Tropical Plant Biol. (2009) 2:111–121
DOI 10.1007/s12042-009-9033-6

Growing More Potatoes with Less Water

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Received: 27 February 2009 / Accepted: 3 August 2009 /

Abstract Demand for potato is steadily rising in developing countries, where actual per-hectare production levels reach mere fractions of the yields achieved in Europe or North America. Improving abiotic stress tolerance, e.g., against drought, could increase these low potato yields and thus help to satisfy the growing demand for this crop. Hypotheses about genes and traits that could mitigate yield decreases caused by drought have been driven by information obtained from model plants and have recently been complemented with data of high throughput gene expression profiling and metabolite studies on potato genotypes under water stress. Principal tolerance traits that could diminish the vulnerability of potato yields to drought stress include improved detoxification of reactive oxygen species produced during stress, optimized stomatal control under drought to reduce water loss but at the same time allow for continuous CO_2 access for photosynthesis, and mechanisms to protect proteins and membranes from damage by water stress. Candidate genes underlying these traits as well as genotypes that express them are available and, after appropriate validation, could be used for breeding.

Keywords Breeding · Drought resistance · Potato · Tolerance genes · Yield maintenance under drought

Abbreviations

ABA	Abscisic acid
HSP	Heat-shock protein
LEA	Late embryo abundant
masl	Meters above sea level
ROS	Reactive oxygen species
SNP	Single nucleotide polymorphism
WUE	Water use efficiency

Communicated by: Paul Moore

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Introduction

On a global scale, demand for potato (*Solanum tuberosum* L.) is steadily rising. Slight decreases in potato consumption in developed countries are overcompensated by strong increases in developing countries, where potato production has tripled between 1960 and 2000 and will need to grow continuously to satisfy unremitting demand [16, 29]. Most of the production increase will have to come from yield increases as new cultivable area is scarce. Many potato production areas in developing countries are located in semi-arid areas, where drought spells contribute to large harvest losses. In these regions, where the yields range around 30% of the global mean, adapted drought-tolerant potato varieties could improve yield considerably.

The critical level of soil moisture tension for potato yield and quality ranges around −0.7 bar [76]. Average tuber yield reduction per mm water deficit has been estimated at 117 kg/ha [107]. Nevertheless, potato water productivity on dry weight basis is two times higher that of wheat or maize and three times higher than that of rice [28, 103]. Water stress at virtually any stage of potato development decreases yield, but, depending on the timing, drought may have different effects on plant growth and tuber yield. Drought at early developmental stages, before tuberization, reduces the stolon number per stem without affecting the number of tubers initiated per stolon [41]. It was suggested that drought during tuberization lowers tuber number, and during bulking it lowers both tuber number and size [70]. In field trials tuber yield reduction was greatest either under drought during tuber initiation [23, 55, 68] or during tuber bulking [63, 64], probably due to differences in phenology of the tested genotypes. Besides yield, drought may also affect tuber quality. Water stress causes an increase of glycoalkaloid contents, especially of α-solanine and α-chaconine in many varieties [14]; moreover, water stress might cause tuber defects such as cracking, secondary growth, malformations, hollow heart, and internal brown spot [69].

Tuber yield depends primarily on the amount of radiation intercepted by the plant and on water availability [3]. Plants with a large canopy intercept more light, but also have a larger surface exposed to transpiration. Drought generally reduces canopy size [24, 102]. Leaf growth stops at a certain threshold of transpirable soil water. These threshold values range between 40% and 50% for many crops, but in potato, leaf growth ceases when the fraction of transpirable soil water declines to only 60%, illustrating the susceptibility of potato to water stress [111]. Reduction of canopy size helps the plant diminish the evaporative demand and improves plant survival under water stress, but, on the other hand, results in yield decreases due to the smaller leaf area available for photosynthesis. Early leaf appearance combined with the ability to sustain leaf growth with increasing soil moisture deficit would improve productivity in the presence of drought [48]. Deeper and denser roots could improve water availability to the plant and contribute sustaining leaf growth and plant productivity under drought, where water still remains available in deeper soil layers. Tuber yield, reduction of stomatal conductance, photosynthesis, and leaf area are significantly correlated to root dry mass under stressed conditions. Consequently, root mass in the plow layer could be used as a selection criterion for enhancing tolerance of potato to drought [44, 56]. A good indicator of drought adaptation is increased root-shoot ratio under water stress [13, 40, 46].

Drought Tolerance Breeding in Potato

Available variation of drought tolerance and water use efficiency in potato germplasm opens the path to enhance yields under water-limiting conditions by breeding, but the success of this approach has been limited by both the inconsistency of natural drought events and the complexity of plant drought stress responses. Selecting for drought tolerance under natural conditions is challenging, as the occurrence of stress is unpredictable due to day-to-day and year-to-year variation of climate. Different stress intensities and timing from one year to the next can lead to elicitation of distinct drought responses in different selection cycles, resulting in limited breeding progress. Therefore, in early breeding stages, breeders often prefer to select for high yield in favorable environments and expect that this will also increase yields under abiotic stress conditions. This might be true for environments with weak stress, but if the target environment is commonly affected by severe stress, selection gains in an unstressed target environment are of little or no help in improving yields in stress environments. Finally, when genotypes are selected mainly under favorable conditions, much useful genetic variation for stress tolerance may be lost [7]. In addition, direct selection for drought tolerance under water-stressed conditions is hampered by low heritability, polygenic control, and epistasis of many drought tolerance traits.

Breeding to reduce the gap between yield potential and yield in drought-prone environments requires highly productive water-stress-tolerant parental material that expresses tolerance traits likely to improve drought tolerance without diminishing yield potential. Not surprisingly, greatest tolerance levels have been found in Andean native potato and wild tuber bearing potato species [5, 87] that evolved in harsh environments at high altitudes above 3,000 masl and were regularly exposed to drought during their evolution. However, native Andean potato genotypes generally have low yields and are not adapted for most commercial potato production systems, and wild potato species harbor many agronomically unfavorable traits. Hybridizing adapted with non-adapted material usually conserves chromosomal regions containing large amounts of undesirable genes. Linkage of undesirable genes with favorable gene combinations may need a large number of sexual crosses to separate and therefore require considerable time and effort to recover previous yield levels. Consequently, breeders are reluctant to introduce unadapted parents such as wild potato species into breeding programs, unless they can target a specific trait from the unadapted parent. Therefore, successful breeding requires exact information on effective tolerance traits, their heritability and their genotype-by-environment interaction, plus suitable selection tools for the traits of interest.

According to Levitt [58], drought resistance can be based on (1) drought stress tolerance, (2) drought stress avoidance, (3) drought escape, or (4) on a combination of these mechanisms. Drought escape means that the plant life cycle is complete before drought stress inhibits further plant growth. Indeed, Levy [60] observed that early-maturing potato varieties had lower yield losses under drought than later maturing ones, but this finding is valid only for late-season drought events. Drought stress tolerance implies that plants are tolerant to desiccation to some extent, and that moderate short-term disturbances of plant water balance do not immediately affect yield. This could be accomplished by protecting cell components from the adverse effects of water loss through expression of cell rescue mechanisms and through increased capacity of leaves to recover after wilting. Drought stress avoidance has two components: reduction of water loss and improvement of water uptake. While improvement of water uptake allows the plant to meet transpirational demand under lower soil water contents, increasing evaporation resistance by closing stomata or decreasing the evaporative surface, i.e., leaf area, reduces transpiration and water loss. Crop yield is intrinsically linked to transpiration, and reduced transpiration generally lowers biomass accumulation. Therefore, selection for drought stress avoidance genotypes with low transpiration generally results in diminished yields under optimum conditions [93]. Increasing the amount of harvested biomass per unit of transpired water, i.e., water use efficiency (WUE), would be an option to mitigate the yield penalty caused by reduced transpiration. Favorable leaf anatomy as well as optimal regulation of stomatal and mesophyll conductance for continued CO_2 diffusion to the chloroplasts and increased Calvin cycle activities might increase intrinsic WUE, while improvement of harvest index under water stress would contribute to increased crop WUE. Plants with high WUE would be highly desirable for irrigated potato cultivation in regions where water resources are scarce. For areas with frequent drought spells, in addition to increased WUE, drought tolerance traits that help the plants survive and produce under water stress would be highly beneficial.

Potato breeding for tropical environments presents a particular challenge. Temperatures in the lowland tropics are often too high, irradiance excessive, and precipitation insufficient to sustain potato growth. So in addition to drought tolerance, heat tolerance is an important breeding target for potato improvement for tropical areas. The combined effect of drought and heat stress differs markedly from that of individual drought or heat stress [81, 82]; consequently, many drought tolerance traits might not be effective when a combination of drought and heat affects the plant.

Drought Stress Signaling in Plants

Drought stress activates a wide array of responses in plants, which together with constitutive traits determine whether a plant is more tolerant or susceptible to drought. About 10% of the transcriptome is differentially regulated under drought [18, 79, 97]. The number of genes implicated in yield maintenance under drought might be nearly as large as the number of genes implicated with yield in general.

How plants perceive water stress is not yet clearly defined. A general model describing plant responses to stress starts with the perception of signals from the environment, followed by the generation of second messengers such as inositol phosphates, phospholipids, and reactive oxygen species. In yeast, an osmotic stress-sensing pathway involving receptor kinases perceives osmotic stress at the membrane level and transmits the signal to MAP-kinases [38]. Putative orthologs to osmotic stress-sensing kinases of yeast have been found in plants [21, 105], where it is probable that a multitude of sensors is involved in water stress perception and signal transduction, triggering an array of responses through secondary messengers such as hormones, phospholipids, calcium ions, and other signals. The different water stress signaling pathways may interact with one another using shared components generating an intertwined network (reviewed by Wu et al. [112]).

For potato it was conclusively shown that roots sense soil water deficits well before any loss of turgor occurs [62]. In response to slight water potential decreases in roots, abscisic acid (ABA) is produced in root tips and is subsequently transported through the xylem to leaves and causes growth attenuation and stomatal closing well before drops in leaf water content or water potential appear in this organ [62]. ABA accumulation in the xylem then triggers an array of reactions, including liberation of ABA from sugar complexes, leaf and shoot growth attenuation, transcriptional induction of a battery of genes that presumably protect the cells from damage under prolonged stress, as well as more general adaptive shoot and root responses (reviewed by Wasilevska et al. [109]. At least four independent regulatory systems for gene expression changes in response to water stress have been identified, two are ABA-dependent and two are ABA-independent [91].

Drought Stress Tolerance Candidate Genes and Traits in Potato

Microarray-based gene expression profiling in drought-exposed plants revealed a large number of drought-induced and repressed genes that inform us about plant stress responses at molecular level [18, 79]. During recent years, results of several microarray experiments assessing gene expression changes in drought-stressed plants also became available for potato. Most analyses were targeted towards leaves; only one study was addressed toward tubers and leaves [110]. Up to now, no molecular data on root or stolon responses of potato to drought have been published.

Drought adaptation and acclimation responses on gene transcriptional level in native Andean potato derived from true seed were described in Watkinson et al. [110]. Schafleitner et al. [87], Vasquez-Robinet et al. [106] and Mane et al. [87] reported gene expression changes and metabolite accumulation in native Andean potato clones exposed to prolonged drought stress. In most studies the TIGR 10 k potato cDNA microarray was used [81]. Mane et al. [87] applied the POCI 44 k oligonucleotide chip [53]. In the studies on clonal material, clone Sullu was used as the drought-tolerant genotype and drought susceptible controls were either SA2563, Ccompis, or Negra Ojosa. Each of these articles includes lists of drought-induced and repressed genes of potato. Additionally, the gene expression data obtained with the TIGR 10 K are publically available in the Solanaceae Gene Expression Database (http://www.jcvi.org/cgi-bin/potato/study/sol_study.pl).

Together with agronomic, physiological, and biochemical assessments, gene expression data have given valuable insight into drought responses of different potato genotypes with different drought susceptibility levels. The tolerance traits suggested by gene expression profiling include features involved with signaling; transcription regulation; photosynthesis; carbohydrate, amino acid, and lipid metabolism and transport; hormone biosynthesis, degradation and transport; and cell rescue. However, microarray studies typically are performed on a small number of clones and, in spite of thorough statistical analysis, are prone to errors resulting in false positive candidate genes, and, more importantly, might fail to pinpoint important tolerance genes. Furthermore, it might be difficult to discern whether up-regulation of a specific gene points towards its role in a tolerance mechanism or transcriptional induction merely reflects a stress response without impact on drought tolerance. The microarray studies on drought stress responses in potato were carried out comparing expression patterns in tolerant and susceptible genotypes, which facilitates the discrimination of putative tolerance genes from stress-responsive genes without a role in drought tolerance. Verifying the expression patterns of candidate genes over a larger number of accessions with varying tolerance would help to confirm the value of putative candidate genes. Coupling gene expression studies with genetic linkage analysis, where expression levels are treated as quantitative phenotypes, would be another means to validate the impact of gene expression changes on the drought tolerance phenotype, provided that gene expression differences between stressed and control plants are heritable [61]. But none of these approaches substitutes the experimental proof that a candidate gene indeed provides improved tolerance. Testing the large number of candidate genes by transgenic over-expression or gene silencing and phenotyping of the resultant transgenic plants would be a very laborious task. Model plants such as *Arabidopsis thaliana* mutants or knock-out lines are very helpful for candidate gene validation, but the effect of a specific candidate trait on tuber yield maintenance can only be accomplished in potato, as the popular model plants do not produce tubers. Furthermore, a specific candidate tolerance gene might interact with an array of other genes and thus is only operational in a specific genetic background. In spite of all these limitations, gene expression studies are apt to identify candidate genes for tolerance and allow establishing hypotheses on pathways conferring drought tolerance in plants.

Genes Involved with Drought Stress Signaling in Potato

Little is known about signaling factors involved with water stress tolerance in potato. Gene expression measurement revealed an array of up-regulated genes functioning in signaling such as Ca^{2+}-binding and GTP-binding factors, kinases, and phosphatases, but no studies have been performed in potato to confirm the involvement of these factors in tolerance mechanisms. Microarray gene expression analysis pinpointed a protein phosphatase 2C gene of potato, an ortholog to ABI2 of *A. thaliana*, that is involved with ABA sensing and signaling [36]. High expression of this gene was correlated with yield maintenance under field conditions [86]. Inositol phosphates and their turnover products have been implicated to play important roles in stress signaling. Constitutive transgenic expression of an *Arabidopsis* inositol polyphosphate 6-/3-kinase in tobacco improved tolerance to diverse abiotic stresses [116]. An ortholog to the inositol polyphosphate kinase is present and expressed in potato, but its implication in abiotic stress signaling has not yet been addressed. Inositol polyphosphate kinase was expressed, but was not significantly up-regulated in potato under prolonged drought stress. The conducted microarray studies assessed drought stress responses taking place several days and weeks after drought stress onset, and therefore fail to identify early signaling events water stress.

Phytohormones play a key role in drought stress signaling. While ABA-responsive genes were found induced in drought-stressed potato, no ABA-metabolizing genes were differentially regulated under prolonged water stress. In contrast, transcripts encoding gibberellin-degrading enzymes accumulated under drought [87]. Gibberellins act as growth promoters and increased degradation of this hormone might contribute with decreased shoot and leaf growth under drought. Increased ethylene biosynthesis gene expression, which was observed predominantly in drought-susceptible potato, might be associated with increased stress perception. Ethylene, together with ABA, is involved with leaf growth attenuation under water stress [92].

Transcription Factors Involved in Drought Signaling and Response

In potato, differential regulation of several transcription factor families was found under drought conditions.

Evidence for the action of some of the water-stress inducible transcription factors of potato such as MYC, MYB, Nam, NF-Y, DREB, GAI and ASR family members is available from other plant systems [1, 2, 43, 77, 84]. High expression of a DREB transcription factor in potato, an ortholog to DREB1D of *A. thaliana*, was associated with increased drought tolerance in a trial on 16 improved potato varieties and breeding clones [86]. The abscisic acid, stress ripening gene (ASR) family comprises at least four genes in Solanaceae [30]. The first identified drought-induced gene of potato, DS2, belongs to this gene family [26]. The best-characterized gene family member, ASR1, as well as ASR2 are strongly up-regulated in potato under drought [87]. ASR1 has a dual function: in the nucleus it acts as a transcription factor and regulates the expression of a hexose transporter, while in the cytosol it functions as chaperone and stabilizes proteins under abiotic stress conditions [117]. Further transcription factor families found up-regulated in drought-tolerant potato comprised GATA, bZIP, WRKY1, and TAF-3 transcription factors, suggesting a role for these factors in the establishment of drought tolerance in this crop [87, 106, 110].

Recently, CSPA and CSPB, bacterial RNA chaperones that resolve RNAs that have been kinetically trapped in miss-folded form, were shown to promote stress adaptation in multiple plant species [20]. RNA chaperones are ubiquitous proteins and homologs of CSPA were found in wheat [51] and *A. thaliana* [52]. In potato, a putative homolog to CSPA was slightly induced under drought. CSP-like genes might merit a more thorough investigation of their role in stress tolerance of potato and of their use in crop improvement.

Photosynthesis and Respiration

Dependending on the kind and timing of drought, reduced leaf area may affect net photosynthesis more than inhibition of photosynthesis itself. Nevertheless, maintenance of photosynthetic activity under water stress and recovery from drought-stress associated drop of photosynthetic activity is a key element of plant drought tolerance. Under drought, photosynthetic efficiency decreases and CO_2 assimilation is greatly reduced in susceptible genotypes, while resistant genotypes can continue with photosynthesis for weeks after drought onset [110], indicating that reduction of photosynthetic activity under drought is highly genotype-dependent. Photosynthesis in water-stressed plants may be restricted by stomatal limitations, i.e., in how much CO_2 remains available for the photosynthetic apparatus, when stomatal conductance is kept low to avoid excessive transpiration. There may also be non-stomatal limitations, such as metabolic impairment including reduced ribulose bisphosphate carboxylase regeneration and ATP synthesis that inflict carbon assimilation under drought. Mesophyll conductance for CO_2 also may change dramatically under drought and, together with stomatal closure, limit the access of CO_2 to the chloroplasts (reviewed by Warren [108]). Under moderate drought, stomatal limitations prevail, while under extreme drought stress metabolic impairment may occur.

Stomatal conductance declines faster than photosynthetic capacity. Liu et al. [62] observed that photosynthesis did not significantly decrease when stomatal conductance decreased from 0.7 to ca. 0.4 mol m^{-2} s^{-1}, while the relationship between photosynthetic efficiency and stomatal conductance increased approximately 1.7-fold, demonstrating that photosynthetic WUE of potato increases at moderate soil water deficits by partial stomatal closure. Variation in stomatal density has been observed between different potato varieties and low stomatal density was proposed to be associated with drought tolerance in potato [10]. Masle et al. [71] reported the isolation of the ERECTA gene of *A. thaliana*, a leucine-rich repeat, receptor-like kinase that controls transpiration efficiency and has effects on stomatal density, epidermal cell expansion, mesophyll cell proliferation and cell–cell contact. It remains to be tested whether genotypic variation of the potato ortholog to this gene has an impact on stomatal density and transpiration efficiency in potato. Decreased stomatal density was also observed in potato transformed with trehalose-6-phosphate synthase from yeast [94]. These plants showed retarded wilting of excised leaves and lower CO_2 assimilation.

On the gene expression level, photosynthesis-related genes such as chlorophyll-binding proteins or photosystem components are up-regulated under drought in resistant genotypes and down-regulated in susceptible genotypes [87]. The significance of the differential expression of these genes for tolerance is unclear. During recovery from drought events, resistant accessions induce genes involved with thylakoid-associated processes, including genes encoding photosystem I and II proteins and chloroplast envelope protein genes, ribulose bisphosphate carboxylase, thioredoxin-responsive plastidic glyceraldehyde-3-phosphate dehydrogenase and fructose-1,6-bisphosphatase genes, and enzymes of photosynthetic carbon fixation [67]. These gene expression changes indicate that photosynthetic recovery might require de novo synthesis of photosynthetic proteins.

Reactive Oxygen Species

Under stress, the photosynthetic machinery, like other cell compartments, is affected by increased concentrations of reactive oxygen species (ROS) [88]. The primary sources of ROS in chloroplasts are the Mehler reaction and the antenna pigments [6]. Other sources of ROS in plant cells under stress include the photorespiratory pathway in peroxisomes, detoxifying reactions catalyzed by cytochromes in both the cytoplasm and the endoplasmic reticulum, and oxidative processes in mitochondria. The high energy consumption of the plant's stress response increases respiration rate with a linked production of ROS [101]. ROS are toxic to cells as they can cause oxidative damage to proteins, DNA, and lipids. On the other hand, ROS act also as signaling molecules for regulating development and various physiological responses [75]. How plants control this dual role is largely unknown, but it is clear that the steady-state level of ROS in cells needs to be tightly regulated. Major ROS-scavenging enzymes in chloroplasts include superoxide dismutase, ascorbate peroxidase, catalase, glutathione peroxidase, and peroxiredoxin. Members of all these gene families were up-regulated in tolerant potato under drought [67, 87, 106]. CDSP 32 and CDSP34 are other chloroplast-localized proteins involved with ROS detoxification [19, 57]. Additionally glutathione synthetase, glutathione-S-transferase, glutathione transporter, as well as two thioredoxins were induced in drought tolerant Sullu, pinpointing the increased capacity of ROS detoxification of this clone. During drought recovery, four thioredoxin-related chloroplast targeted genes were induced in a drought-resistant accession only.

Mitochondria are other targets of oxidative stress, as the interaction of O_2 with reduced components of the electron transport chain and fatty acid peroxidation leads to ROS formation. Under drought, we observed up-regulation of an antiquitin family aldehyde dehydrogenase 7 gene previously suggested to be involved in the detoxification of reactive aldehyde species generated by oxidative stress-associated lipid peroxidation [83], which is a good candidate for mitigating oxidative stress in mitochondria. Another important drought-inducible mitochondrial function concerns alternative oxidase 1a, which also is strongly upregulated in potato under drought. Respiration is generally enhanced by drought, the drought-induced increase in oxygen uptake being due mostly to a twofold increase in the capacity of the alternative oxidase pathway. This pathway has been shown to play a broad role in determining the normal redox balance in the cell and is important in maintaining photosynthetic electron transport under stress, either through direct consumption of reducing power, through sustained production of CO_2, or by allowing other power-consuming processes (e.g., photorespiration) to operate [35]. An increased respiration rate seems necessary for photosynthesis recovery after a period of water stress. This might be the reason genes encoding mitochondrial proteins such as carrier proteins, ubiquinol-cytochrome c reductase and an epsilon subunit of mitochondrial F1-ATPase are up-regulated during drought recovery in tolerant potato [67].

The up-regulation of ROS detoxifying enzyme genes and the accumulation of antioxidants in tolerant varieties point towards a crucial function of ROS detoxification in drought tolerance. Transgenic over-expression of nucleoside dikinase 2, Cu/Zn superoxide dismutase, and ascorbate peroxidase, which neutralize ROS-mitigated deleterious effects of free oxygen radicals, improves drought tolerance and thus provides further evidence for the importance of ROS detoxification in water stress tolerance [73, 98, 99]. Therefore, genes that have the potential to protect the cell from oxidative stress are good candidates for drought tolerance genes.

Changes in Carbohydrate Flux Under Drought

It has been noted that water stress causes changes in the concentration of numerous metabolites in plants. In drought-stressed potato, alterations in metabolite steady state levels, as well as in metabolite flux, have been noted in tubers and leaves. Under water stress, sucrose supply to tubers is reduced and tuber growth and starch biosynthesis is repressed. While in turgid tubers, starch biosynthesis is favored and sucrose phosphate synthase is inhibited, mild water deficits lead to a rapid switch from starch biosynthesis and net sucrose degradation to activation of sucrose phosphate synthase and net sucrose synthesis [33]. The shift from starch to sucrose resynthesis is controlled by redox-dependent, trehalose-6-phosphate mediated activation of ADP-glucose pyrophosphorylase [54].

A shift in carbohydrate partition towards tubers has been observed under laboratory drought conditions [34], while increased harvest index appears to be genotype dependent under field drought conditions. The ability to increase dry matter allocation to tubers might depend on the increased sucrose phosphate synthase-mediated sucrose resynthesis under water stress that might attract water to tubers and sustain growth during water deficits [34].

More candidate genes for improving harvest index under drought have been proposed, e.g., SNF1-related protein kinase, which plays a key role in carbon partition [66], but more research is needed to identify factors that promote preferred carbon allocation in tubers during water stress under field conditions.

Osmotic Adjustment

A net increase of solute concentrations in plants in response to a fall in the water potential of the cell's environment results in a decrease of the osmotic potential in plant cells, which in turn attracts water into the cell to maintain turgor pressure. Osmotic adjustment often is mentioned as a desirable trait in plant drought tolerance [42, 47, 59]. It takes place in leaf, root, and tuber tissue of drought-tolerant and -susceptible potato genotypes. While Jefferies [47] reports osmotic adjustment in leaves in ranges between 0.01 and 0.16 MPa, Coleman [22] measured a maximum value for osmotic adjustment of 0.54 MPa in young expanding leaves of an improved potato variety. The difference in the osmotic adjustment between these two reports is probably due to the low osmotic potential in the control plants used by Jefferies [47]. Basu et al. [12] observed a decrease in water potential from −0.2 to −1.0 MPa in potato under drought. These data demonstrate that osmotic adjustment depends on the kind and strength of stress as well as of the potato genotype. As demonstrated by Serraj and Sinclair [89], the contribution of osmotic adjustment to increased water uptake from drying soils is very limited, therefore osmotic adjustment might be more important for protecting proteins and membranes (reviewed by Yancey [115]) than as a means to acquire more water. The value of osmotic adjustment as a drought tolerance trait is controversial since turgor maintenance could result in maintenance of green leaf area and delay the activation of water-conserving mechanisms such as stomatal closure and leaf abscission, thus exposing the plant to even stronger stress when drought prevails [89]. However, under transient water stress, turgor maintenance may have a function in sustaining tissue metabolic activity. Osmotic adjustment does not take place homogenously in the whole plant. Instead, active roots and young leaves show greatest decreases in osmotic potential. Therefore osmotic adjustment might favor turgor maintenance particularly in young and essential parts of the plant and thus improve plant survival, regeneration, and productivity under drought.

A large array of metabolites has been proposed to contribute to osmotic adjustment in potato, including all kinds of plant-compatible solutes, such as metal ions, organic acids, polyamines, sugars, sugar alcohols, amino acids and their derivates, and proteins [39]. Proline was proposed to play a key role in osmotic adjustment, as its concentration in plants strongly increases under water stress [25]. In drought-stressed potato, genes of proline biosynthesis such as Δ^1-pyrroline 5 carboxylate synthase and Δ^1-pyrroline 5 carboxylate dehydrogenase were found induced, but no correlation between proline content and drought tolerance could be established [11, 85]. It was proposed that proline accumulation is more an indicator of injury by drought than a tolerance factor [8, 72]. However, there is evidence that proline biosynthesis intermediates act in drought stress signaling [45]. Amino acids other than proline did not accumulate in the drought-tolerant landrace Sullu under stress, but concentration of amines such as ethanolamine and putrescine was increased [67]. Organic acid content was much higher in Sullu than in a susceptible control, with significant drought-mediated increases of high basal concentrations of caffeic acid, a putative strong antioxidant and chlorogenic acid precursor [4, 114], and citric acid [106]. Sucrose accumulation in leaves of tolerant potato was inconsistent between experiments, ranging from no accumulation and even slight decline in resistant Sullu [87] to very high sucrose concentrations in drought-stressed leaves of the same clone [67]. Similarly, trehalose accumulation in Sullu varied between different drought trials from no detected changes to accumulation of moderate levels [106]. Further osmolytes accumulating in drought-tolerant potato that are considered to be involved with drought tolerance in plants are galactinol, raffinose, pinitol, and inositol [67, 87, 90, 95, 97, 106]. Sugar alcohols also may act as antioxidants in stressed plant cells. Corresponding biosynthesis genes were found up-regulated under stress [67, 87].

Stabilization of Proteins and Membranes

An array of genes encoding proteins putatively involved with maintaining the hydration of cellular compounds such as proteins and membranes are up-regulated under water stress. Several genes encoding late embryo abundant (LEA) and dehydrin genes, particularly LEA5 and LEA 18, were induced in potato under drought [87]. These proteins prevent protein aggregation under stress and thus could be of use for breeding drought-tolerant crops [9].

Protein chaperones of the DnaJ family as well as an array of heat shock proteins (HSP) have similar roles as LEA proteins and their expression is also increased under drought stress in potato [87, 106, 110]. In vitro studies have shown that HSPs can bind selectively to denatured proteins, prevent their aggregation, and maintain them in a competent state for refolding by other chaperones [31]. DnaJ-like proteins belong to a large and diverse family of chaperones. Drought-induced expression of these genes has been observed in many plant species [74] and might contribute to plant performance under water stress. Expression of both gene families was induced in potato under drought; however, while HSP genes were up-regulated in both drought-tolerant and -susceptible cultivars, DnaJ-like protein genes were much stronger expressed in tolerant potato [87, 106]. One of the drought-induced potato HSPs is an ortholog to the *Arabidopsis* HSP At5g12030 that previously has been shown to enhance drought tolerance [96]. Furthermore, an ATP-dependent metalloprotease and chaperone found induced in potato has been associated with drought tolerance [27].

The cell and organelle membranes are susceptible to injury by water stress. Limiting membrane damage during desiccation and membrane regeneration are critical features of tolerance. The extent of membrane damage is commonly used as a measure of tolerance to drought [15]. In potato, the ability of the adapted cells to maintain cellular and subcellular membrane integrity under conditions of severe water stress was found to be associated with a reduced level of unsaturated fatty acids in the membrane lipids [37]. Expression analysis pointed to non-specific lipid transfer proteins that are highly induced in tolerant potato [87]. Further studies will be required to assess membrane-stabilizing and regenerating processes in drought tolerant potato.

Future Directions

The present knowledge on the physiological and genetic basis of water stress tolerance in other crops as well as in potato helps us to better understand the drought tolerance trait network. For some of the proposed traits, such as increased root mass and enhanced ROS detoxification, strong evidence for their beneficial effect in drought tolerance is already available, while for other candidate traits, such as osmotic adjustment or protein and membrane stabilization-related mechanisms, direct proof for their function in yield maintenance under stress in potato is still missing. To determine the functionality of candidate genes and traits, thorough agronomical, physiological, and genetic analysis of candidate traits will be required in germplasm panels or segregating populations. One way to speed up candidate gene validation and efficiently narrow down the number of candidate genes obtained in microarray studies could be accomplished by quantitative trait loci (QTL) analysis of specific drought tolerance traits, similar to that described by Gebhardt et al. [32]. For this purpose, publicly available databases of potato gene sequences, e.g., the TIGR Potato Gene Index (http://compbio.dfci.harvard.edu/tgi/cgi-bin/tgi/gimain.pl?gudb=potato), could be mined for single nucleotide polymorphisms (SNPs) in a number of candidate genes that are presumably evenly spread over the potato genome. Cost-effective methods such as high resolution melting would allow screening of large germplsm panels or populations for SNPs in candidate genes [113]. The resulting candidate gene-based markers could be used together with available anonymous markers, such microsatellite markers that would help to identify homologous groups, for a QTL approach or association genetics analysis to identify candidate gene loci that are co-localized with QTLs for specific drought tolerance traits. Chromosomal regions explaining diversity of a specific trait have been successfully identified in tetraploid potato [17, 65, 80]. Examples of drought tolerance traits that have been targeted in QTL studies using anonymous markers in crops were WUE [50], osmotic adjustment [100], delayed senescence [49], deep rooting [78], or cell membrane stability under drought stress [104]. Using markers derived from candidate genes instead of anonymous markers could indicate links between genes and QTLs and thus pinpoint involvement of candidate genes with specific tolerance traits. The alleles associated with a specific drought parameter might offer a favorable allele for this trait and can be used for marker-assisted selection in breeding. Although this approach does not provide direct evidence that the candidate gene marker linked with the QTL is indeed the gene underlying this QTL, this method can strengthen hypotheses on gene functions in specific drought tolerance traits and at the same time yields gene markers linked to traits of interest.

For many traits, a strong genotype by environment interaction might limit their use to improve drought tolerance over a broad range of environments; therefore it is very improbable that one single tolerant potato variety can be successful in all drought environments. However, it can be assumed that ROS detoxification, which provides benefits under many stress conditions, could be a suitable drought tolerance trait for a broad range of environments. In contrast, larger roots or high osmotic adjustment may be useful only for specific drought environments, either for situations where water remains available in deeper soil layers or in cases where regeneration after drought periods is crucial for yield maintenance. For breeding well-adapted potato that yields well in a specific drought environment, we need deeper insight into the potential impacts of different tolerance traits on yield maintenance in the target environment. For this purpose, materials expressing different drought tolerance traits need to be tested in multi-location trials to filter out tolerance traits and trait combinations that are effective either in a broad or narrow range of environments. Systematic characterization of soil and climate variables of target environments parallel to trait capture and validation would facilitate identifying the best trait options for each environment and allow better targeting of tolerance traits to specific drought environments.

Acknowledgements Many thanks to all collaborators and colleagues who contributed data and information for this review and to the two anonymous reviewers of this paper for their helpful comments. The work performed at CIP cited in this review has been supported by the governments of Austria and Luxembourg and by the Generation Challenge Program.

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