



Review

Drought tolerance in potato (*S. tuberosum* L.) Can we learn from drought tolerance research in cereals?

Philippe Monneveux^{a,*}, David A. Ramírez^a, María-Teresa Pino^b^a International Potato Center, Lima 12, Peru^b Fisiología & Genética Vegetal, Instituto Nacional de Investigaciones Agropecuarias (INIA), Santa Rosa 11610, Chile

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ABSTRACT

Drought tolerance is a complex trait of increasing importance in potato. Our knowledge is summarized concerning drought tolerance and water use efficiency in this crop. We describe the effects of water restriction on physiological characteristics, examine the main traits involved, report the attempts to improve drought tolerance through *in vitro* screening and marker assisted selection, list the main genes involved and analyze the potential interest of native and wild potatoes to improve drought tolerance. Drought tolerance has received more attention in cereals than in potato. The review compares these crops for indirect selection methods available for assessment of drought tolerance related traits, use of genetic resources, progress in genomics, application of water saving techniques and availability of models to anticipate the effects of climate change on yield. It is concluded that drought tolerance improvement in potato could greatly benefit from the transfer of research achievements in cereals. Several promising research directions are presented, such as the use of fluorescence, reflectance, color and thermal imaging and stable isotope techniques to assess drought tolerance related traits, the application of the partial root-zone drying technique to improve efficiency of water supply and the exploitation of stressful memory to enhance hardiness.

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* Corresponding author. Tel.: +51 1 349 6017x3133; fax: +51 1 317 5354.

E-mail addresses: p.monneveux@cgiar.org (P. Monneveux), d.ramirez@cgiar.org (D.A. Ramírez), mtpino@inia.cl (M.-T. Pino).

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1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth most important food crop in the world. It is cultivated on 19 million ha and its annual production is around 325 million tons [1]. Developing countries produce more than half of the total world potato production [2]. Potato is often cultivated by resource-poor farmers in remote, often marginal areas with limited access to farm inputs [3]. It accounts for large quantities of dietary daily energy intake compared to other crops [4] and contributes to hunger reduction and improved nutrition [5]. Potato is also progressively fetching higher market value thus contributing to poverty reduction [4]. An increasing part of the production is transformed by industry (French fries, chips) particularly in Asia [6].

Potato regularly suffers transient water deficit in most of the rainfed growing regions due to erratic rainfall or inadequate supplemental irrigation techniques [5]. This is the case in temperate northern China which accounts for 45% of the Chinese production and around 10% of the world production [6] and has experienced severe and prolonged dry periods since the late 1990s [7]. Sub-tropical lowlands potato is normally produced in the short days of the winter season between harvesting and planting of rice. Grown with residual moisture following the monsoon it would often need supplementary irrigation, a resource unavailable at many locations [8].

The impacts of water restriction on potato production will likely increase over the next decades, due to climate change and the extension of potato cultivation in drought prone areas. The potato growing area considerably expanded in tropical and sub-tropical environments [1] as a winter crop exposed to drought events. Climate change is likely to increase the frequency of drought events in many regions, affecting drought-sensitive crops [9]. Severity and duration of water scarcity periods may vary more from year to year making it difficult for plants to adapt [10]. 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 [11]. Enhancement of transient drought tolerance in potato through conventional breeding and biotechnology should therefore receive high priority. For this purpose, it may be advisable to learn from the experience gained in crops such as cereals for which drought tolerance improvement has received more attention. Thus, the objectives of the present review are to (i) examine our present knowledge of drought tolerance in potato, (ii) compare the research advances made in this crop to those in cereals and (iii) propose novel research oriented to improve drought tolerance in potato.

2. Drought tolerance in potato

2.1. Potato, an efficient water user but drought susceptible crop

Potato, under rainfed conditions, yields more food per unit of water than other major crops [2]. For every m³ of water applied to the crop, potato produces 5600 kcal of dietary energy, compared

to 3860 in maize, 2300 in wheat and 2000 in rice [12]. Because of its high nutritional productivity, potato is gaining support among policymakers and land use planners as a substitute for less water efficient cereal crops. Water use efficiency (WUE) in potato is in fact widely variable, depending on environmental conditions and temporal and spatial scales of measurement (Table 1). A substantial increase of the efficiency of applied water has been achieved by implementing different irrigation methods, like drip irrigation or the partial root-zone drying technique which consists of an alternated irrigation of the root-zone by watering of one furrow and keeping the adjacent one dry until the next watering cycle (Fig. 1). Partial root-zone drying can allow a 29–50% of water saving with a similar tuber yield and a concomitant water use efficiency increase [14,16,17,22]. Potato is however a drought-sensitive crop [24]. Its drought vulnerability has been mainly attributed to its shallow root system and low capacity of recuperation after a period of water stress [25].

2.2. Drought effects on the potato crop

The magnitude of drought effects on potato production depends on the phenological timing, duration and severity of the stress [26]. Emergence and tuberization (sink strength) are two critical periods where water stress most affects final tuber yield [27]. Drought decreases plant growth [28], shortens the growth cycle [29] and reduces the number [30] and size [31] of tubers. Short periods of drought during tuber bulking lead to dumbbell-shaped, knobby, or

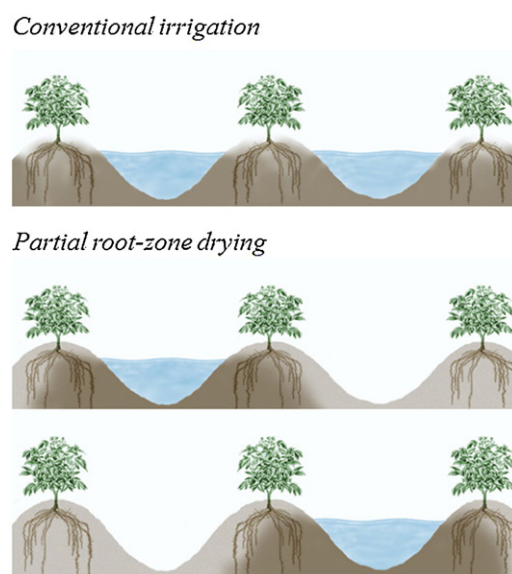


Fig. 1. Description of the partial root-zone drying (PRD) irrigation technique (compared to the conventional irrigation technique) which consists in an alternated irrigation of the root-zone by watering of one furrow and keeping dry the adjacent one until the next watering cycle.

Table 1
Range of values and kinds of water use efficiency (WUE) assessed at different scales in potato.

Scale	WUE type	Calculation	Range	Authors	Country
Leaves	Intrinsic WUE	A/g_s (mmol mol^{-1})	9.0–38.4	[13]	Denmark
	Transpiration efficiency	A/E ($\mu\text{mol mol}^{-1}$)	2.2–11.4	[14]	Denmark
				0.9–1.0	[15]
Individual plants	Transpiration efficiency	Y/T (kg m^{-3})	4.3–5.1	Yactayo (<i>pers. comm.</i>)	Peru
	Transpiration efficiency	Y/W (kg m^{-3})	5.4–8.0	[16]	UK
Crop	Crop or irrigation WUE	Y/W (kg m^{-3})	0.6–2.5	[17]	China
			2.2–2.6	[18]	Peru
	Crop or irrigation WUE	Y/ET (kg m^{-3})	1.9–5.3	[19]	Iran USA
			4.9–9.3 5.0–9.8	[20] [13,14]	Denmark
			6.0–14.0	[21]	Tunisia
			7.7–15.6	Yactayo (<i>pers. comm.</i>)	Peru
			19.6–37.8	[22]	Denmark
Crop or irrigation WUE	SB/T (kg m^{-3})	3.6–5.5	[23]	USA	

A = net photosynthesis, g_s = stomatal conductance, E = transpiration rate, T = individual transpiration, W = amount of water applied, ET = evapotranspiration or plant water used, Y = yield. SB = shoot biomass.

pointed-end tubers [32]. Water limitation reduces leaf growth [33], leaf area index [22], ground coverage [34], rate of photosynthesis per unit of leaf area ($\mu\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) [35] and harvest index [36].

Decline in photosynthetic rate is fast and substantial, even at relatively high water potentials (-0.3 to -0.5 MPa [37]). By reducing transpiration, drought leads to an increase in plant temperature that in turn is detrimental to tuber formation [38]. Drought also decreases nitrate reductase activity and consequently affects nitrogen uptake [31]. Conversely, previous exposure to drought improves the response of potato plants to drought stress [39]. Pre-stressed plants exhibit higher relative water content at zero turgor potential than unstressed plants [40].

2.3. Measurement of drought tolerance related traits

The variation of putative drought tolerance related traits and their relationship with tuber yield under drought have been studied using diverse methods with the aim of better understanding the mechanisms underlying drought tolerance.

2.3.1. Gas exchange

Stomatal conductance is driven by abscisic acid (ABA) regulation under mild water stress conditions and is more sensible to water depletion than the rate of photosynthesis, relative water content, and leaf water potential [41]. Drought reduces stomatal conductance in potato when leaf water potential values fall below -0.6 MPa [42]. A range of photosynthetic rate values between 1 and $3.6 \mu\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ has been used to describe water stress condition in potted potato grown in greenhouses under natural light [43]. Seasonal integrated rate of photosynthesis and maximum net photosynthesis (estimated from light-curves response assessed before flowering) have a positive relationship with tuber yield in greenhouse [44] and field conditions [45]. In well-tuberized potatoes the response of photosynthetic rate to drought in potato depends on leaf sugar content [46], the strength of the demand of carbohydrates by the sink [46], mesophyll conductance [47], relative water content and light intensity [46].

2.3.2. Fluorescence

Knowing the kinetics of this variable allows the assessment of the state of photosynthetic apparatus *in vivo* and the dissipation of excess of light energy (by xanthophyll cycle, photorespiration or water–water cycle [48]). High dehydration resistance of photosystem II has been noted in potato, the maximum quantum yield being affected only at relative water content below 40% [49]. Variation in chlorophyll fluorescence among genotypes has also been reported [50]. However, in most studies carried out under water

stress, fluorescence parameters did not discriminate effectively between genotypes and consequently did not correlate with yield [31].

2.3.3. Color imaging

Images of individual plants taken in controlled environments with digital color cameras have been used to estimate biomass, quantify relative growth rates and quantify chlorophyll concentration and degree of senescence [51]. Reflectance spectral indices measure a general stress level of the plant canopy discriminating plant from background soil reflectance, which is important in early and late stages of growth when the plants do not entirely cover the ground [52]. Multispectral imaging (bands 550, 710 and 810 nm) has been successfully used in potato for determination of chlorophyll in leaves (linear relationship with $r^2 > 0.95$) [53].

2.3.4. Carbon isotope discrimination

Carbon isotope discrimination, calculated from the ratio of the two stable carbon isotopes ^{12}C and ^{13}C , negatively correlates with transpiration efficiency in C_3 species [54]. 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 [55]. In root and tuber crops, the variation of carbon isotope discrimination and its potential utilization for estimating transpiration efficiency or drought tolerance has been poorly explored. There is a positive correlation between carbon isotope discrimination and stomatal conductance among potato clones [56]. Carbon isotope discrimination also correlates to drought tolerance (defined as dry weight tuber yield under water limitation relative to dry weight tuber yield under irrigated conditions) suggesting the use of this trait for indirect selection for yield under drought [36].

2.3.5. Plant water status

The degree of osmotic adjustment in response to drought seems to be limited in potato and thus might not contribute efficiently to the maintenance of leaf expansion with increasing soil moisture deficit [57]. Potato varieties showing higher tuber yield under water restriction had a higher osmotic adjustment [45]. Accumulation of potential osmolytes has been poorly investigated in potato. Proline levels increase earlier in drought susceptible varieties than in more tolerant ones [58]. It has been suggested that proline could protect plants from dehydration by stabilizing proteins and membranes, and are a source of carbon, nitrogen and energy during cell rehydration [59].

2.3.6. Root traits

Improvement in root traits like root depth and root length density is important for developing drought tolerant genotypes [60]. Tolerant cultivars have deeper root systems [61] and higher root dry weight [62]. Measurement of root traits in field-grown plants is however laborious and time-consuming. Root pulling resistance has been proposed as a practical measure to quantify root development. This trait varies widely and its use was suggested as a quick way to select for drought avoidance [63]. A significant relationship between root pulling resistance and tuber yield was observed under moderate drought [63]. Root mass correlates well with leaf mass and tuber yield [64]. A selection for root mass in the low soil layer was developed, leading to the Konyu cultivars that had less reduction of leaf conductance and rate of photosynthesis, leaf area and tuber yield under drought stress than commercial cultivars [64]. High root mass was associated with low number of root branches and high leaf to stem ratio. They are characteristics of genotypes with high yield stability across drought prone environments [65]. Root volume and root length also correlated with drought recovery [66].

2.3.7. Infrared thermometry

Canopy temperature relative to air temperature is an indication of transpiration driven cooling of the leaves. The relationships between canopy and air temperatures and transpiration are not simple, involving atmospheric, soil and plant conditions. Relatively lower canopy temperature in a given genotype may indicate its relatively better capacity for taking up soil moisture and maintaining a relatively better plant water status [67]. Canopy temperature increase caused by water deficit varies among cultivars [50]. In potato, genotypes with warmer canopies under irrigated conditions were less susceptible to drought than genotypes with cooler canopies [68]. No information is available concerning variation of canopy temperature under drought conditions and its association with yield.

2.3.8. Canopy reflectance

Reflectance indices have been used in several crops, mostly to estimate biomass [69] and changes in leaf water content [70]. Indices calculated from the visible and near-infrared light reflected by vegetation have proved to be suitable to accurately assess some drought response traits. Relative vegetation index (reflectance at 800 nm/reflectance at 650 nm) and normalized difference vegetation index (NDVI) $([\text{reflectance at } 800 \text{ nm} - \text{reflectance at } 650 \text{ nm}] / [\text{reflectance at } 800 \text{ nm} + \text{reflectance at } 650 \text{ nm}])$ strongly correlate with leaf area index and biomass in potato [31]. Specifically designed NDVI spectrometers are commercially available. An advantage of these instruments is the ease of use and their wide application in the assessment of plant health in response to stress conditions [71]. As in early stages of crop growth, normalized difference vegetation index can be biased by soil reflectance, other indices such as the weighted difference vegetation index $(\text{NIR} - g \times R)$, where NIR and R are reflectance in the near infrared and red respectively, and g is the soil line slope) which corrects for soil background and differences in soil moisture content have been proposed [72].

2.4. In vitro screening

Evaluating the relative field performance of cultivars in sites under dry conditions highly depends on weather variability and is very cumbersome. Screening under *in vitro* conditions is consequently an attractive option, particularly in potato, a crop highly amenable to tissue culture [73]. It represents a highly controlled and homogeneous procedure to quickly induce osmotic stress [74]. The general effect of water stress on *in vitro* plant growth is similar

to the effects observed under field conditions (reduction of stem and foliage weight, root number and root-dry weight) [75]. *In vitro* osmotic stress, induced by polyethylene glycol, has been used to evaluate root and shoot traits at the juvenile stage and for recovery potential [76] even if no commercial variety has been bred until now using this technique. Polyethylene glycol is a non-ionic polymer produced in a range of molecular weights (ranging from 1500 to 8000), and its uptake rate into shoots and roots depend on the species, concentration and time exposure. Polyethylene glycol of large molecular weight is taken up slower by plants plant, thus representing a better osmoticum for use in hydroponics root medium [77,78]. Mannitol solution is also used for inducing drought stress in tissue culture. It is however taken up into plant tissues in maize [79], wheat, rape and potato [80], causing artifact effects.

2.5. Marker assisted selection

Selection for drought tolerance through visible phenotypic drought tolerance traits is time consuming. The use of molecular markers to identify and locate genomic regions that control drought tolerance traits may accelerate selection. The first potato genetic maps were constructed by following the segregation of restriction fragment length polymorphism markers in different genetic backgrounds [81,82]. As the large genome size and co-existence of several homoeologous genomes in cultivated wheats present a huge challenge for the genetic dissection of phenotype–genotype relationships, the efficiency of association mapping is much higher in diploid than in polyploid species. As a consequence, most of the quantitative trait loci (QTL) mapping studies in potato have been performed on diploid populations. Target traits included leaf senescence [83], tuberization [84] and tuber shape, eye depth and flesh color [85]. Recently, quantitative trait loci have also been identified in tetraploid populations for traits such as plant height, maturity, crop emergence, tuber size, and tuber quality traits [86,87]. Under *in vitro* osmotic stress (induced by polyethylene glycol), three quantitative trait loci involved in the control of root to shoot ratio were identified which explained 41.1% of the variance for this trait [88].

2.6. Gene expression

Changes in the gene expression profiles are induced in response to drought stress and several genes are regulated up or down with osmotic stress. A first category includes genes directly involved in protection against environmental stresses, encoding proteins with a role in biosynthesis of compatible osmolytes, chaperones, late embryogenesis abundant proteins, proteinases and enzymes involved in detoxification (Table 2).

A second category refers to genes which regulate other genes involved in drought response, including the synthesis of protein kinases and transcription factors such as dehydration responsive element binding, Basic Leucine Zipper Domain, or myeloblastosis oncogene [102,103]. Several studies also reported genes associated to compatible solutes (sugars, proline, and glycine-betaine) biosynthesis. Andean potatoes adapted to drought stress show higher expression of genes inducing antioxidants, flavonoid genes, heat shock protein and late embryogenesis abundant proteins [39,58]. Some studies suggested that $\Delta 1$ -pyrroline-5-carboxylate synthetase over-expression was associated with better root development [59,104]. Stress-responsive dehydrins have been associated to drought stress. Dehydrins act as chaperones stabilizing vesicles, proteins, and membrane structures in stressed plants [105,106]. Most dehydrins are induced by drought or abscisic acid, like the barley dehydrins DHN1, DHN2, DHN3, DHN4, DHN6 and DHN9 [107]. Early dehydrin like gene expression has been associated to drought tolerance in wheat [108] and cold-regulated gene expression in potato [109].

Table 2
Genes for drought tolerance tested in transgenic potato plants.

Gene	Gene function	Abiotic stress tolerance	Reference
(a) Genes involved in Regulation with role in drought tolerance			
CaPF1	ERF/AP2-type pepper transcription factor gene	Oxidative stress and others	[89]
NDPK1	Nucleoside diphosphate kinase 2	Multiple stress resistance	[90]
StMYB1R-1	MYB-Like Domain Transcription Factor, activation of drought-related genes	Drought resistance via reduced water loss	[91]
DREB1B	Transcription factor	Enhanced drought and freezing tolerance	[92]
(b) Genes involved in metabolites and osmolytes biosynthesis in drought stress			
SST/FFT	Fructan accumulation	Reduced proline accumulation at low water status	[93]
TPS1	Trehalose synthesis	Delayed wilting under drought	[94]
TaSTRG	Fructan accumulation	Increased proline accumulation under drought stress	[93]
codA	Synthesize GB in chloroplast	Enhanced oxidative, salt, and drought tolerance	[95]
BADH	GN synthesis	Enhanced drought and salinity tolerance	[96]
(c) Other genes participating in drought stress			
StPPI1	Proton pump interactor from <i>Solanum tuberosum</i> involved in several physiological processes	Drought and others abiotic stresses	[97]
Tomato Cu, Zn superoxide dismutases	Enhanced oxidative stress defense	Enhanced drought-osmotic tolerance	[98]
Cu/Zn SOD and APX (SWPA2 promoter)	Enhanced antioxidative mechanism of chloroplasts	Enhanced oxidative stress and heat stress tolerance	[99]
AtDHAR1	Membrane integrity, protecting chlorophyll against degradation, and allowing faster removal of H ₂ O ₂	Enhanced herbicide, drought and salt stress tolerance	[100]
AtGR1	Elevation GSH contents	Enhanced tolerance to multiple environmental stresses, including drought stress	[101]

The last group of genes includes transcription factors such as C-repeat binding factors/dehydration responsive element binding. In *Arabidopsis thaliana*, C-repeat binding factors bind to the cold/dehydration responsive regulatory motif, presents also in the promoter of many drought and cold responsive genes such as those associated with osmo-protectant biosynthesis-protein [110,111]. Thus, C-repeat binding factors over-expression has been associated to proline synthesis in rice [112] and potato [113,114]. Over-expression of the C-repeat binding factors regulon increases cold, salinity and drought tolerances in different plant species [115]. Transgenic potato plants over-expressing *Arabidopsis* C-repeat binding factors 3/dehydration responsive element binding 1A under a stress-inducible responsive to dehydration 29A promoter exhibits tolerance to drought and other abiotic stresses [116]. Recent studies confirmed the existence of the C-repeat binding factors regulon in *Solanum commersonii*, a wild potato species highly tolerant to abiotic stress. *S. commersonii* C-repeat binding factors induced genes similar to those induced by C-repeat binding factors transcription factors from *Arabidopsis* [117,118]. Over-expression of potato R1-type myeloblastosis oncogene transcription factor gene reduces water loss (Table 2) and enhances the expression of other drought regulated genes [91]. These findings, however, have not yet translated in the development of transformed clones with improved drought tolerance.

2.7. Utilization of native and wild potatoes for improving drought tolerance

The modern *S. tuberosum* L. potato varieties are highly susceptible to drought stress [119]. In contrast, landraces of Andean potato species and wild potatoes occurring in the Americas, from Colorado (United States) to Chile and Uruguay [120], are predominantly better adapted to harsh environments and regularly exposed to water-scarce conditions [58]. Genes from this germplasm should contribute to the improvement of potato for current and future needs [121]. However, information about drought tolerance of Andean native potatoes and wild potatoes is still scarce (Table 3).

The relatively limited use of native potatoes in breeding programs is largely due to undesirable effects of genes linked to the introgressed trait or gene (phenomenon generally referred to as linkage drag) and to the fact that some of the traits contributing to drought tolerance in native and wild potatoes are themselves associated with low yield potential [124]. Also, photoperiod requirements of modern varieties and native potato are different, which could explain why plants from inter-crosses and back-crosses often have undesirable agronomic characteristics such as lower yield, small tuber number, late maturity, poorer foliage and tuber appearance when grown under non suitable photoperiods [127].

3. Specificity of drought tolerance research in potato compared to cereals

3.1. What do we know about drought tolerance in potato compared to cereals?

Research and selection for enhanced drought tolerance started much earlier in cereals than in potato. The first agricultural scientists who addressed drought adaptation in wheat and maize were R. Gaus and M.T. Jenkins respectively, both working at the beginning of the 20th century, and the first dissection of drought tolerance in cereals, in terms of crop physiology, was done by J.H. Martin in 1930 [128].

Conversely, research on drought tolerance in potato only started in the 60–80's with the pioneer works of Steckel and Gray [61], Burton [129,130] and Tanner [23]. This is probably because drought was not considered as a major yield limiting factor in potato for a long time [5]. Potato was not considered as a crop of major importance in drought prone production systems [131,132]. The situation drastically changed over the last few years due to the increasing importance of drought for potato production and the recognized interest in developing potato cultivars able to perform well in drought prone areas. Our knowledge of physiological mechanisms underlying drought tolerance in potato (e.g., role of abscisic

Table 3
Drought tolerant potato landraces and wild species.

Target trait	Species	Accession	Reference
Landraces			
Tuber yield	<i>Solanum juzepczukii</i> Bukasov		[122]
Tuberization	Andigenum group of <i>S. tuberosum</i>	Sipancachi	[123]
Senescence	Stenotomum group of <i>S. tuberosum</i>	Yema de Huevo	[123]
Drought susceptibility	<i>Solanum juzepczukii</i> Bukasov	–	[124]
Combination low drought susceptibility and high irrigated yield	<i>Solanum curtilobum</i> Juz. & Bukasov	Choquepito	[124]
Combination low drought susceptibility and high irrigated yield	Stenotomum group of <i>S. tuberosum</i>	Titerite	[124]
Combination low drought susceptibility and high irrigated yield	Andigenum group of <i>S. tuberosum</i>	Puca Allqu, Venancia, Rosita, Renacimiento, Chava Negra, Calvache, Criolla	[124]
Combination low drought susceptibility and high irrigated yield	Chaucha group of <i>S. tuberosum</i>	Color Unkhuña, Muru Warkatina, Puqya, Puca Botijuela, Yana Rucunag	[124]
Wild species			
Tuber yield	<i>Solanum cardiophyllum</i>	–	[125]
Transpiration vegetative growth	<i>Solanum gandarillasii</i>	–	[126]
Tuber yield	<i>Solanum tarjense</i>	CLS 1802 Norte	[123]

acid, osmotic adjustment, or rooting patterns) is however still poor compared with cereals.

3.2. Are drought tolerance related traits assessment methods equally applicable to potato and cereals?

In cereals selection for drought tolerance has been first carried out by selecting for high-yielding lines in the field. However, direct selection for yield may select for a myriad of secondary traits that have little to do with drought-tolerance *per se*. Developing a better understanding of traits that are required for adaptation to a certain type of drought is therefore paramount. The mechanisms underlying drought tolerance are quite well elucidated in cereals, the importance of intensity and timing of stress have been highlighted [55] and the contribution of different traits to grain yield under different environments and drought scenarios well described [133]. Indirect selection for yield, based on the use of secondary traits genetically associated with grain yield under drought and highly heritable, has been initiated several decades ago [134]. Conversely, most of the selection for drought tolerance in potato has been carried out based on direct selection for yield [124]. Secondary traits have been generally analyzed on limited number of genotypes and their genetic variation and heritability poorly studied [88].

Drought tolerance related trait assessment methods actually available and used in cereals are applicable to potato. They include fluorescence, thermometry, reflectance and the use of stable isotopes. However, most of them have still been scarcely applied to potato. Fluorescence techniques have been mainly used in potato to analyze the effects of thermal stresses on photosystem II [135] but remains poorly investigated thereafter as a tool for high throughput phenotyping under drought and/or heat conditions. Canopy temperature, widely used to screen for drought tolerance in cereals [136], has been used in potato more for scheduling irrigation than for detecting genotypic differences [137]. As a consequence, information about genetic variation for this trait is scarce [50]. Despite promising results [31], the use of reflectance measurements techniques is still modest in potato, while this method is widely used in cereals and particularly in wheat [138]. Tolerance to photo-inhibition (caused by light excess and water stress) driven by xanthophylls cycle could be assessed by some reflectance indexes taking account some recent experiences in rice [139]. Carbon isotope discrimination has been poorly investigated in potato, compared to cereals. Most studies concerned a limited number of genotypes and no information is available about carbon isotope discrimination variation associated to the type of stress, sampled organs and stage of sampling while these factors considerably influence the association between carbon isotope discrimination and

yield. In cereals for example, the strongest association was found between carbon isotope discrimination of the grain at maturity and yield under post-anthesis water stress [55].

3.3. The use of genetic resources in potato and cereals

Accessing genetic diversity in breeding programs is a way to capture new drought tolerance traits. Potato breeders have in theory access to a tremendous diversity. The International Potato Center genebank conserves around 4500 accessions of cultivated species, landraces and more than 2500 accessions of wild potatoes [140]. Drought tolerance accessions identified in Andean potatoes [122–124] have been barely used in breeding programs worldwide, because of their adaptation to the short-day conditions prevalent in the low latitudes [141]. Some attempts have been made to transfer drought tolerance genes from wild to cultivated potato species via traditional breeding. However, inserting the specific genes associated with drought tolerance is challenging. Gene introgression from wild to cultivated potato highly depends on the ploidy level and the endosperm balance number and many wild species are sexually incompatible with cultivated potato [142]. As an alternative, potato breeders have used somatic fusion, embryo rescue, and bridging strategies to overcome the natural barriers from interspecific crossing between wild and cultivated species. Also, linkage drag still limits the use of wild potatoes because many exotic genes and undesirable traits, e.g., high alkaloid content or long stolons, can be transferred along with the acquisition of drought tolerance and multiple cycles of backcrosses and selection are required to remove these traits. Therefore, successful breeding schemes require time-consuming backcrosses, evaluations, and phenotypic selections to obtain an improved cultivated phenotype [143,144].

Drought tolerance is a complex quantitative trait controlled by several, as yet unknown, combinations of genes and gene families which are not easy to select simultaneously. Thus, this trait and the potential yield over the back-cross cycles and the physiological and biochemical bases of potato drought tolerance need to be studied more to find reliable selection markers. Progenies derived from the interspecific hybrids between drought tolerant and sensitive potato species can provide valuable information on the mechanisms underlying drought tolerance in cultivated potato. Interspecific crosses have been more extensively used to enhance diversity and introgress useful traits in wheat. An example among others of the successful application of the creation of synthetic wheat cultivars is provided by the crossing between durum wheat (*Triticum durum* Desf.) and the diploid ancestor *Aegilops tauschii* Coss. [145]. More than 60% of the new germplasm generated by the International Maize and Wheat Improvement Center today used

synthetic wheat as parents. Four synthetic-derived varieties have been released in the Sichuan province (China) since 2003. The variety Chuanmai 42 which out-yields a commercial check variety by 23% has been grown on more than 100 000 ha since 2006 [146].

3.4. Comparative progress of genomics in potato and cereals

Many more drought response genes have been identified in wheat, rice and maize than in potato. The majority of gene over-expression studies in response to drought stress have been reported in the mentioned cereals and significantly fewer studies have been reported in potato (Table 2). The identification of genes controlling drought responses in potato really started in 2007 with the somatostatin/fructosyltransferase genes increasing fructane accumulation under drought stress [93] and some progress has been made over the last few years. With the first results obtained by the potato genome sequencing consortium, 30% of potato sequences were completed and a total of 39,031 genes have been annotated in the doubled monoploid *Solanum phureja* clone (DM1-3516R44) genome [147]. Some microarrays transcriptional expression profiling studies have been reported for potato and genes driving potato tuber initiation and growth were identified based on Potato Oligo Chip Initiative array [148]. Several candidate genes in Andean potatoes are associated with osmotic adjustment and are involved in changes in carbohydrate metabolism, membrane modifications, strengthening of cuticle and cell rescue mechanisms [43,58].

3.5. Advances in generating drought tolerant germplasm in potato and cereals

The early-maturing wheat cultivars Bobs, Purple Straw and Federation developed by William James Farrer at the beginning of the 20th century allowed a considerable increase of yield in the drought-prone areas of Australia. Release of drought tolerant maize hybrids occurred as early 30's [149]. In potato, the first references to cultivars with enhanced tolerance are from the 70's [61]. The documented impact of drought tolerant germplasm has been reported even more recently, with the International Potato Center potato cultivar Tacna, selected under the drought conditions of Southern Peru, introduced in China in 1994, released in 2006 under the name of Jizhangshu 8 and now widely cultivated in drought-prone areas of that country [140].

A lot of information about drought tolerance in potato has been collected over the last two decades [124], but yield genetic gains obtained through selection are poorly documented. This situation dramatically contrasts with cereals. In maize for example, the yield genetic gains obtained under drought by combining the use of secondary traits and recurrent selection in populations with high diversity have been quantified and the variation of selected and non-selected traits has been described [134,150]. Some conceptual models and theoretical ideotypes for drought tolerance have been proposed in wheat [133] and maize [151] but not so far in potato.

3.6. Advances in the application of water saving techniques in potato and cereals

The recent application to irrigated potato of the partial root drying technique has proven to be an efficient mean to reduce water supply and increase water use efficiency (see above) and in some cases to even increase tuber yield [45]. In both irrigated and rain-fed potato, water use efficiency can also be improved by reducing soil evaporation through mulching and no-tillage. Significant effect of mulching on potato yield has been observed in drought prone areas [17]. In cereals, the application of water saving techniques has been considered long time ago, with the development of conservation agriculture techniques. Conservation agriculture defined as

minimal soil disturbance (no-till) and permanent soil cover (mulch) combined with rotation [152] is practiced on over 108 million ha globally under different production systems and ecologies [153]. In irrigated wheat cropping systems, additional techniques have also been proposed and implemented to increase irrigation efficiency, such as permanent raised bed planting [154]. However, potato occupies only a small proportion of conservation agriculture area, mainly in rice-potato cropping systems in South China. The benefits of the application of conservation agriculture in potato are still poorly documented and are largely focused on pest control [155].

3.7. Potato and cereals in the face of climate change

The modeling of the impact of climate change on wheat yield at the global level has been widely developed [156]. Conversely, such studies are scarce for potato [11] and most have been done at the regional level. These studies predict a strong impact of climate change on potato production, higher than in cereals. Potato production at low latitudes is expected to decrease from 18 to 32% without adaptation of planting date and varieties and from 9 to 18% with adaptation. Potato production in India is estimated to decline by 10 and 16% by 2020 and 2050, respectively, if no adaptation strategy is implemented [157].

4. Research perspectives

4.1. Crop management

A challenging aspect in the implementation of limited irrigation techniques in potato is to find the most appropriate definition of both the timing of water shortage initiation and its duration in order to promote the triggering of tolerance mechanisms (osmotic adjustment, xanthophyll cycle, antioxidant synthesis) without compromising tuber yield [45]. A better knowledge of the molecular and physiological mechanisms responsible for tuberization and drought tolerance in different genotypes and environments is needed to face this challenge. The partial root-zone drying technique is effective in potato. Notwithstanding, there are key unresolved issues. It is not clear when the alternation of the irrigation would optimize water savings and tuber yield in field conditions. In addition, it is not well established which variable or variable combinations (water soil condition, xylem-ABA concentration, root functioning performance) to use to decide when to switch the irrigation from the wet to the dry side to optimize tuber yield. Selection of cultivars with good adaptation to partial root drying should also be initiated. Partial root drying causes a mild or false water stress in crops [45]. Under this kind of controlled water supply, "opportunistic" or "risky" cultivars (*i.e.*, those able to maintain photosynthesis [158]) are likely to have better growth and tuber yield. Nonetheless, this hypothesis should be experimentally validated. In a similar vein, conservation agriculture would also benefit from clones selected for this management strategy.

4.2. Crop improvement

As mentioned above, there is a need to better know different traits respond to changes in timing, duration and intensities of water stress. The challenge is also, as in other cereals [159], to find the yield components that are critically affected by water stress and the combination of traits that enhance drought tolerance without penalizing tuber yield. Drought tolerance tends to be environment specific and dependent upon soil type, light intensity, and evaporative demands, among others [158]. Therefore, it is convenient to normalize the assessed trait values by the vapour pressure

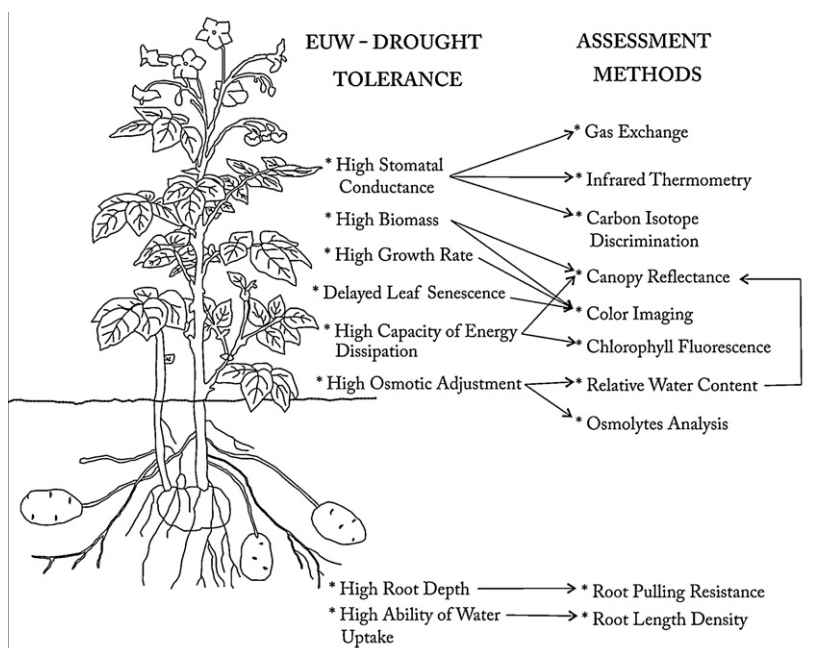


Fig. 2. Conceptual model for effective use of water (EUW) and drought tolerance in potato, showing related traits and methods used for their assessment.

deficit (e.g., transpiration in potato [130]) or leaf-meristem temperature (e.g., leaf elongation in some cereals using thermal time or degree days [160]), aiming at characterizing the expected drought response with respect to the target environments.

Methods to assess the response of traits under drought stress, particularly those non-invasive and non-destructive techniques warrant special attention. Root growth, architecture and functionality in response to drought are measurements that must be incorporated in potato breeding programs [64]. *In situ* root imaging is a technology being used in other crops and in potato [161,162]. Magnetic resonance imaging (MRI) can be used to study root architecture in early stages of potato development (A. Posadas, *pers. comm.*). Color imaging and infrared thermometry could complement existing methods based on vegetation indices. Thermal cameras offer several benefits compared to infrared thermometers, particularly in terms of spatial resolution, precision of measurements and reduction of errors due to changing environmental conditions between measurements [163]. Attempts are actually made to apply thermal imaging in potato breeding [164]. Since noticeable changes in fluorescence only occur under severe water stress conditions, fluorescence imaging on its own does not seem suitable for the early detection of water stress. This technique has however the potential to complement other imaging techniques and provide information about responses to heat or severe drought. The use of carbon isotope discrimination assessments should be re-analyzed in the light of the experience in cereals. The variation of this trait in different organs and under different stress intensities and timings should be investigated, allowing a better definition of conditions in which it could be used as an indirect selection criterion for yield. It would be useful to develop conceptual models and theoretical ideotypes for potato in order to address critical drought tolerant related traits and implement corresponding assessment methods in an integrative way. A first attempt is proposed in Fig. 2. Selections based on *in vitro* experiments merit further development at least as a pre-screening method, to be validated against selection under field conditions.

Among the mechanisms that could determine drought tolerance improvement in plants, epigenetic stressful memory is an issue that is currently debated and formalized in the scientific community [165]. Plant memory and specifically “stressful memory”

involves some processes that allow an improved stressful response in individuals that previously have undergone acclimation and hardiness to the same stress driver [165]. Stressful memory is caused by epigenetic changes such as modification of DNA activation by methylation or acetylation, histones alteration and chromatin remodeling that result in gene silencing and/or gene activation [166]. Drought stress memory studies have been carried out in potato to test and compare water response and tolerance of some varieties [39,43]. Activation of genes that take part in abscisic acid biosynthesis metabolic pathways, heat-shock proteins, xanthophylls, anthocyanins and other anti-oxidants glutathione-related were detected. Nevertheless, there is a need to compare memory effects on seeds from fruits (botanic seeds), seedlings and adult plants, and investigate the potential of trans-generation memory of stress.

Modern potato varieties are generally highly susceptible to drought. Thus, there is an increased interest in exploring and exploiting the wide genetic variation that exists for abiotic stresses tolerance in native potatoes. Selecting for drought tolerance while maintaining maximum productivity under optimal conditions is difficult as plant attributes involved in drought tolerance can be counter-productive under favorable conditions. The exciting results obtained in increasing abiotic stress tolerance in wheat by introgressing genes from related species [145,146] should stimulate similar efforts in potato.

Recent biotechnological approaches offer new alternatives to improve drought tolerance in several plants species, including potato; in terms of the identification of signaling pathways and master genes regulating drought tolerance. Genomic tools for identifying genome regions and genes involved in the control of drought tolerance should be more extensively used in potato. More detailed information will become available in the future using the metabolomics and proteomics techniques together with integrated bioinformatics systems. These advances will facilitate the genetic engineering of single or multiple targets to create a cultivated phenotype with high-yielding potential under drought stress conditions. Although cereal drought research may indeed have taken of earlier in cereals than in potato, there are exciting opportunities to transfer the rich knowledge accumulated in cereals into potato research. Many traits and screening methodologies have

been developed over the years in cereals and these may be applied to potato research as well. Taking advantage of the experience in cereals, careful scrutiny is needed to define the environment and the type of drought stress potato crops are really experiencing.

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