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Drought and Heat Tolerance Evaluation in Potato (*Solanum tuberosum* L.)

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Abstract The impacts of water restriction and high temperatures on potato production will increase over the next decades, due to climate change and the extension of cultivation in drought and heat prone areas. We review recent achievements and describe new avenues in the evaluation of tolerance to these abiotic stresses in potato, focusing on the definition of target populations of environments, choice and characterization of the managed stress environment, stress monitoring, and secondary traits measurement.

Keywords Drought · Heat · Managed stress environments · Phenotyping · Secondary traits · *Solanum tuberosum* L. · Target populations of environments

Introduction

Potato is the world's fourth most produced food crop (370 million tonnes) after rice, wheat, and maize. It is grown on 19 million ha worldwide (FAOSTAT 2013). Developing countries are responsible for more than half of the total world potato production (FAO 2009) and together with soybean constitute the only crops where contribution from developing countries to world production is growing (Walker et al. 2011). Potato is often cultivated in remote and marginal areas by resource-poor farmers with limited access to farm inputs (Scott 1985). In these regions, it largely contributes to dietary daily energy intake (Scott et al. 2000) and hunger reduction (Thiele et al. 2010). Potato is also progressively acquiring higher market value, thus contributing to poverty reduction (Scott et al. 2000). An increasing part of the production is transformed by industry (French fries, chips) particularly in Asia (Janski et al. 2009).

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In developing countries, increase in production is mainly due to an increase in cultivated area, yield annual growth rates remaining stagnant (Walker et al. 2011). In many areas, potato regularly suffers transient water stress due to erratic rainfall or inadequate irrigation techniques (Thiele et al. 2010). It also often faces heat stress, particularly in the tropics and subtropics (Simmonds 1971). The impacts of water shortage and high temperatures on potato production will likely enhance over the next decades, due to climate change and the extension of potato cultivation in drought and heat prone areas (Hijmans 2003).

Climate change is expected to increase the frequency of drought events in many regions, affecting drought susceptible crops like potato (Simelton et al. 2012). Potato yield losses in the world due to climate change are expected to range between 18 and 32% during the first three decades of this century (Hijmans 2003), although this study does not consider the mitigation effect of CO_2. Climate change could also affect tuber quality by reducing dry matter and increasing reducing sugar concentration (Haverkort and Verhagen 2008).

Since 1950, the potato growing area considerably expanded at low latitudes as a winter crop exposed to high temperatures and drought events (Thiele et al. 2008) and field studies have revealed the scope for further extension of potato production in these regions (Minhas et al. 2011). Temperature in these regions is often supra-optimal for potato growth. There is also a potential for intensifying wheat-based systems in Central Asia by cultivating potato as a summer crop that will consequently face increased heat and drought stress (Carli et al. 2014).

Potato is susceptible to both drought (Monneveux et al. 2013) and heat (Levy and Veilleux 2007). Drought susceptibility of potato has been mainly attributed to its shallow root system and low capacity of recuperation after a period of water stress (Iwama and Yamaguchi 2006). Drought decreases plant growth (Deblonde and Ledent 2001), shortens the growth cycle (Kumar et al. 2007), and reduces the number (Eiasu et al. 2007) and size (Schafleitner et al. 2007) of tubers. The magnitude of drought effects on potato production depends on the phenological timing, duration, and severity of the stress (Jeffery 1995; Schafleitner 2009). Emergence and tuberization are two critical periods where water stress most affects final tuber yield (Martínez and Moreno 1992).

High temperature drastically affects potato production (Gregory 1965; Slater 1968). Soil temperature higher than 18 °C tends to reduce tuber yield, especially when combined with high ambient air temperature (30 °C day/23 °C night). When heat stress accompanies drought stress, pronounced declines in tuber yield and tuber quality are noted with notable differences among cultivars (Ahn et al. 2004). Heat stress creates imbalances in source-sink relations, delays in tuber initiation and bulking, and malformation and necrosis of tubers (Levy and Veilleux 2007). Heat tolerance is an important trait for further development of potato in subtropical India (Gaur and Pandey 2000), the semi-arid Middle East (Levy et al. 2001), and the tropics (Minhas et al. 2011).

For a long time, potato was not considered as a crop of major importance in drought- and heat-prone production systems (Hyman et al. 2008; Li et al. 2011) and breeders consequently did not consider tolerance to these stresses as priority objectives (Thiele et al. 2010; Monneveux et al. 2013). Today, the progresses of genomics and bioinformatics offer real opportunities for dissecting the genetic basis of drought and heat tolerance into component traits and select plants with favorable alleles at the underlying genes (Tuberosa 2012). An important quantity of genes involved in drought and heat tolerance have been identified in the past few decades in potato (Monneveux et al. 2013). Availability of genome sequence and high throughput marker systems enriched the genomic resources that were used to develop genetic and physical maps (Kumar et al. 2013). Recently, studies also reported identification of QTLs for drought tolerance in a diploid genetic background (Anithakumari et al. 2011). Further progress in developing drought tolerant germplasm and increasing plant performance in drought and heat prone areas however depends largely on our capacity to generate the high-quality quantitative data that are needed for genetic analysis and gene identification and transfer (Tuberosa 2012).

Phenotyping, the Main Bottleneck in Breeding for Abiotic Stress Tolerance

Plant phenotyping (from the Greek *phainein*, to show) is the basic measurement of individual quantitative parameters that form the basis for more complex traits such as growth, development, tolerance, resistance, architecture, and yield. Plant phenotyping—based on experience and intuition—has been performed by farmers since crop domestication and by breeders during the last century. Over the last two decades, progress was done in the development of more reproducible measurements reducing the individual subjectivity factor of the phenotyper. However, the basic attributes of a good phenotyping approach are not just the accuracy and precision of measurements, but also the relevancy of experimental conditions. Efficient phenotyping implies accurate i) definition of target population of environments, ii) characterization of the testing environment or managed stress environments, iii) stress monitoring, and iv) measurement of secondary traits.

Definition of Potato Target Populations of Environments

Any variety is adapted to several environments. This group of environments is referred by Fischer et al. (2003) as target population of environments (TPE). Deploying different cultivars in different TPEs is the only way to reduce genotype by environment interactions (GEI). A TPE can be defined as the set of all environments in which an improved variety is expected to perform well (Cooper et al. 1997). An important objective for breeders is consequently to clearly define the TPE for which each variety is developed. The environments constituting a TPE must be sufficiently similar for one genotype to perform well in all of them. There are several complementary ways to define the TPE.

Mega-Environments or Agro-Ecological Zones

The definition of a mega-environment (ME) is mainly based on spatial information about environmental constraints (including drought and heat) (Rajaram et al. 1995). It requires previous information about crop distribution, environmental constraints, and the factors to which the crop is susceptible.

Information about potato distribution over the world has been insufficient for a long time. A first (but rather incomplete) map of global potato distribution was published by

Finch and Baker (1917). Global potato distribution maps were further published by Van Royen (1954) and Bertin et al. (1971). A better description of the global distribution of potato area was obtained by merging statistics at country-level, and subnational information with geo-referenced databases (Hijmans 2001; Theisen and Thiele 2008). Monfreda et al. (2008) used the previous approach and excluded non cropland defined by NDVI. Temperature and photoperiod play a key role in the distribution, growth, and development of potato (Kooman and Haverkort 1995; Struik et al. 1999). Dry matter accumulation depends on the amount of solar radiation intercepted by the crop while dry matter distribution between the various organs is determined by temperature and photoperiod (van Keulen and Stol 1995). Short day length and low temperatures (especially at night) enhance tuber initiation and increase the number of tubers while low solar radiation restricts tuber formation (Ewing et al. 2004). Potato growth and development are slow at lower temperatures while daily average temperatures above 21 °C (generally coinciding with day-night temperatures of 27–15 °C), leading to increased respiration and foliar development, are detrimental for potato growth. As a consequence, yield of potato highly depend on latitude and altitude that determine length of the growing period and photoperiod (Haverkort 1989). A global zonification taking into account these two last variables was developed at CIP (Fig. 1) to assist in the distribution of improved potato populations to several regions.

Based on the requirements of the crop and the constraints faced in different regions, potato agro-ecological zones have been also defined. By 1979, CIP potato breeding strategy focused on just two ME, tropical highlands and warm tropics. In 1992, three priority agro-ecologies were defined for potato breeding, the highlands, temperate, and subtropical lowlands regions agro-ecological analysis was used to reprioritize CIP's research (Thiele et al. 2008). In 2013, three main "strategic objectives" were defined (Table 1).

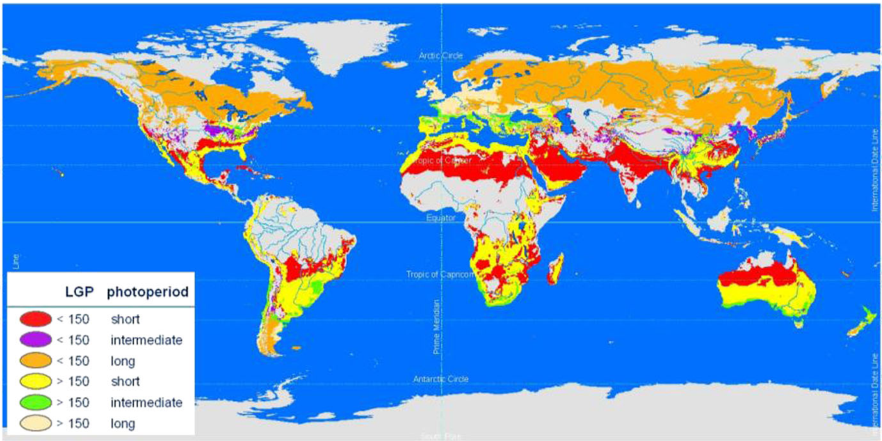

Fig. 1 Global zonification based on length of growing period (LGP) and photoperiod at tuberization. A latitude layer for calculating photoperiods in suitable areas for production was established by using threshold temperatures (minimum between 4 to 18 °C and a maximum below 30 °C) and duration of the growing season (pixels selection depend on if they show the indicated threshold temperatures during three consecutive months). LGP and photoperiod were classified in two (≤150 and >150 days) and three classes (short: ≤13 h, intermediate: 13–15 h and long: >15 h) respectively

Table 1 Main potato mega-environments at the global level were their main characteristic length of growing period and photoperiod, corresponding locations, system characteristics, major constraints, required varietal characteristics and CIP strategic objectives (SO) concerned

Agro-ecological zones (mega-environments)	Definition (Hijmans 2001)	Length of growing period and photoperiod(1)	Major locations	System characteristics and major constraints	Required varietal characteristics	Strategic objectives
Tropical highlands	Altitude >1000 m	Short growing period and short photoperiod	Andean highlands	Small farm size, vulnerability to stress and, increasingly, extreme weather events linked to climate change	Cold tolerance, drought tolerance, biofortification with iron and zinc	SO5
			Nepal, Northeast India, Bhutan, South China, North-West Vietnam, East Indonesia, Philippines	Staple and cash crop in mixed farming systems	High yield, late blight resistance, drought tolerance, biofortification with iron and zinc	SO2
			Africa, elevations between 1500 and 4000 meters	Mixed farming systems (maize, legumes, vegetables) with frequent potato monocropping	Resistance to soil-borne pests and diseases	SO3
Temperate	45°<latitude <57°	Short growing period and long photoperiod	N. China, Central Asia and Caucasus, Korean peninsula, Mongolia	Summer crop, moderate to high temperatures. In the lowlands, alternative to fallow between two consecutive winter wheat crops. In the highlands, alternative to spring wheat/barley	90- to 100-day, resistant to viruses and tolerant to heat, drought, and salinity	SO2
Subtropical lowlands	23°<latitude <34°	Long growing period and short photoperiod	S. China, N. Vietnam, India, Bangladesh, plains of Nepal, East Pakistan	Winter crop at sea level, summer crop at altitudes >1500 m. Cereal-based systems with short fallows appropriate for intensification	70- to 90-day, high dry matter, processing quality, tolerant to heat, resistant to virus	SO2

SO2, enhancing food security in Asia through the intensification of local cereal-based systems through the adoption of the early-maturing agile potato; SO3, improving livelihoods of potato farmers in Africa by tackling deteriorated seed quality through an integrated approach; SO5, addressing the food security challenge through roots and tubers: transforming vulnerability to resilience. (1) See Fig. 1

However, the ME and agro-ecological zones do not always offer a sufficient level of resolution in the definition of TPE. Genotype by environment interaction analysis, spatial analysis, and modeling are useful tools to refine the TPE definition.

Use of Genotype by Environment Interaction Analysis

An important objective by implementing ME and analyzing GEI is, besides describing the behavior of genotypes across different environments, to define clusters of locations sharing the same best cultivar(s), i.e., showing little or no crossover (Yan and Rajcan 2002). The biplot analysis and the AMMI (additive main effects and multiplicative interaction) and GGE (genotype main effects and genotype by environment interaction effects) models have been used in several crops for clustering location and defining TPE (Basford and Cooper 1998; Yan et al. 2007).

A compromise should be searched between precisely defining the TPE and achieving enough replication within it. If the TPE is too narrowly defined, few trials will be conducted within each TPE, and least significant difference values will be very large, preventing accurate evaluations and reducing progress from selection. Since each new TPE will need additional breeding and testing resources, there is a practical limit to the number of TPE used in a breeding program, and breeders should rely on the spillover of a variety from another TPE. The subdivision of a target region into uniform subregions will only increase selection efficiency if genotype-by-subregion interactions are repeatable (Atlin et al. 2001), genotypic correlation among subregions is low (Presterl et al. 2003), and increase in genotypic variance can counterbalance loss in precision of genotypic means associated with division of testing resources (Windhausen et al. 2012).

As there is a large non-predictable component of GEI associated with year-to-year variation, it is sometimes difficult to define consistent patterns for the grouping on the basis of locations (Cooper et al. 1999), and substantial datasets (twenty or more varieties evaluated over several years) are consequently required to accurately estimate the best clustering. The high temporal variability in climatic variable can be addressed using long-term historical (Qiao et al. 2004; Loffler et al. 2005) or simulated/predicted climatic records (CCAFS 2011).

In potato, GEI analysis have been widely used to describe adaptation of potato varieties in specific environments and characterize their stability but poorly exploited for clustering environments. In some crops like wheat breeding programs routinely collected data from ME and historical sets of data are available at the global level (Peterson and Pfeiffer 1989). This is unfortunately not the case in potato, partially because of the constraints related to seeds exchange and distribution.

Use of Spatial Analysis and Modeling

As information about GEI is scarce in potato, CIP invested over the last years in the use of spatial analysis and the development of models to better define TPE. Several advances over the last few decades in the development of computer hardware and software, and availability of climate data in digital formats allowed sophisticated statistical analysis of GEI (Crossa et al. 2004) and development of precise agro-ecological zoning maps (Hyman et al. 2013). By using soil and climate information on the trial sites, it is possible to classify locations into more or less homogenous environment types (DeLacy et al. 1994; Roozeboom et al. 2008). Linking individual trial sites to larger regions for which they are representative is very useful for developing maps of TPE and, ultimately, for introducing varieties into environments where they are expected to perform well (Gauch and Zobel 1997).

In cereals, a great advance in the study of TPE has been attained using long-term climatic records as an input of crop growth models with the aim to analyze patterns of water deficit based on crop water availability (Heinemann et al. 2008; Chenu et al. 2011). This approach permits to identify model parameters, run the model under different climatic scenarios, and test it in the multi-environment trials (Tardieu 2012).

Following the mentioned perspective in potato, long-term precipitation records were collected from the daily TRMM 3B42 v7 data base and corrected with a limited number of gauged data (Heidinger et al. 2012). This information allowed defining the probability of drought as the percentage of years when the precipitation does not cover the crop water demand. Assuming obligatory irrigation until tuber initiation, drought probability was estimated for three phenological stages: after tuber initiation, tuber bulking, and senescence (Fig. 2). Crop growth model parameterization using SOLANUM model (Condori et al. 2010, 2014; Harahagazwe et al. 2012) with promisory potato clones in drought prone areas (Carli et al. 2014) served as a raw material for spatial models that simulated water demand and crop responses in water-limited environments and establish the requested environmental classification. Finally, field MET could serve to test simulation results.

Choice and Characterization of the Managed Stress Environment

Choice of the Managed Stress Environment

As breeding facilities (fields, equipments) are generally not available in the TPE and genetic resources cannot easily be transferred, phenotyping and screening need to be done in a managed stress environment (MSE) that can be the main experimental station(s) of the national program, private company, or international center. Ideally, the choice of the MSE should take into account its representativeness with regard to edaphic and climatic conditions of the TPE, based on historical weather data and soil features (Gomide et al. 2011). The MSE should mimic as far as possible the TPE for water distribution and profiles, potential evapotranspiration rates, and physical and chemical soil properties. Any deviation may result in significant GEI between TPE and MSE, and genetic gains achieved in the MSE may not be expressed in the TPE.

Geographic information system (GIS) tools and models can help considerably in describing the relationships between TPE and MSE. Homology maps have been generated that show the degree of similarity between any set of stations or a continuous surface through spatial interpolation of climate data (Hyman et al. 2013). Notwithstanding, the challenge is to try finding the most appropriate formal models based on key traits that drive the phenotypic responses to each environmental condition (Cooper et al. 2002). Some pitfalls that limit the aforementioned aim are related to the disruptive effect of sampling variation and the lack of representativeness of the MET used as homologues of TPE, among others (Basford and Cooper 1998).

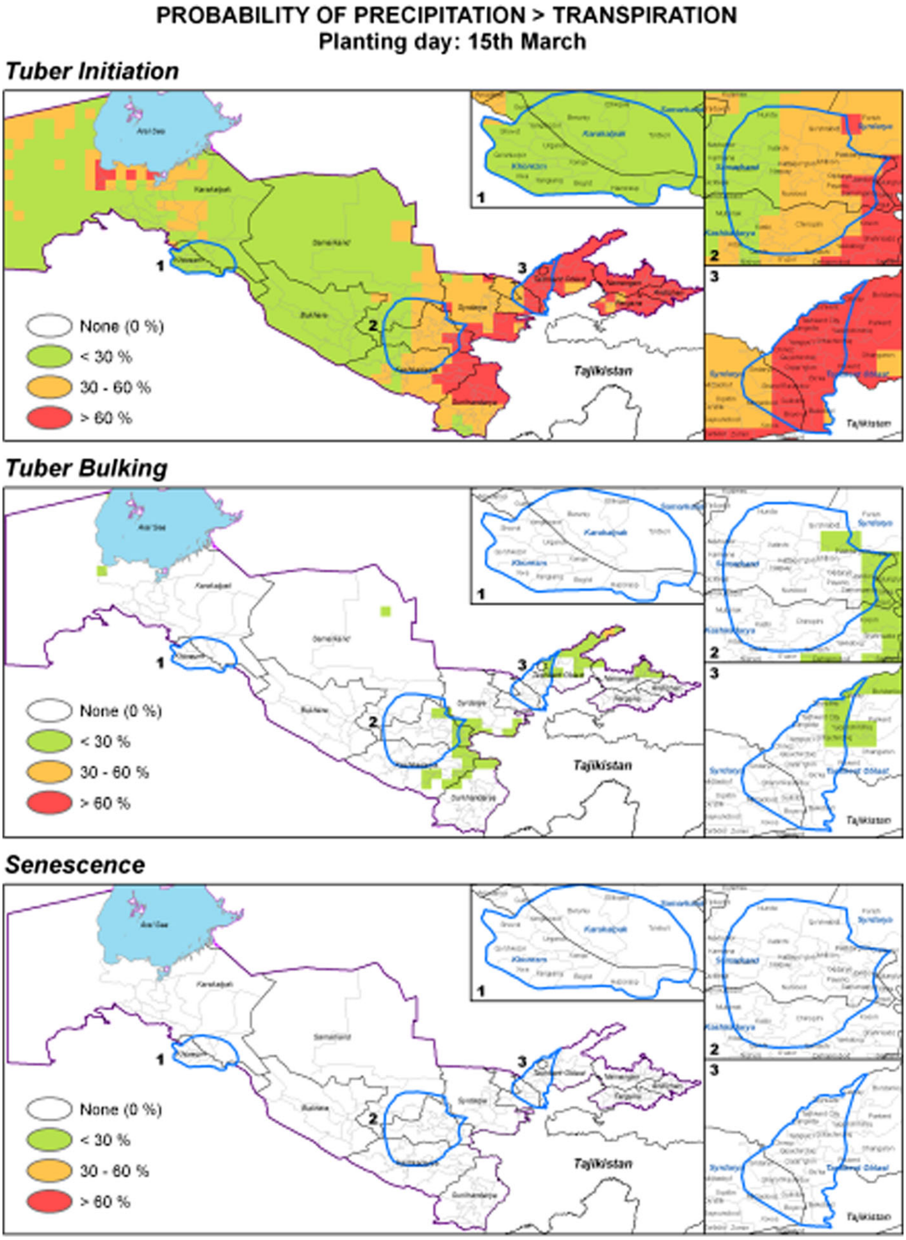

Fig. 2 Main potato cropping area in the lowlands of Uzbekistan (patches defined by *blue lines*) and probability of drought (precipitation/crop transpiration) at three crop developmental stages: tuber initiation, tuber bulking, and senescence during the March–June cropping season

Characterization of Managed Stress Environments

Actual environmental climatic characterization is essential to quantify evapotranspiration and crop water requirements, in order to control the different water regime treatments and estimate the corresponding crop stress levels. The main atmospheric parameters to be registered by means of an automatic or a standard weather station are air temperature, global solar radiation, air relative humidity, wind speed, air water vapor pressure deficit, and precipitation. Soil characterization is equally important as differences in soil depth and water holding capacity can affect the imposition of stress. Soil depth affects rooting volume and consequently nutrient and water availability. Compaction, aluminum toxicity, and soil acidity also reduce root depth. Soil texture is a major determinant of water holding capacity and water release characteristics (Gomide et al. 2011). A list of the climatic and soil parameters assessed and methods used at CIP to characterize the MSE is provided in Table 2.

As far as the aim is to develop varieties with adaptation to water constraints, it is important to know more about the patterns of water supply and the type of drought faced by the MSE. Water balance models are highly valuable tools to characterize environments based on predicted water availability (e.g., aquacrop, see Quiroz et al. 2012 and http://www.fao.org/nr/water/aquacrop.html).

Reducing Noise Factors

Any crop facing drought or heat stress simultaneously experiences a number of additional stresses (e.g., micronutrient deficiency, soil compaction, salinity, and pathogens) that impair root growth, reduce water availability, affect source capacity, and finally exacerbate the effects of the studied stresses. Genetic variability among the tested germplasm for tolerance to these stresses inevitably biases an accurate evaluation of the effects of drought or heat. Soil surveys permit to describe the within-site distribution of these confounding factors (Cairns et al. 2009). In case of interaction between drought and heat stress, additional trials (e.g, trial under full irrigation in heat prone areas) may be needed to isolate the specific effect of each stress.

Table 2 Methods used at CIP to characterize soil and climate conditions in managed stress environments

MSE characterization	Methods
Climate characterization	Weather station HOBO U30, Onset, Bourne, MA, USA, for measuring air temperature, relative humidity, dew point, rainfall, soil moisture, solar radiation, wind speed, and direction, barometric pressure, and more.
	Weather station HOBO U23, Onset, Bourne, MA, USA, for temperature and relative humidity, weatherproof data loggers for use in outdoor/condensing environments
Soil characterization	Soil sample analysis: sent to outside laboratory to determine texture, pH, salinity, organic matter, and other cations and anions. Salinity also mapped with corrected EM38 measurements
	503TDR HYDROPROBE, 2830 Howe Road Martinez, CA, USA for measuring soil moisture
	PR2 Soil Moisture Profile Probe, Delta-T Devices Ltd, Cambridge, UK, for measuring soil moisture in different water profiles in all soil types at 4 depths down to 40 cm
	WATERMARK 200SS, Irrometer, Riverside, CA, USA, for measuring soil water tension in centibars (cb) or kilopascals (kPa); (0–200 Centibar range)

Experimental conditions of the MSE should also ensure minimal environmental heterogeneity to reduce unwanted experimental error. Spatial variability affects the detection of treatment differences by inflating the estimated experimental error variance and limiting the value of data acquired (Masuka et al. 2012). Moreover, the effects of soil heterogeneity become more apparent under drought (Gomide et al. 2011). Direct assessment of soil variability within a field site can be made through destructive soil sampling positioned by a Global Positioning System (Campos et al. 2011). For purposes of water balance, physical and chemical properties of soil samples should be analyzed through the soil profile (or layers) (at a minimum for texture, pH, bulk density, macro and micro-nutrients). High-throughput techniques are also available for mapping variability within field sites based on penetrometers (Cairns et al. 2011), soil electrical conductivity and electromagnetic induction sensors (Cairns et al. 2012; Brunner et al. 2004; Jhonston et al. 1997), spectral reflectance (Dang et al. 2011), and thermal imagery of plant canopies (Campos et al. 2011). At CIP, assessment of soil variability through reflectance measurements allowed discarding fields contaminated by nematodes and electromagnetic induction for mapping salinity.

Stress Monitoring

The ability to manage the timing, frequency, and intensity of the stress is a key factor in mimicking the environmental conditions prevailing in the TPE and ensuring accurate drought phenotyping (Tuberosa 2012).

An increasing number of breeding programs are conducting drought trials in dry locations or “out-of-season”, i.e., in seasons that are not the cropping season of the crop and are characterized by very low rainfall. Under such conditions, the dynamics of drought episodes can be tightly controlled through the frequency and volume of irrigation treatments. The dry season should be sufficiently long to cover the whole growth cycle. Furthermore, conditions during the dry season generally do not reflect the environmental conditions (radiation, temperature, vapor pressure deficit) plants would experience during a natural drought in the main (wet) season (Jagadish et al. 2011). These differences lead to genotype-by-season interactions and limit the extrapolation of results. Late or delayed planting can represent an interesting alternative option, particularly in the case of heat stress.

Static or moveable rainout shelters constitute another alternative of investigating the adaptive response of crops to a desired level of drought stress, avoiding the bias of unpredictable rainfall patterns (Tuberosa 2012). Major inconveniences are, in addition to the high construction and operating costs, i) the usually rather limited area protected by a shelter which, in turn, limits the number and size of experimental plots that can be tested and ii) shelters do not consider the water dynamic under the soil.

Phenotyping potted plants in greenhouses or growth chambers with robotized systems, and advanced image analysis software permits to assess traits in a quicker and more reproducible manner limiting undesirable environmental influences on phenotype expression (Furbank and Tester 2011; Fiorani and Schurr 2013). It represents an interesting option for the analysis of drought and heat tolerance underlying mechanisms. However, controlled conditions tend to be very different to those prevailing in the TPE and may limit the application of results in germplasm development. In particular, irrigation in pots creates a situation that is very distinct from that occurring under field conditions

(Passioura 2005), potted plants being exposed to earlier and stronger stress (Wahbi and Sinclair 2005). Additional factors to be also considered are the more uniform pore distribution in potting mixtures which can lead to hypoxia and the temperature of the substrate that can be different from field soil temperature (Passioura 2005).

At CIP, abiotic stress tolerance evaluations are actually made in field conditions with late planting, in static and moveable rainout shelters, and in growth chambers, according to the objective of the evaluation.

To apply a similar drought stress (in terms of timing, frequency, and intensity) in the MSE as experienced in the TPE, irrigation should be withheld at the correct phenological stage. As drought stress is imposed at the same time across all genotypes, genotypes with different phenologies are expected to face different stress durations what biases the interpretation of the influence of drought-adaptive traits on yield (Tuberosa 2012). To overcome this difficulty, genotypes can be grouped into subsets of similar maturity to ensure phenological synchronization across genotypes at the crucial stage when drought stress is imposed. Another option is to use the information on phenology as a covariate adjustment. Finally, irrigation methods must be carefully chosen to ensure optimum control of the irrigation water (Gomide et al. 2011). Drip irrigation is utilized at CIP to allow plot level control of irrigation.

An accurate management of irrigation and sound interpretation of drought response require an adequate characterization and monitoring of soil and plant water status. Jones (2007) highlighted that over half of the published papers focusing on the effects of drought on gene expression or transgenes did not include measurement of plant or soil water status. Soil or plant water status can be monitored by measuring water potential (Blum 2009) or relative water content (Riga and Vartanian 1999). Methods for measuring the amount of water stored in the soil include the gravimetric method, the polymer-based tensiometer (van der Ploeg et al. 2008), the neutron probe (Hignett and Evett 2008), the capacity probe (Nagy et al. 2008), the time-domain reflectometry (Noborio 2001), the single and multi-sensor capacitance probe systems (Fares and Polyakov 2006), and the two dimensional geo-electrical tomography (Werban et al. 2008).

Efficiency of breeding is largely due to accurate phenotyping of large numbers of plots, made possible by more sophisticated and high-throughput experimental machinery (e.g., plot combines able to measure yield directly in the field), as well as the automation of tedious manual operations. The labeling of a large number of plots and samples, data collection, and storage are now facilitated by the use of electronics (e.g., bar-coding) and dedicated software (e.g., spreadsheets, databases, etc.). The effectiveness of field experiments and the management and interpretation of phenotypic data can be enhanced through the utilization of the most appropriate experimental designs (Federer and Crossa 2011) to allow for better control of within-replicate variability and reduce or remove spatial trends.

Traits Measurement

General Requirements

After having used yield under drought as an exclusive breeding objective, most breeders progressively replaced this empirical approach by indirect selection (Jackson et al. 1996), based on the selection for “secondary traits” or plant characteristics that provide additional information about how the plant performs under a given environment (Lafitte et al. 2003). To be useful in breeding programs, a secondary trait should ideally be (Edmeades et al. 1997) (i) genetically associated with yield under drought; (ii) genetically variable; (iii) highly heritable; (iv) easy, inexpensive, and fast to observe or measure; (v) non-destructive; (vi) stable over the measurement period; and (vii) not associated with yield loss under unstressed conditions. The heritability of indirect traits itself varies according to the genetic make-up of the materials under investigation, the conditions under which the materials are investigated and the accuracy and precision of the phenotypic data. The accuracy of secondary traits measurement is closely related to precision or repeatability, the degree to which further measurements show the same or similar results (Tuberosa 2012).

Most of the traits currently mentioned in the literature associated with drought and heat adaptation in potato are shown in Table 3, classified according to their relationship to drought escape, growth and biomass, partitioning, water status, and photoprotection.

A Need of More Integrative Measurements

Most traits mentioned in Table 3 are assessed through “instantaneous methods” which depend on environmental conditions during measurement, what strongly limits the number of individuals assessed. Most traits are also assessed on individual plants or even on particular organs of individual plants what poses a problem of representativeness of the sampling. In addition, these methods are cumbersome. There is consequently a need of traits assessment methods that are more integrative, both in time and space (Jarvis 1995). Some promising approaches are presented below.

Remote Sensing

Remote sensing is defined as the set of techniques to collect information about an object without having physical contact with it. From the analysis of physical parameters such as the reflectance of radiant energy that interacts with plant tissues in plants, it is possible to get information from biological variables such as biomass, nutritional deficiencies of nitrogen in the leaves, water stress, the presence of pests and diseases, among others. Because green leaves reflect a small portion of the incident radiation in the red and a high proportion in the infrared, vegetation indices can be used as tools to estimate the condition of the crop or the presence of different types of stress in plants (Peñuelas et al. 1997; Suárez et al. 2009) and even anticipate their presence before symptoms are visible, due to the increased spectral sensitivity of the sensors in comparison with our view. In an experiment conducted in CIP Lima for example, the presence of "yellowing veins" virus (PYVV) on potato plants inoculated with virus was detected 14 days before symptoms were detected by a trained eye (Chavez et al. 2009).

To facilitate remote-sensing measurements, CIP is developing the use of unmanned aerial vehicles (UAV) with eight rotors transporting small and light cameras and radiometers. The processing of the acquired images includes the following steps: log file (superimpose and align images acquired with cameras adapted with interference filters centered in the near infrared and red, respectively, to obtain a multispectral image), geometric correction, mosaicking (or image stitching), and georeferencing (Fig. 3).

Table 3 Main secondary traits that can be used to improve drought tolerance in potato, associated characteristics, measurement methods, references, ease of use, and main target environment of application

Secondary trait	Associated characteristics	Measurement methods	References	Heritability	Ease of use	Target environment	Comments
Drought tolerance							
Traits related to drought escape							
Earliness	Drought escape	Scoring	Rana et al. (2011)	High	+++	Temperate, lowland subtropics	Empirically used by breeders, possible negative association with potential yield
Traits related to growth and biomass							
Ground cover decrease	Decrease of evaporation, increase of radiation use	Scoring, reflectance, plant canopy analyzer, digital commercial cameras	Bouman et al. (1992), Boyd et al. (2002), Shah et al. (2004)	Moderate	+++	High evaporative demand and low radiation	
Aboveground biomass/leaf area index	Carbon assimilation and allocation	Allometric relationships (height, volume, stem diameters, number of stems and leaves), remote sensing	Deblonde and Ledent (2001), Ray et al. (2006), Schafleitner et al. (2007), Islam and Bala (2008), Herrmann et al. (2011), Papadavid et al. (2011)	Low	++	All	
Leaf area	First morphological effect of drought	Leaf area meter	Gordon et al. (1997), Fleisher et al. (2008)	High	+	All	Associated with greater vein density?
Traits related to partitioning to tubers							
Tuber volume	Sink strength	Scan	Dannoura et al. (2008)	Moderate	+		
Traits relating to water status							

Table 3 (continued)

Secondary trait	Associated characteristics	Measurement methods	References	Heritability	Ease of use	Target environment	Comments
Root depth and mass	Water uptake, (root mass generally associated with high leaf mass, low number of root branches and high leaf to stem ratio)	Direct observation methods	Steckel and Gray (1979), Rossouw and Waghmarae (1995), Lahlou and Ledent (2005), Iwama (2008), Deguchi et al. (2010)	Low	+		Associated to drought recovery
Root pulling resistance	Water uptake	Dynamometry	Ekanayake and Midmore (1989)	Moderate	++	All	Cumbersome
Gas exchange	Stomatal conductance, transpiration and CO_2 assimilation	Porometry, infra-red gas analyzers, (indirect through canopy temperature depression and carbon isotope discrimination)	Vos and Oyarzun (1987), Jefferies (1992a, b), Vacher (1998), Liu et al. (2006a, 2006b, 2009)	Moderate	+		Instantaneous estimation through gas exchange measurements is slow and depends on environmental conditions during measurement
ABA	Stomata aperture	ELISA test	Liu et al. (2006b)	Low	+++		Difficult under field conditions
Canopy temperature	Transpiration	Infra-red thermometry	Levy et al. (2013), Prashar et al. (2013)	Moderate	+++	Hot conditions	Accurate measurement needs absence of clouds and wind
Osmotic adjustment	Minimization water loss	Measurement of RWC and water potential, osmolyte accumulation	Xu et al. (2011), Yactayo et al. (2013)	Moderate	+	Moderate drought	Difficult under field conditions and poorly investigated

Table 3 (continued)

Secondary trait	Associated characteristics	Measurement methods	References	Heritability	Ease of use	Target environment	Comments
		Analysis of osmolytes	Proline (Schafleitner et al. 2007), sucrose (Bethke et al. 2009; Eldredge et al. 1996)	Moderate	+	Moderate drought	
Senescence	Stay-green, partitioning	SPAD	Ramírez et al. (2014)	Moderate	++	–	Some attributes of chlorophyll concentration are closely related with final yield under water restriction conditions
Traits relating to photo protection and tolerance to heat							
Chlorophyll fluorescence	Activity of thermal energy dissipation in photosystem II	Fluorimetry	Mauromicale et al. (2006)	High	++	Severe drought	
Antioxidants (superoxide dismutase, ascorbate peroxidise)		Biochemical analysis		Moderate	++	–	Poorly investigated

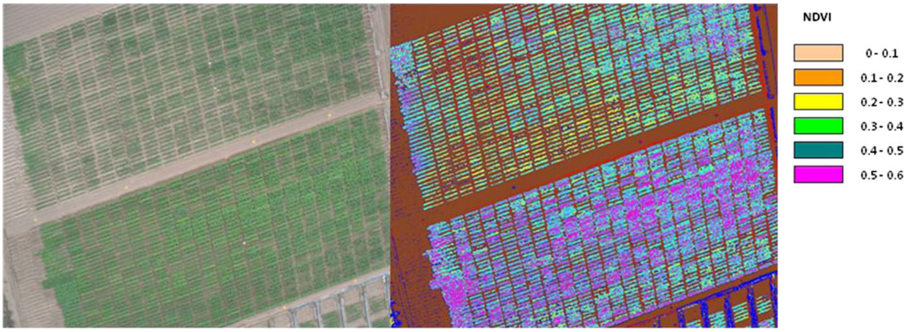

Fig. 3 Optical (*left*) and spectral *(right)* images of a potato experimental field taken from an unmanned aerial vehicle

Carbon Isotope Discrimination

Carbon isotope discrimination (Δ) in plant tissues, calculated from the ratio of the two stable carbon isotopes ^{12}C and ^{13}C, negatively correlates with transpiration efficiency in C_3 species (Johnson et al. 1990). This allows an integrated measure of this trait during the entire period in which the sample tissue was growing. In cereals, an association was found between carbon isotope discrimination and yield (Monneveux et al. 2005). The potential utilization for estimating transpiration efficiency or drought tolerance has been poorly explored in root and tuber crops. Jefferies and MacKerron (1997) reported a positive correlation between Δ and stomatal conductance among potato clones while Deblonde et al. (1999) found an association between Δ and drought tolerance (tuber yield under water limitation relative to tuber yield under irrigated conditions). Recently, Δ has been proposed in potato as an indicator of photosynthetic capacity and yield potential (Ramírez, unpublished).

Fluorescence

In addition to the reflected energy, a small fraction of the energy absorbed by the plants is emitted as chlorophyll fluorescence. The particularity of the fluorescence of plants is that their dynamics are related to changes in the photochemical conversion. The importance of chlorophyll fluorescence for the study of photosynthesis is well documented and is widely used in laboratory (Krause and Weis 1991; Schreiber et al. 1994) proving to be a sensitive indicator of a stress response to water scarcity (Flexas et al. 1999). Today, large commercial instrumentation measures the performance of fluorescence at leaf-level in the laboratory, but its assessment in open field conditions and at the canopy level is still a challenge. Works such as those by Zarco-Tejada et al. (2009) and Zarco-Tejada et al. (2012) suggest the possibility of remotely obtaining chlorophyll fluorescence images using the discrimination method of Fraunhofer lines in the absorption bands of atmospheric oxygen (Moya et al. 1998), a promising technique since it would provide information at different levels of integration, from a leaf to the whole canopy (Moya and Cerovic 2004).

Conclusion

Drought is expected to increasingly affect potato production, with potential consequences on food security. Genomics approaches to improve drought tolerance will bring new opportunities over the next few years, but their impact in farmer's fields will mainly depend on the actual progress in our understanding of the physiology and genetic basis of drought-adaptive traits. The effective implementation in breeding programs of accurate and cost-effective phenotyping methods will be consequently essential to ensure research impact.

Efforts should focus on a more precise definition of TPE, a better control of the stress monitoring in the MSE and a more accurate assessment of drought-tolerance-related traits. GIS system tools, remote sensing information, growth crop modeling, new equipments for the measurement of soil and plant water content, and more integrative drought-tolerance-related traits assessment methods can contribute largely in these efforts. Success will also depend on a closer cooperation among partners. Collaborative efforts could include development of free-access long-term climatic databases, multi-local and multi-institutional trials including common sets of cultivars, establishment of a well-documented database of potato MSE and field data, web-sharing of experiences, and organization of training courses. The development of networks among different partners and establishment of shared phenotyping platforms will allow quicker evaluation of germplasm in diversified environments, broader dissemination of germplasm products, and larger impact of breeding efforts.

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