



Exploring possibilities of enhancing water use efficiency in potato: A review

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Abstract: Climate change threatens the global agriculture sustainability. Among different kinds of abiotic stresses, water stress is the most devastating component which curtails potato crop productivity. Our recent knowledge is limited concerning water stress tolerance and water use efficiency in potato. Many efforts are being made by the scientific community to reduce water use and to produce “more crop per drop”. This review elaborates quantitative and qualitative aspects of multiple stress mechanisms and their regulating system related to present scenario of water use efficiency (WUE) requirements. WUE can only be improved by using multidisciplinary promising research approaches like molecular breeding, high throughput genotyping, multi-gene transfer and bioinformatics applications to unleash the information needed to exploitation of required traits in potato.

Keywords: Genomics, Genotype, Proteomics, Stress, Water use efficiency

INTRODUCTION

Potato (*Solanum tuberosum* L.) is the most important non-cereal food crop worldwide (Pino *et al.*, 2007). It is grown in more than 125 countries and consumed almost daily by more than a billion people. Being a versatile crop, potato is not only utilized as a food and feed crop but also as a raw material in many industries (Ortiz and Watanabe, 2004). Potato crop is vulnerable to numerous biotic and abiotic stresses but, because of its shallow root system, it is more prone to water stress (Jefferies, 1993) and insufficient moisture availability leads in reduction of quality and quantity as well (Devaux *et al.*, 2010). Approximately 85 % root length is concentrated in the upper layer (0.3-0.4m) of the soil. Therefore, sufficient water availability is a critical issue for the targeted production of potato crop (Fabeiro *et al.*, 2001). Global water usage has increased six-folds in the past 100 years and it is forecasted that the water requirement will get double before 2030, mainly because of irrigation practices (Wang *et al.*, 2014). The water demand is increasing constantly for agriculture, but available water resources are decreasing due to continuous rise in world population, changing patterns of rainfall because of global climate change and evaporative demand in many cultivated areas. In the future, agriculture may not be a priority for water use, because of competition with other uses such as human consumption, urbanization, industrialization etc. So there will be a demand for new potato varieties with higher water use efficiency and drought resistance which require less irrigation

as compared to the presently cultivated genotypes. To understand the mechanism of water use efficiency (WUE) in potato, trait specific study from morpho-physiological to molecular level is the need of hour, so that the desired traits can be introgress in modern cultivars to enhance the productivity under water deficit conditions (Kaminski *et al.*, 2015; WWAP, 2015).

Water use efficiency (WUE) can simply be defined as the ratio of outputs to input. Output includes increasing biomass / yield / energy content / saleable product / financial return etc. and inputs includes rainfall / irrigation / transpired water / evapotranspiration etc. But, in general WUE of a crop is the amount of dry matter produced per unit of water transpired. In the era, when water rather than land area is limiting, the required crops should produce a higher yield with the same water input, or the same yield with a lower water input. N. E. Borlaug (2000) said, how can we continue to expand food production for a growing world population within the parameters of limited water availability? The answer is that humankind will need to bring about a ‘Blue Revolution –more crops for every drop’ in the 21st century to complement the Green revolution in the 20th century.

The pioneer research studies related to WUE were initiated by Briggs and Shantz in 1913. They first studied the water requirement of different species (corn, sorghum, millet, wheat, oat, barley, potato, alfalfa and soybean) for a whole growth period (Briggs and Shantz, 1914; Shantz and Piemeisel, 1927). They also explored difference in the water requirements between different varieties of the same crop, and suggested the

possibility of developing plant varieties, which are still more efficient in water use. But, the focused research for potato under water deficit scenario was started in 60-80's by Burton (Burton 1966; Burton, 1981). Some species of potato like *S. curtilobum* Juz, *S. curtilobum* Bukasov and *S. andigenum* and *Chaucha* group of *Solanum tuberosum* were reported to have low drought susceptibility traits (Monneveux *et al.*, 2013). After identification of key traits, the main target is to reduce the gap between yield potential and actual yield in drought prone environments. The basis of identification, selection and genesis of new variety should be based on the combined screening at different phenological levels. A direct link between stomatal function, transpiration and carbon assimilation was supported by many research groups (Willmer and Fricker, 1996; Farquhar *et al.*, 2001; Hetherington and Woodward 2003; Lawson *et al.*, 2011). Stomatal conductance is directly related to WUE and by manipulating the stomatal characteristics we can easily manipulate WUE (Rebetzke *et al.*, 2002; Masle *et al.*, 2005; Eisenach *et al.*, 2012). Further studies conclude that partial closure of stomata tends to increase photosynthetic water use efficiency, which can be defined as a ratio of photosynthesis (A) to stomatal conductance (g_s). Jones (1992), suggested that the optimal opening of stomatal aperture gives higher WUE without compromising at yield level. For controlling the stomatal aperture, guard cell membrane transporters are the important targets for genetic manipulation to improve crop performance under water limited regime. Besides these, several other traits which should be studied to come up with a plant type with higher WUE (Bita and Gerats, 2013). Improved WUE and a deep understanding of crop responses to water stress will help to reduce input requirements and lead to money saving for farmers (Saravia *et al.*, 2016). This review paper explains the basis of WUE at physiological, biochemical and molecular levels for exploiting the natural genetic variation present within the species and also from the species other than potato, so as to get better yield even under water deficit conditions.

Physiological and biochemical responses under water stress: Due to the sessile life cycle, plants have evolved adaptive mechanisms to face adverse environmental variations during their life cycle. These adaptation includes numerous physiological and biochemical changes which generally vary with plant genotype and growth stages. Plant height, number of green leaves and leaf area are considered as most sensitive parameters to moderate drought conditions (Deblonde and Ledent, 2001). The depth of root penetration in the soil is directly related to water absorption as well water stress tolerance (Lahlou and Ledent, 2005). Tolerance of a plant under limited water regime has been associated with the control of growth, carbon transfer (Tourneux *et al.*, 2003), osmotic adjustment (Heuer

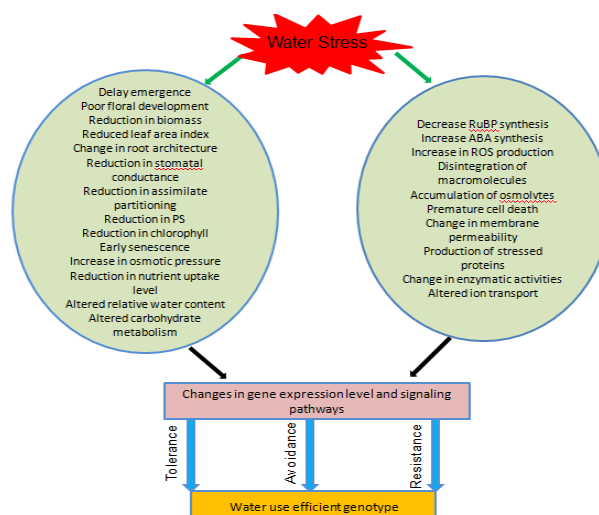


Fig. 1. Morphological, physiological, biochemical and molecular responses of a plant under water deficient condition.

and Nadler, 1998) and finally with enhanced water use efficiency (Alva *et al.*, 2012). Reduced water uptake also decreases nutrient absorption and transport to the roots by inducing root shrinkage and breakage of root soil contact (He and Dijkstra, 2014; Ahmad *et al.*, 2013). So, WUE is a critical factor to determine the plant productivity under water deficit condition. Comparatively shallow spreading root architecture of potato is an undesirable trait under limited moisture availability conditions (Harris, 1992; Kleinkopf and Westermann, 1981; Bailey, 2000). Water scarcity not only imposes other abiotic stresses like drought and salinity but also limits the yield and quality of the produce. In potato, water stress during vegetative stage reduces plant height, leaf area, root development and this finally results in reduced/delay canopy development. Reduced root development causes a significant reduction in the number of tubers per plant which ultimately leads to decrease productivity. After the vegetative growth, the most critical stage for water deficiency is tuberization because water stress during tuberization will form pointed tuber ends, multiple knobs and other malformations. Water stress during tuber bulking stage increases the percentage of undersized tubers, decrease specific gravity and increase dark ends. Under water deficit condition, osmotic stress is the main factor which damages the structure of cell and cell organelles and disturbs the normal metabolic activities. Plant productivity under drought is closely associated with the osmotic adjustments made by the plant species such as Sorghum (Tangpremsri *et al.*, 1995), Brassica sp. (Kumar and Singh, 1998) and Wheat (Morgan, 1984; El Hafid *et al.*, 1998). At biochemical level, accumulation of reactive oxygen species (ROS) in plants, including superoxide radical ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) under water stress is a common adaptive phenomenon. Higher production of ROS can disrupt normal functioning and plant metabolic activities

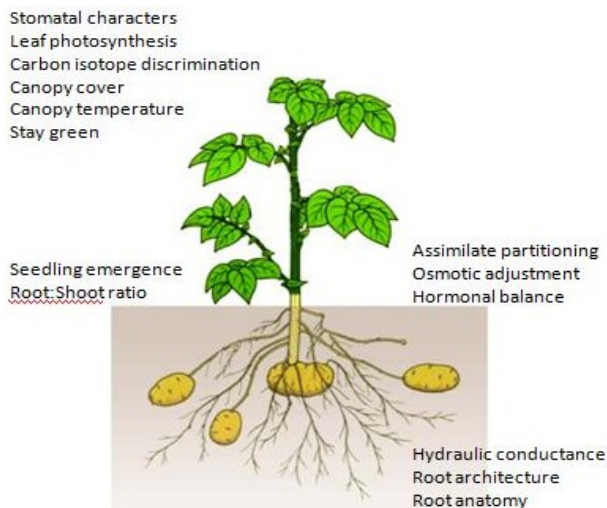


Fig. 2. Traits to be studied for water use efficiency.

through impaired enzyme activity due to oxidative damage, protein degradation, membrane lipid peroxidation and damage of DNA and RNA, which can ultimately culminate in cell death (Finkel and Holbrook, 2000). To limit ROS production, plants produce various types of antioxidants like superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR) and peroxidase (POX) etc. Proline acts as a non-enzymatic antioxidant to counteract the negative effects of numerous ROS and also as a signaling molecule in various metabolic activities which help plant to recover under severe stresses (Szabados and Savoure, 2010; Vankova *et al.*, 2012). Besides, Proline, sugar alcohols, hexoses, pinitol, and metabolites like carotenoids, glutathione, ascorbic acid and α -tocopherol have been found to be associated with water deficit tolerance in potato along with many other crops (Bansal and Nagrajan, 1986; Bohnert *et al.*, 1995; Sairam *et al.*, 2000). The higher production of antioxidant in response to oxidative stress induced by water stress is associated with the degree of stress tolerance of various plant species (Sunkar *et al.*, 2006). Although, in case of potato it was reported by Wegener and Jansen (2013) that the level may increase, decrease or remain stable depending on the genotypic variability and type of antioxidant. Morphophysiological, biochemical and molecular responses of a plant under water deficient condition are illustrated in Fig 1.

Molecular responses under water stress: The most crucial line of defense under any kind of stress works at genetic level. The genes which are induced because of water stress can protect the plant by several means like, enhancing the production of osmoprotectants (proline, glycine betaine, sugars, polyamines), modifying metabolic proteins and regulating signal transduction pathway accordingly. Water stress induces a decrease in leaf water potential and stomatal conductance which will cause the down regulation of photosynthe-

sis related genes. A gene *mrp51* (Mitochondrial Ribosomal Protein), is associated with stomatal conductance and the transformed arabidopsis plants having *mrp5-1*, was found to have higher WUE (Klein *et al.*, 2003; Ghasem *et al.*, 2009). Glycinebetaine, a compatible solute, whose biosynthesis is catalyzed by choline oxidase (COD), acts as a scavenger for ROS and efficiently protects different components of photosynthetic machinery, like Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase), photosystem II (PSII) from different types of stresses including the water stress. Cheng *et al.* (2013) studied the expression of choline oxidase (COD) under drought and found enhanced tolerance for water stress in transgenic potato plants bearing *codA* gene as compared to the non-transgenics. This COD gene was also introduced in many other plants like arabidopsis (Sulpice *et al.*, 2003), tobacco (Huang *et al.*, 2000), rice (Mohanty *et al.*, 2002; Kathuria *et al.*, 2009), tomato (Park *et al.*, 2007; Goel *et al.*, 2011; Li *et al.*, 2011) and potato (Ahmad *et al.*, 2008) to improve stress tolerance. Enhanced tolerance for drought and high temperature due to introduction of BADH (Betaine aldehyde dehydrogenase) gene in tomato (Jia *et al.*, 2002), wheat (Guo *et al.*, 2000) and potato (Zhang *et al.*, 2009) has also been reported. The expression of Arabidopsis HARDY (HRD) gene in rice improves the water use efficiency by enhancing the assimilation of photosynthates and reducing transpiration. HRD over expression produces roots with enhanced strength, branching and thicker leaves with more chlorophyll bearing mesophyll cells which contribute towards enhanced WUE. HVA1, an ABA responsive barley gene was introduced into wheat and the transgenic showed higher WUE (Sivamani *et al.*, 2000).

Root is the most susceptible part for water deficit in a tuber crop like potato, so modifications in root architecture can be an effective way to enhance the yield and production. Uga *et al.* (2013) demonstrated an increase in root growth angle by altering a rice quantitative trait locus (QTL), DEEPER ROOTING 1 (DRO1) through cloning and characterization. Higher expression of DRO1 increases the root growth angle so the roots grow in a more downward direction to reach up to the deeper soil layers for absorbing more water. Introducing DRO1 in a shallow root system like potato can be helpful in maintaining high water use efficiency under deficit irrigation. There are many transgenics with improved WUE in various crop plants. Various transcription factor (TF) related to abiotic stress have also been identified viz., MYB, MYC, DREB/CBF, ABF/AREB, WRKY (Wang *et al.*, 2016). The transcription factor DREB1A transferred from Arabidopsis to peanut resulted in 40% higher transpiration efficiency (TE) than the untransformed control (Bhatnagar-Mathur *et al.*, 2007). In transgenic potato overexpression of DREB/CBF TFs has been reported to enhance

drought tolerance (Iwaki *et al.*, 2013).

Transcriptomics and proteomics studies have identified the involvement of water stress tolerance related gene with various physiological processes. These studies resulted into the identification of various ABA biosynthesis related genes, chaperons, ROS related genes, iron homeostasis, late embryogenesis abundant (LEA). Some novel type of transcription factor like DST (drought and salt tolerance), a C₂H₄ type TF, which control the expression of H₂O₂ homeostasis related genes and mediate stomatal closure were identified by Huang *et al.* (2009). In *Solanum commersonii*, (a wild potato variety) the over expression of C-repeat binding factors has been found to be associated with proline synthesis in potato (Pino *et al.*, 2007, 2008). NFYA5, a drought-inducible nuclear TF has been reported in Arabidopsis which controls the stomatal aperture and hence proved to be linked with water stress tolerance (Li *et al.*, 2008). The cap-binding protein 80 (CBP80), also known as Abscisic Acid Hypersensitive 1, (ABH1) gene in *Arabidopsis thaliana* is involved in the regulation of the ABA transduction pathway and in drought tolerance. SNAC1 (STRESS-RESPONSIVE NAC1) is a rice guard cell related gene and its over expression enhanced ABA sensitivity and stomatal closure both under drought and salt stress in rice (Hu *et al.*, 2006). MYB60, MYB61 TFs of Arabidopsis regulate stomatal aperture and water stress tolerance (Cominelli *et al.*, 2005). AHK1, an Arabidopsis histidine kinase (AHK1) localized to the plasma mem-

brane, functions as osmosensor. The over expression of AHK1 enhanced water stress tolerance in Arabidopsis. WUE is a multigenic trait, so transferring only a single gene, which is specific to a specific kind of stress, may not be sufficient to reach the required level of tolerance (Bohnert *et al.*, 1995). The only approach is through multigene transfer, to enhance the WUE in potato (Chinnusamy *et al.*, 2005).

Traits required for better selection of a water use efficient variety: Plants responses to water stress are not similar among different cultivars (Hassanpanah, 2010), as a function of stress occurrence period (Kashyap and Panda, 2003). There are many traits which are required for a better understanding of mechanisms underlying tolerance under water stress like gaseous exchange, fluorescence, carbon isotope discrimination, plant water status, root traits, canopy reflectance etc. Gas exchange occurs mainly through stomata and the stomatal conductance is mainly influenced by CO₂ absorption and thus affects photosynthesis and other developmental process as well. ABA is the key regulator for stomatal conductance and more sensitive for water depletion. Endogenous ABA is produced rapidly during water stress so as to trigger a cascade of physiological responses. ABA mediated plant responses can be used for better selection. Recently, McAusland *et al.* (2013) combined thermal imaging and chlorophyll fluorescence technique to develop a screening method to measure alterations in intrinsic WUE. This approach is of dual significance

Table 1. Genes for drought tolerance tested in transgenic potato plants.

Gene	Gene function	Abiotic stress tolerance	Reference
StMYB1R-1	MYB-Like Domain Transcription Factor, activation of drought-related genes	Reduced water loss and provide tolerance under water deficit	Shin <i>et al.</i> , 2011
DREB1B	Transcription factor	Enhanced water stress tolerance Enhanced freezing tolerance	Movahedi <i>et al.</i> , 2012
TPS1	Trehalose synthesis	Delayed wilting under water stress	Stiller <i>et al.</i> , 2008
SST/FFT	Fructan accumulation	Reduced proline accumulation at low water availability	Knipp <i>et al.</i> , 2006
TaSTRG	Fructan accumulation	Enhanced proline accumulation under drought stress	Knipp <i>et al.</i> , 2006
codA	Synthesize GB in chloroplast	Enhanced salt tolerance Enhanced drought tolerance	Ahmad <i>et al.</i> , 2008
BADH	GN synthesis	Enhanced tolerance to drought and salinity	Zhang <i>et al.</i> , 2011
StPPII	Proton pump interactor from <i>Solanum tuberosum</i> involved in several physiological processes	Enhanced tolerance to water stress and others abiotic stresses	Garcia <i>et al.</i> , 2011
Tomato Cu, Zn superoxide dismutases	Enhanced oxidative stress defense	Enhanced drought-osmotic tolerance	Perl <i>et al.</i> , 1993
AtDHAR1	Membrane integrity, protecting chlorophyll against degradation, and allowing faster removal of H ₂ O ₂	Enhanced herbicide, water and salt stress tolerance	Eltayeb <i>et al.</i> , 2011
AtGR1	Elevation GSH contents	Enhanced tolerance to multiple environmental stresses, including drought	Eltayeb <i>et al.</i> , 2010
Cytosolic glutamine synthase	Reduced photorespiration	Limiting N loss due to photorespiration under well-watered and well-fertilized conditions	Kaminski <i>et al.</i> , 2015

because it provides both spatial and temporal images of stomatal conductance and carbon assimilation. Hence, we can access both, stomatal response and speed simultaneously with rates of photosynthesis, which would be suitable for identifying plants with faster stomata movement with no impairment in carbon assimilation. Another important parameter to identify a genotype for higher WUE is Carbon isotope discrimination (CID). It is the ratio of two stable C isotopes i.e. ^{12}C and ^{13}C , which are negatively correlated with transpiration efficiency of any C_3 species. CID also correlated well with water deficit conditions suggesting that it is a potential tool that can be used to identify a tolerant variety within the germplasm of any crop species. The variability in intrinsic photosynthetic capacity can be exploited for screening under water deficit conditions in potato (Minhas *et al.*, 2003). Plant water status and its degree of osmotic adjustment with response to available soil water are critical to mark a variety as water stress tolerant. For selecting a genotype with higher WUE, it is important to evaluate it under well watered conditions along with the stressed one (Topbjerg *et al.*, 2014). Small root length in the soil profile may be an important component of the potato plant's sensitivity to stress (Iwama and Yamaguchi, 2006). For a tuber crop like potato, root traits like deeper root system, high root dry weight and density are desirable. Deguchi *et al.* (2015) reported the correlation between hydraulic conductance in potato crop and its root system under water deficit conditions. It suggests that improved total root length enhances hydraulic conductance and increases leaf water potential. For maintaining higher yield under restricted irrigation, early vigorous root proliferation may be considered a useful selection trait, because it rapidly secures access to water available in deep soil layers (Puertolas *et al.*, 2014).

Many workers proposed root pulling resistance as a quality parameter to quantify root development since a direct correlation was observed by Ekanayake *et al.* (1989) between tuber yield and root pulling resistance. Rolando *et al.* (2015) suggested leaf greenness as a water stress tolerant trait in potato as it indicates reduced chlorophyll degradation. When senescence is delayed, this stay green may reflect more photosynthetic activity along with re-mobilization of assimilates towards tubers. Figure 2 represents the traits to be studied for enhancing water use efficiency.

Partial root zone drying and water use efficiency: A new irrigation strategy termed as Partial Root-zone Drying (PRD) being investigated in many countries (Kang and Zhang, 2004). PRD is based on the assumption that by providing a partial water stress to the roots, we can control the stomatal opening which may reduce water loss substantially with a minimum loss of CO_2 uptake (Jones, 1992). PRD involves irrigating only part of the root zone and leaving the other parts dry to

a predetermined level before the next irrigation. PRD works on the principal of induction of the abscisic acid (ABA) based root to shoot chemical signaling system to regulate growth under water limited conditions. On the other side these alternative watering cycles also induce the growth of secondary roots, which decreases the pressure of drought stress (Loveys *et al.*, 2001). So, this PRD thereby, increase WUE with a minimum cost of yield reduction (Davies *et al.*, 2002). PRD has been shown to be successful in grapevines conserving up to 50% of water (Stoll *et al.*, 2000; Loveys *et al.*, 2001). The alternative cycle of drying and irrigation may stimulate the mineralization of organic N, enhance aeration and moisture condition to complement microbial activities in the soil and are essential for the continuous signal networking from the root to shoot because a drought-primed root cannot sustain ABA production for a longer duration (Davies and Hartung, 2004). Shahnazari *et al.* (2008) observed stay green habit late in the season under PRD treatment in potato contributing towards high yield. In wheat and maize also an enhanced N uptake has been observed in PRD experiments (Kirda *et al.*, 2005; Li *et al.*, 2005; Li *et al.*, 2007). An increase in the number of secondary root hairs was also reported under PRD (Liang *et al.*, 1996, Mingo *et al.*, 2004). Implementation of such kind of irrigation practices at field level enhances WUE.

Although there is a reduction in total yield but the yield obtained per unit of water used in irrigation increases, which make PRD a promising tool for water scarce areas. The concept of lateral PRD (Liu *et al.*, 2006) has now been replaced with vertical PRD (Puertolas *et al.*, 2014) to understand the differential patterns of ABA accumulation under vertical and horizontal soil moisture gradients and it has been observed that horizontal partial root-zone drying (HPRD) might better trigger a long-distance ABA signal than vertical partial root-zone drying (VPRD) under conditions allowing simultaneous high (ABA) root and relatively high root water uptake (RWU) fraction (Puertolas *et al.*, 2015). So, selection and use of PRD based cultivars in breeding programs can be a fruitful approach to develop water use efficient variety.

Present scenario: Multiple strategies have been proposed to enhance the potato productivity via increasing photosynthesis, controlling stomatal conductance and understanding gene expression (Obidiegwu *et al.*, 2015). But the target of "more crop per drop" can only be achieved by increasing WUE. Potato yield is more likely to be source limited instead of sink during tuber bulking because water availability is a key production management factor and interaction between water and nitrogen influence potato yield mainly through affecting source capacity via the net photosynthetic rate, total leaf area and leaf life span (Li *et al.*, 2016). Recent biotechnological approaches provide

new alternatives to improve WUE in crop plants including potato. The search for identification of genes responsible for high water stress tolerance in potato was started in 2007 with fructosyltransferase gene, increasing fructane accumulation under water deficit condition. Because of wide genetic variations present in the plant kingdom, there is a wide scope for exploring, exploiting and engineering WUE related genes. Several genes have been identified and transformed in potato to produce highly water use efficient plants (Table.1). Recent genome analysis research of plant water use efficiency is focused on the naturally occurring variation in the isotopic composition of plants. Measurements of component traits such as leaf nitrogen content, biomass allocation, and plant hydraulic conductance are now proved as reliable tools to understand the phenotypic mechanisms associated with quality trait loci (QTL) for WUE.

Another interesting approach for enhancing WUE is the introduction of crassulacean and metabolism into C₃ plants. Water requirement for CAM is 20% of that required for C₃ or C₄ plants. Although there are several knowledge gaps to understand the temporal enzyme action and signaling pathway to control stomatal closing during day and opening at night (Tuberosa and salvi, 2006). Institute of Integrative Biology is working in collaboration with US scientists to develop a systems level view of the CAM pathway by developing a detailed understanding of the genes, proteins and metabolites involved in CAM. Comprehensive knowledge of the CAM 'parts-list' will permit forward engineering of CAM into C₃ crops. To generate crop varieties with improved WUE, suited for better production under reduced water inputs, the key rate-limiting step in ABA synthesis is 9-cis-epoxycarotenoid dioxygenase (NCED). Over-expression of NCED in plants using constitutive promoter causes increased ABA accumulation and a range of physiological changes including improved WUE. Tissue-specific over production of ABA, root-to-shoot signalling, the generation of random alterations in NCED expression and exploitation of natural allelic variation in ABA biosynthetic genes is the most extensively studied research area. Eight putative StYUC (*Solanum tuberosum* YUCCA) genes were identified and transgenic potato plants overexpressing AtYUC6 showed enhanced drought tolerance, reduced water loss and levels of reactive oxygen species in leaves. Hence, YUCCA pathway of auxin biosynthesis in potato may be exploited against abiotic environment stresses (Kim *et al.*, 2013).

Recently, in a diploid backcross progeny (DMDD) of potato, a dense genetic and physical map has been constructed with a total of 2469 markers, including single nucleotide polymorphism (SNP), simple sequence repeats (SSRs) and diversity array technology (DArT) (Sharma *et al.*, 2013). By using two parental

genetic maps constructed using this already published genotypic data, and quantitative trait locus (QTL) analysis. Khan *et al.* (2015) identified 45 genomic regions associated with nine traits in well-watered and terminal drought treatments and 26 potentially associated with drought stress both in greenhouse and field trials. They also showed that in potato QTLs reflects multigenic control of traits related to water stress conditions. A QTL was identified on chromosome 1 containing three genes encoding isoforms of cytosolic glutamine synthase genes and these were identified for controlling the nitrogen loss due to photorespiration and hence contributing towards enhanced WUE and photosynthetic efficiency in potato (Kaminski *et al.*, 2015). *S. tuberosum* has diverse wild relatives that can exchange genetic traits. These wild *Solanum* species have been used as donors for introgression of biotic and abiotic stress tolerance to *S. tuberosum* (Kikuchi *et al.*, 2015).

Conclusion

WUE is a quantitative index of drought tolerance, drought resistance, drought avoidance and many other adaptive traits. Enhancement of a polygenic trait is interplay of the interaction of multiple interactive pathways. To develop water use efficient genotype identification and selection of a drought resistance genotype which uses water efficiently under to produce more biomass and better partitioning towards sink (tuber) is the prerequisite for future breeding programs. Wild species can act as donor for this purpose. There is a need to develop a reliable technology that can measure plant WUE efficiently by using quantifiable stress indicators. Adequate RWC for longer period, decrease in meristematic activity, increased root: shoot ratio are some key screening feature for a water use efficient genotype. In parallel, identification of key molecules involved in signaling mechanism, development of new biotechnological and bioinformatics tools may help us to dissect out the whole pathway. A lot of work has been done on potato but no theoretical ideotype or conceptual model has been proposed yet for potato. In future we believe that the genes directly controlling WUE, signaling under water deficit conditions and yield will be transferred to potato for improving productivity. High throughput genotyping linked with phenotypic methods like use of infrared thermo sensors, hyperspectral imaging, visible RBG imaging, chlorophyll fluorescence imaging (CFIM) can be utilized as a scalable screening base for WUE. Current scenario of below ground research adds an idea to study the interaction of root with soil microbes because microbes are notorious enough to reshape the root physiology. Multigene transfer should be the future strategy for limited irrigation agriculture. Dissecting the genetic architecture to identify QTLs, genome editing technology, mutagenesis and transgenic development are the new areas which should be ex-

ploited for desirable modifications, so as to make a plant tolerant to environmental stresses including water stress.

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