] Treatment	4	219810[b]	15.05 ns	4008.61[b]	26.20[b]

Statistic significance: [a]significant at 0.01; [b]significant at 0.05 and *ns* no significant

In landraces, a highly significant group effect was found on tuber yield, number, size and dry matter (Table 3). The Andean *S. tuberosum* cultivar groups Andigenum and Chaucha, the species *S. curtilobum* and the non Andean *S. tuberosum* accessions had higher tuber yield in average than *S. ajanhuiri* and *S. juzepczukii*, both under irrigated and drought conditions (Table 4). These last species had higher tuber number than *S. curtilobum* and the *S. tuberosum* cultivar groups Andigenum, Phureja and Stenotomum, both under irrigated and drought conditions. The highest tuber weights were noted in *S. curtilobum* and the non Andean *S. tuberosum* and the lowest in *S. ajanhuiri*. The highest tuber dry matter was observed in *S. juzepczukii* and the lowest in the *S. tuberosum* cultivar group Andigenum.

A larger variation was noted for drought susceptibility index (DSI) in genetic stocks and landraces, compared to improved varieties (Fig. 1). Within the subset of improved varieties, higher DSI was found for the LBR and LTVR accessions, compared to the foreign varieties (Fig. 2a). Within the subset of genetic stocks, a higher DSI and a broader variation for this trait were noted among PD accessions (Fig. 2b). Among landraces, *S. juzepczukii* had the lowest DSI value (Fig. 2c). A broader variation for DSI was found in this group and to a lesser extent, in *S. curtilobum* and *S. ajanhuiri*.

Accessions combining high yield under irrigated conditions and low DSI were found mainly among improved varieties and landraces (Fig. 3). Table 5 provides a list of improved varieties, genetic stocks and landraces with tuber yield under irrigated conditions superior to their median, and DSI lower to their median. Among the checks, Revolucion had lower yield under drought and higher DSI than Compis, as expected. Achirana had the lowest DSI. The improved varieties possessing these traits (38 accessions) included 6 foreign varieties and 17 and 15 accessions extracted from the LBR and LTVR populations, respectively. Most of improved varieties had higher yield, both under irrigated and drought conditions, than the checks. The subset of genetic stocks (13) only involved BCT clones, characterized by low yield and low DSI. The landraces with high tuber yield under irrigated conditions and low DSI (114 accessions) included accessions from the cultivar groups Andigenum (58), Ajanhuiri (1), Chaucha (25), Curtilobum (5), Goniocalyx (7), Phureja (6), Stenotomum (7) as well as non Andean *S. tuberosum* accessions (5). They did not include *S. juzepczukii* accessions because of their low yield under irrigated conditions.

Discussion

Highly significant differences for tuber yield, number of tubers, average tuber weight and tuber dry matter were found among the tested accessions, both under irrigated and drought conditions. The reduction of around 62 % of water supply resulted in reduction of 58, 80 and 71 % of tuber yield, tuber number, and average tuber weight, respectively. However, the effect of water shortage highly differed among the subsets of germplasm used in this study. Within the subset of improved varieties, the drought treatment resulted in a reduction of 48 % in tuber yield, 22 % in tuber number and 35 % in average tuber weight in comparison to full irrigation. Within the subset of genetic stocks, the reduction was 52 % in tuber yield, 30 % in tuber number and 30 % in average tuber weight. Finally, within the subset of landraces, water shortage resulted in 38 %, 20 % and 26 % reduction in tuber yield, number and weight, respectively, indicating lower yield loss under drought particularly in comparison with improved varieties. This increase in drought susceptibility observed from landraces to improved varieties could reflect a gradual narrowing of the genetic base.

As pointed out by Ober et al. (2004), it is important to differentiate between genotypes that have high yield under drought stress simply because of high inherent yield potential and those that also have greater drought tolerance *per se*, here estimated from the drought susceptibility index (DSI). In the present study, accessions with high yield under irrigated conditions also tended to yield well under drought conditions.

Table 3 Variance analysis for tuber yield, tuber number, tuber weight and tuber dry matter in landraces

Source	Degrees of freedom	Tuber yield	Tuber number	Tuber size	Tuber dry matter
Year	4	776966 ns	2576.92 ns	6149.14 ns	530.98 ns
Cultivar group	8	1636319[a]	2147.80[a]	6100.19[a]	255.40[a]
Treatment	1	8368878[b]	3068.27 ns	18366 ns	909.90 ns
Year[b] Cultivar group	22	213813 ns	426.01[b]	1212.34[b]	33.92[a]
Year[b] Treatment	4	1361218[a]	959.57[a]	7754.46[a]	244.65[a]
Treatment[b] Cultivar group	8	244227[b]	279.02 ns	584.49 ns	8.86 ns
Year[b] Treatment[b] Cultivar group	22	113527.91[b]	171.30 ns	576.38[b]	10.17 ns
R(year)	11	449306.91[a]	125.56 ns	1549.18[a]	24.94[b]

Statistic significance: [a]significant at 0.01; [b]significant at 0.05 and *ns* no significant

Table 4 Ranking of cultivar groups for tuber yield, tuber number, tuber weight and tuber dry matter

	Tuber yield (g)		Tuber number		Tuber weight (g)		Tuber dry matter (%)	
Species and Cultivar groups (ploidy)	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought	Irrigated	Drought
Solanum ajanhuiri Juz. & Bukasov ($2n=2x=24$)	201.6^{c}	121.1^{d}	9.0^{cd}	7.4^{c}	20.0^{c}	14.8^{c}	24.2^{a}	25.5^{b}
Solanum curtilobum Juz. & Bukasov ($2n=5x=60$)	606.7^{a}	379.0^{a}	17.7^{ab}	15.2^{ab}	51.9^{a}	28.1^{b}	21.8^{b}	24.7^{b}
Solanum juzepczukii Bukasov ($2n=3x=36$)	170.2^{c}	168.2^{cd}	7.1^{d}	7.3^{c}	23.5^{bc}	23.3^{bc}	25.2^{a}	27.2^{a}
Solanum tuberosum L.								
Andigenum ($2n=4x=48$)	558.6^{a}	347.4^{ab}	22.5^{a}	17.8^{a}	28.6^{bc}	22.5^{bc}	19.3^{c}	20.5^{e}
Chaucha ($2n=3x=36$)	568.2^{a}	338.6^{ab}	13.8^{bc}	12.6^{abc}	44.3^{a}	29.5^{b}	20.4^{bc}	22.6^{cd}
Goniocalyx ($2n=2x=24$)	382.5^{b}	231.5^{bcd}	13.4^{bc}	10.9^{bc}	30.6^{b}	22.7^{bc}	20.3^{bc}	21.7^{de}
Phureja ($2n=2x=24$)	370.6^{b}	215.0^{bcd}	17.6^{ab}	14.0^{ab}	21.5^{bc}	16.3^{c}	19.1^{c}	24.0^{bc}
Stenotomum ($2n=2x=24$)	378.7^{b}	269.2^{abc}	15.1^{b}	13.3^{ab}	28.3^{bc}	22.4^{bc}	21.1^{b}	22.7^{cd}
Non Andean Tuberosum ($2n=4x=48$)	526.1^{a}	334.9^{ab}	12.3^{bcd}	9.8^{bc}	52.0^{a}	39.8^{a}	21.2^{b}	22.9^{cd}
Mean	418.1^{a}	267.2^{b}	14.3^{a}	12.0^{a}	33.4^{a}	24.4^{b}	21.4^{a}	23.5^{b}

This suggested that potential yield explained an important part of the productivity under drought stress, but also that yield under both irrigated and drought conditions depended on the adaptation of the different varieties (most of them adapted to high altitude environments) to the conditions of the testing location. Despite the general linear relationship between drought stress and irrigate tuber yields, there was sufficient dispersion to indicate that not all accessions responded similarly to drought. This was confirmed by the significant treatment by accession interaction for tuber yield in improved varieties, genetic stocks and landraces and the large variation for DSI across subsets and accessions.

Potato landraces cultivated in a large range of agro-ecological conditions and subjected to very diverse selection pressures (Ritter et al. 2008) had higher variation for DSI than improved varieties, confirming their value as a reservoir of potentially useful drought tolerance genes. Among improved varieties, higher DSI in LBR and LTVR accessions, compared to foreign varieties, is likely to be due to the high moisture selection pressure applied to screen for late blight and virus resistance in these populations (Bonierbale et al. 2003). Among genetic stocks, the PD accessions derived from a cross between Andean (Phureja) and non Andean *S. tuberosum*

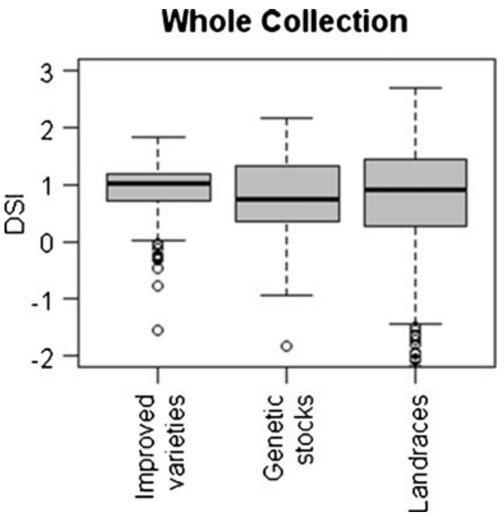


Fig. 1 Boxplot grouping for DSI in the whole collection

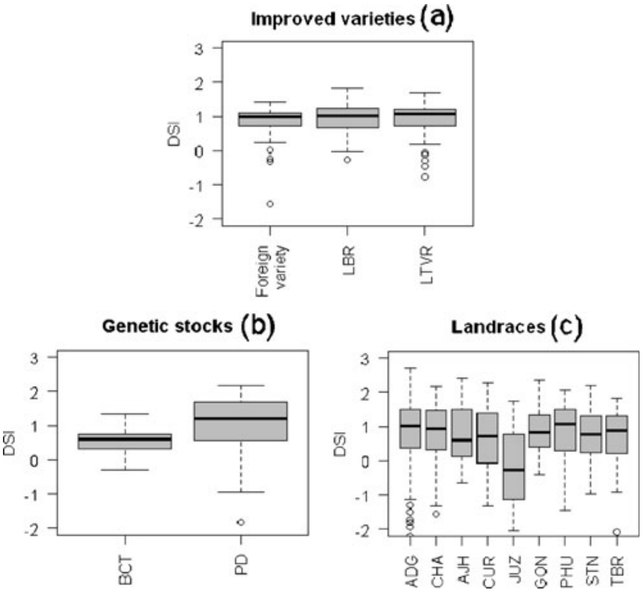
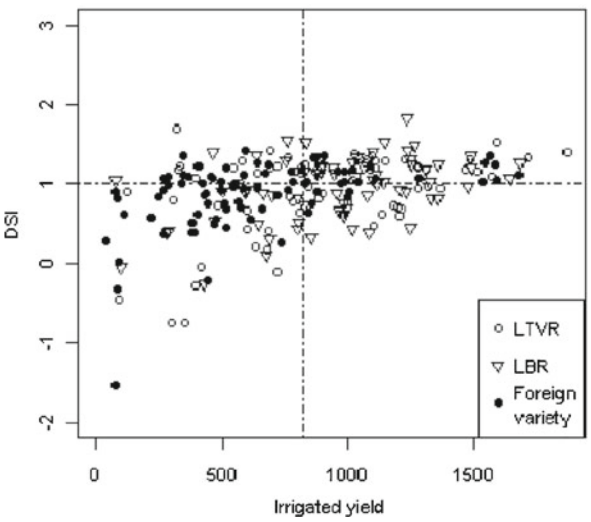
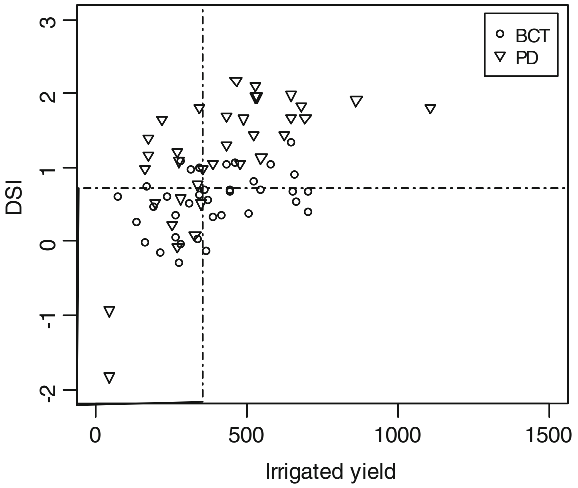


Fig. 2 Boxplot grouping for DSI in the subsets of improved varieties (**a**), genetic stocks (**b**) and landraces (**c**). *LBR* late blight resistant population; *LTVR* lowland tropic virus resistant population; *ADG* andigenum(1); *CHA* chaucha(1); *AJH* ajanhuiri(2); *CUR* curtilobum(3), *JUZ* juzepczukii(4), *GON* goniocalyx(1); *PHU* phureja(1); *STN* stenotomum(1); *TBR* tuberosum(5); for (BCT population and PD see explanations in the text) (1) Andean *Solanum tuberosum* cultivar groups; (2) *Solanum ajanhuiri* Juz. & Bukasov; (3) *Solanum curtilobum* Juz. & Bukasov; (4) *Solanum juzepczukii* Bukasov; (5) Non Andean *Solanum tuberosum* L

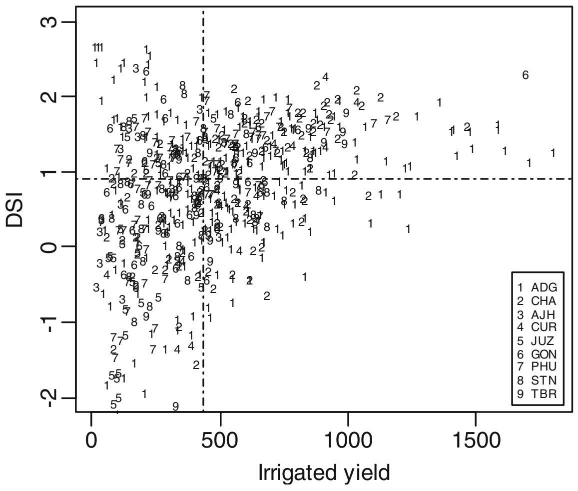
Improved varieties (a)



Genetic stocks (b)



Landraces (c)



◀**Fig. 3** Plotting of accessions according to tuber yield per plant under irrigated conditions and drought susceptibility index within improved varieties (**a**), genetic stocks (**b**) and landraces (**c**). Genotypes with tuber yield under irrigated conditions superior to their median and DSI lower to their median (quadrant on the right and below part of the graphics) represent 16.8 %, 33.7 % and 18.5 % of the improved varieties, genetic stock and landraces, respectively. These genotypes are listed in Table 5. *LBR* late blight resistant population; *LTVR* lowland tropics virus resistant population; *ADG* andigenum(1); *CHA* chaucha(1); *AJH* ajanhuiri(2); *CUR* curtilobum(3), *JUZ* juzepczukii(4), *GON* goniocalyx(1); *PHU* phureja(1); *STN* stenotomum(1); *TBR* tuberosum(5); for BCT population and PD see explanations in the text. (1) Andean *Solanum tuberosum* cultivar groups; (2) *Solanum ajanhuiri* Juz. & Bukasov; (3) *Solanum curtilobum* Juz. & Bukasov (4) *Solanum juzepczukii* Bukasov; (5) Non Andean *Solanum tuberosum* L

accessions (Ghislain et al. 2001) had higher DSI, but also higher variation for this trait than the BCT accessions obtained from a backcross population involving the wild potato species *S. berthaultii* Hawkes.

Comparing DSI and tuber yield under irrigated conditions permitted us to identify accessions combining high productivity and drought tolerance. The proportion of accessions with tuber yield under irrigated conditions superior to the median and DSI lower to their median, regarding to the total number of accessions tested, was slightly higher in landraces (18.5 %) compared to genetic stocks and improved varieties (17.6 and 16.8 %, respectively). Among native Andean potatoes, the highest proportion of accessions combining high yield under irrigated conditions and low DSI were noted in the *S. curtilobum* (33.3 %) and in the *S. tuberosum* cultivar groups Stenotomum (25.0 %), Andigenum (22.2 %) and Chaucha (22.1 %). The high proportion in these groups indicated the potential interest of landraces Andean potato to improve drought tolerance in *S. tuberosum* modern germplasm without affecting potential yield.

S. curtilobum derived from natural hybridization between *S. juzepczukii* Bukasov and Andigenum cultivars of *S. tuberosum* (Hawkes 1990) is considered by Ritter et al. (2008) as one of the most frost resistant group. Potatoes of the Andigenum group of *S. tuberosum* have a wide adaptation, being cultivated throughout the Andes from Venezuela to Northern Argentina (Huamán and Ross 1985) at altitudes between 1,950 and 4,050 m (Ochoa 2003). Sources of heat tolerance have also been identified in this group by Morozova and Volkova (1991). Their tetraploid genome allows for hybrid generation with improved *S. tuberosum* varieties (Kumar and Kang 2006). Therefore, accessions of the Andigenum cultivar group are good candidates for the introgression of drought tolerance traits into *S. tuberosum* modern varieties. Potatoes of the Andean cultivar group Stenotomum are cultivated in Central Peru and Bolivia between 3,200 and 4,000 m. Potatoes of the group Chaucha which resulted from hybridization between Andigenum and Stenotomum potatoes are cultivated in Central Peru and Bolivia from 3,300 to 4,000 m altitudes and have the same area of distribution as *S. curtilobum*.

Table 5 Accessions combining high tuber yield under irrigated and low drought susceptibility index (ranked according to their irrigate yield) in each group

CIP identification number	Name	Tuber yield (g/plant)		Drought susceptibility index
		Irrigated	Drought	
Checks				
720043	Revolución	832.3	415.6	1.148
720088	Achirana	457.1	288.6	0.925
700921	Ccompis	867.4	442.4	0.959
Improved varieties				
Foreign varieties				
800226	BR-69.84	1001.7	562.8	0.906
800972	Katcwekano	993.4	590.5	0.839
720123	MEX 750821	967.5	500.0	0.999
720045	Atzimba	878.0	493.5	0.906
676008	I-1039	856.7	547.2	0.747
800222	BR-63.65	841.1	577.1	0.649
LBR clones				
992020	TPS parent	1475.0	785.7	0.966
384321.3	LB-V	1353.8	820.8	0.814
387224.11	LB-IX	1328.3	808.3	0.810
988139	IP88002	1242.4	971.9	0.450
393371.8	B 22	1227.4	694.0	0.899
391062.72	B3CO (GP-II)	1203.9	662.5	0.930
381178.14	LB-I	1080.0	878.3	0.386
501065.1	CG401L-4.1	1072.0	625.5	0.861
988140	IP88003	1016.7	811.1	0.418
381403.16	A LB Group IV	990.6	660.0	0.690
381379.12	A LB Group III	983.3	702.1	0.591
380389.1	Canchan-INIA	980.6	625.0	0.750
393085.5	B3C1	976.1	678.1	0.631
391047.34	B3C1	963.3	652.8	0.667
596013.29	C96H13.29	953.3	549.4	0.876
380496.6	Chagllina-INIA	852.5	722.2	0.316
391058.175	B3C1	827.2	533.3	0.735
LTVR clones				
395193.4	Advanced clone	1361.1	738.9	0.945
383300.21	TS-4	1316.3	705.6	0.959
395195.7	Advanced clone	1271.7	688.9	0.948
392797.22	UNICA	1205.0	800.0	0.695
382432.2	TM-1	1200.0	847.2	0.608
388972.22	C89.315	1191.1	779.9	0.714
390663.8	C91.628	1180.2	766.7	0.725
392273.8	Advanced clone	1129.2	796.0	0.610
376181.5	H-1	1096.7	850.0	0.465
379693.93	P93	997.2	595.1	0.834
395194.9	Advanced clone	993.8	625.7	0.766
397077.16	WA.077/320.16	895.3	518.0	0.871
385500.3	E86.695	880.0	530.8	0.821
397006.18	102.18	843.3	453.7	0.955
391180.6	C90.266	839.1	445.0	0.971
Genetic stocks				
BCT				
810003.109	N271-109	704.7	585.3	0.395
810003.316	N271-316	702.7	502.7	0.664
810003.26	N271-26	662.4	506.7	0.549
810003.112	N271-112	653.2	467.1	0.665
810003.56	N271-56	544.0	380.6	0.701
810003.205	N271-205	505.9	426.0	0.369
810003.21	N271-210	446.1	316.0	0.681
780628	US-W 2230	444.4	313.5	0.688
780974	HH1-9	418.0	353.9	0.358
810003.15	N271-15	387.4	332.0	0.334
781433	M 200.30	374.7	284.0	0.565
810003.164	N271-164	367.3	387.3	−0.127
810003.129	N271-129	360.2	254.0	0.688
Landraces				
Solanum ajanhuiri Juz. & Bukasov				
706205	Jancko Sisu Yari	498	466.7	0.170
Solanum curtilobum Juz. & Bukasov				
707132	Yana Shiri	645.0	475.0	0.712
704161	Luqui Morada	605.6	477.3	0.572
702282	Choquepito	578.5	581.3	−0.013
706776	Lucki	501.6	391.3	0.594
702615	Lucki Morada	490.0	348.0	0.783
Solanum tuberosum L.				
Andigenum				
706724	Puca Allqu	1235.0	1106.7	0.281
705234	‘- ’	1200.0	870.0	0.743
703456	‘- ’	1130.0	821.7	0.737
704440	Venancia	1088.3	948.3	0.348
705223	Capiro	950.0	718.3	0.659
704365	‘- ’	916.7	653.3	0.776
703502	Rosita	855.0	781.7	0.232
705739	Renacimiento	831.7	944.1	−0.365
701142	Escoleta	830.7	700.7	0.423
704865	Holandesa	818.3	555.4	0.868
700932	Okella Quehuillo	790.7	614.9	0.601
705088	Chava Negra	783.3	683.3	0.345
704626	Puma Maki	757.8	536.1	0.790
705536	Duraznillo	750.0	583.0	0.602
705336	Calvache	747.6	691.7	0.202
705378	Leona Negra	731.3	488.4	0.897
703457	Criolla	727.2	648.0	0.294
704864	Koli	714.2	524.7	0.717
704472	Chilqueño	674.4	492.6	0.728
705548	Yurac Ccompis	673.3	650.0	0.094
702270	‘- ’	672.2	648.3	0.096
704148	Alcona	664.4	689.8	−0.103
701559	Almidona Clucel	655.0	541.7	0.467
705438	Pepino	650.0	554.3	0.398
704143	Roja Ojosa	643.0	582.0	0.256
703426	Wakapa Ñawin	637.2	438.9	0.841
702853	Alca Tarma	630.1	562.6	0.290

Table 5 (continued)

CIP identification number	Name	Tuber yield (g/plant)		Drought susceptibility index
		Irrigated	Drought	
704144	Runa Amarilla	615.9	708.0	−0.404
703431	Nicolasa	610.0	498.7	0.493
704556	Pukuchu	598.3	520.0	0.354
705809	‘- ’	579.0	405.9	0.808
701986	Amaryllo	573.7	406.0	0.790
700787	EE-2057	572.2	436.7	0.640
705772	Viuda Yana Mata	570.9	378.3	0.911
700766	Ocke Suitu	560.0	483.3	0.370
705873	‘- ’	549.2	693.2	−0.709
701544	Aguiza	548.2	442.7	0.520
704987	Yana Runa	548.0	626.1	−0.385
701313	Papa Hueca	546.3	487.5	0.291
700908	Hueqlla	540.7	536.7	0.020
704157	Runa Blanca	535.0	430.0	0.530
700532	Sapa Negra	531.2	496.0	0.179
705447	Yana Suytu	527.8	418.3	0.560
704636	Negra	525.0	403.3	0.626
705601	Yana Palta	518.9	382.1	0.712
703369	Ojo De Buey	511.1	492.0	0.101
704222	Mayme Shicra	496.7	383.3	0.616
702514	Chata Blanca Ojos Morados	487.4	548.9	−0.341
705082	Tocana Rosada	486.1	405.6	0.448
703415	Raiz del Palo	467.1	381.1	0.497
703830	Pamoq	466.7	403.3	0.367
703310	Linlesh	462.7	619.4	−0.915
700915	Ñata	462.4	346.7	0.676
704828	Wila Imilla	460.4	416.7	0.257
704650	Puka Sole	460.0	421.7	0.225
703269	Chaucha Roja	457.5	305.3	0.899
703144	Llamapa Chupam	454.2	584.9	−0.778
700050	Ricran Paltacc	445.0	398.3	0.284
Chaucha				
704591	Yana P’utis	1080.0	790.0	0.725
704104	Tarmeña Roja	833.7	630.9	0.657
704019	P’asña Papa	823.3	620.0	0.667
704327	Color Unkhuña	821.7	706.7	0.378
707135	Puka duraznillo	785.0	561.7	0.769
705490	Muru Warkatina	686.7	843.3	−0.616
706728	Puqya	662.6	655.0	0.031
706727	Duraznillo	645.8	546.7	0.415
704262	Puca Botijuela	630.4	633.3	−0.013
701531	Yana Rucunag	620.0	711.7	−0.399
706343	Sutu Malcachu	617.3	523.3	0.411
700739	Puca Corika	610.7	473.3	0.608
705784	Muru Huayro	602.6	488.3	0.512
706890	Cheqllos	571.7	438.3	0.630
703301	Araq Zapato o Ayaparara	558.7	419.3	0.674
704047	Canastilla	550.0	620.0	−0.344
703300	Paqocha o Muru Ureña	502.4	444.0	0.314
701573	Puca Duraznillo	491.1	382.6	0.597
703648	Kununara	489.3	432.7	0.313
704012	Sawasiray	489.3	341.7	0.815
700361	‘- ‘	488.1	333.3	0.856
703678	Alcca Huachuco	486.7	421.7	0.361
704010	Yuraq T’oqlolo	478.0	569.3	−0.516
701707	Aracc Zapato	454.8	503.3	−0.288
703649	Kulurara	443.3	401.3	0.256
Goniocalyx				
703877	Akaqllupa Pechon	656.7	471.9	0.760
706036	Puka Raso	612.4	405.0	0.915
705575	Llikapa Rurun	600.0	400.0	0.901
703825	China Runtush	495.8	381.1	0.625
703280	Puka Chaucha	490.0	439.0	0.281
704270	Wira Pasña	450.0	518.3	−0.410
706116	Comino	445.6	306.7	0.842
Phureja				
701570	Chaucha	660.7	549.3	0.455
703600	‘- ‘	653.8	448.3	0.849
705079	‘- ‘	613.6	438.4	0.771
703514	‘- ‘	467.7	338.2	0.748
703654	Chaucha Amarilla	461.7	333.3	0.751
705177	‘- ‘	451.5	326.1	0.750
Stenotomun				
705875	Criolla	885.5	625.0	0.795
705940	Larga	752.2	571.7	0.648
700348	‘- ‘	685.0	605.0	0.316
702331	Sutamari	683.3	490.0	0.764
703933	Titerite	635.0	545.0	0.383
704909	Surinama	627.3	520.0	0.462
704797	Laram Pitu Huayaca	561.5	475.1	0.416
Non Andean Tuberosum				
705010	Papa Del Cura	663.3	455.5	0.847
706737	Collareja	565.7	379.0	0.892
704169	‘- ‘	462.7	442.0	0.121
705009	Purranca	462.7	489.3	−0.156
704168	‘- ‘	454.1	422.7	0.187

‘– ‘: Unknown, because the identity name was not available at the collecting time

Conversely, the proportion of accessions with tuber yield under irrigated conditions above the median and DSI lower than the median, with respect to the total number of accessions tested, was low in the the diploid groups Goniocalyx (15.6 %), Phureja (7.5 %), Ajanhuiri (6.7 %) and Juzepczukii (0 %). Goniocalyx is cultivated in Central and Southern Peru, between 3,100 and 4,000 m (Hawkes 1990). Phureja is characterized by the lack of tuber dormancy, a trait reflecting its adaptation to regions free from long periods of frost and drought, like the Andean valleys (Hawkes 1990). *S. ajanhuiri* is cultivated in high altitudes of Peru and Bolivia, and is resistant to frost. *S. juzepczukii*, a natural triploid hybrid between wild potatoes and Stenotomum potatoes, had the lowest potential yield and the highest drought susceptibility values. It is cultivated at very high altitudes (3,800 to 4,000 m) in Central Peru and Bolivia.

The average drought tolerance level of the different groups did not appear to be directly related to their eco-geographic distribution. Both Andigenum and Phureja cultivar groups have a wide area of distribution and are adapted to low altitudes and milder climates. Phureja had, however, higher drought susceptibility index and lower yield potential, compared to Andigenum. Similarly, *S. curtilobum*, *S. ajanhuiri* and *S. juzepczukii* which are cultivated at similar altitudes in Central Peru to Bolivia, had very different drought tolerance levels.

Drought tolerance appeared more related to level of ploidy and evolution of potato. The polyploid species *S. curtilobum* (5x) and polyploid *S. tuberosum* groups Andigenum (4x) and Chaucha (3x) had higher drought tolerance and potential yield than the diploid species and *S. tuberosum* groups. Stenotomum, the most primitive form (Hawkes 1990) was the most tolerant among the diploid groups evaluated. Chaucha and Curtilobum groups could have inherited drought tolerance from their progenitors. The Chaucha cultivar group derived from natural hybridization between Andigenum and Stenotomum potatoes, while *S. curtilobum* results from a cross between *S. juzepczukii* Bukasov and tetraploid cultivars of *S. tuberosum* (Hawkes 1990).

In the present study, the evaluation conducted in the absence of rainfall allowed a perfect control of the quantity of water brought to the crop. However, differential or poor adaptation of the germoplasm samples to lowland conditions could have slightly biaised the evaluation, particularly in the case of landraces, all of which originated from high altitude areas. Further multi-year and multi-locational evaluation of the tested germplasm will permit to confirm the present results, describe the adaptation patterns of the tolerant germplasm and confirm the potential interest of some accessions as potential sources of drought tolerance in breeding programs. We also started to evaluate the collection used in this study for several physiological drought tolerance related traits. The associations that will be observed between traits and yield components will allow identifying traits that could be used for indirect selection. As the accessions tested here have already been genotyped (Ghislain et al. 2004), the results obtained could also be used for genetic association work.

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