Drought stress tolerance traits of potato

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Demand for potato is steadily rising in developing countries, where present per hectare production levels reach merely fractions of the yields achieved in Europe or North America. Many potato production areas in developing countries are located in semi-arid areas, where drought spells account for large harvest losses. In these regions, where the yields actually range around 30% of the global mean, adapted drought tolerant potato varieties could confer considerable yield increments and thus contribute to satisfy the growing demand. Physiological, biochemical and molecular analysis of tolerant and susceptible potato cultivars under water stress pinpoints traits that could mitigate yield drops caused by drought. Principal tolerance traits that could diminish the vulnerability of potato yields to drought stress include improved transpiration efficiency, which is associated with optimized stomatal control under drought to reduce water loss but at the same time allow for continuous CO_2 access for photosynthesis, enhanced detoxification of reactive oxygen species produced during stress, 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 in breeding. Future efforts could address improving photosynthetic efficiency and reducing photorespiration under drought.

Keywords: Potato, drought tolerance, photosynthesis.

Introduction

Potato is a drought-susceptible crop. Nevertheless potato water productivity on dry weight basis is twice as high as that of wheat or maize and three times higher than that of rice (Trebejo and Midmore, 1990; FAO, 2003). Drought decreases both potato yield and quality. Water stress affects potato development at virtually any stage. During early developmental stages, before tuberization, drought may reduce stolon number (Haverkort et al., 1990), while drought during tuberization decreases tuber number and during bulking tuber size (Martin et al., 1992).

Tuber yield is a function of the amount of intercepted light and water availability (Allen and Scott, 1980). Light interception depends on the photosynthetically active leaf area. The larger this area, the larger the surface exposed to transpiration. Drought generally reduces plant growth and canopy size (Deblonde and Ledent, 2001; Tourneux et al., 2003), diminishing the evaporative demand and improving plant survival under water stress. But reduced canopy results in decreased yields due to the smaller leaf area available for photosynthesis. Early leaf appearance combined with the ability to sustain leaf growth under increasing soil moisture deficit would improve productivity in the presence of drought (Jefferies and MacKerron, 1993). Deeper and denser roots would enhance water availability, where water remains available in deeper soil layers.

Maintenance of photosynthetic activity under water stress is a key element of plant drought tolerance. Under water stress, photosynthesis per leaf area is mainly restricted by stomatal and mesophyll limitations, i.e., in how far CO_2 remains available for the photosynthetic apparatus, when stomatal and mesophyll conductance is kept low to avoid excessive transpiration. Only at high stress levels non-stomatal metabolical limitations, such as reduced ribulose bisphosphate carboxylase regeneration and ATP synthesis inflict carbon assimilation under drought. However, at high irradiances RuBP is present in excess and CO_2 should remain the limiting factor for photosynthetic rate (Parry et al. 2007). Low CO_2 availability for the photosynthetic apparatus favors the oxygenase reaction of ribulose bisphosphate carboxylase and photorespiration, resulting in up to 50% reduction in carbon gain compared to well-watered conditions.

Water stress leads to increased production of active oxygen species in plant cells. While active oxygen species have regulative roles, excessive accumulation of these compounds can damage proteins and membranes. Mitigation of oxidative stress therefore can enhance plant survival under water stress.

In the last years we have investigated drought responses in tolerant and susceptible potato cultivars on agronomical, physiological, biochemical and molecular level. These investigations showed variation in water stress sensitivity in potato germplasm and pointed towards mechanisms that confer drought tolerance to this crop.

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Water use efficiency

The amount of harvested biomass per unit of transpired water (i.e., water use efficiency - WUE) under drought and well-watered conditions is a genotype-dependent trait. Large variation of WUE has been found in potato (Fig. 1). Appropriate stomatal control is one of the keys for high water use efficiency. Plants with high WUE would be highly suitable to increase yields where water resources are scarce. An important component of WUE is the regulation of abscissic acid biosynthesis and sensitivity of the plant. Together with an array of other factors, abscissic acid co-regulates growth and stomatal behavior (reviewed by Wasilewska et al. 2008). The right balance between abscissic acid accumulation and sensitivity of the plant is crucial for activating tolerance mechanisms against drought without completely inhibiting plant growth. Variation in abscissic acid content in potato germplasm under drought has not yet been systematically assessed.

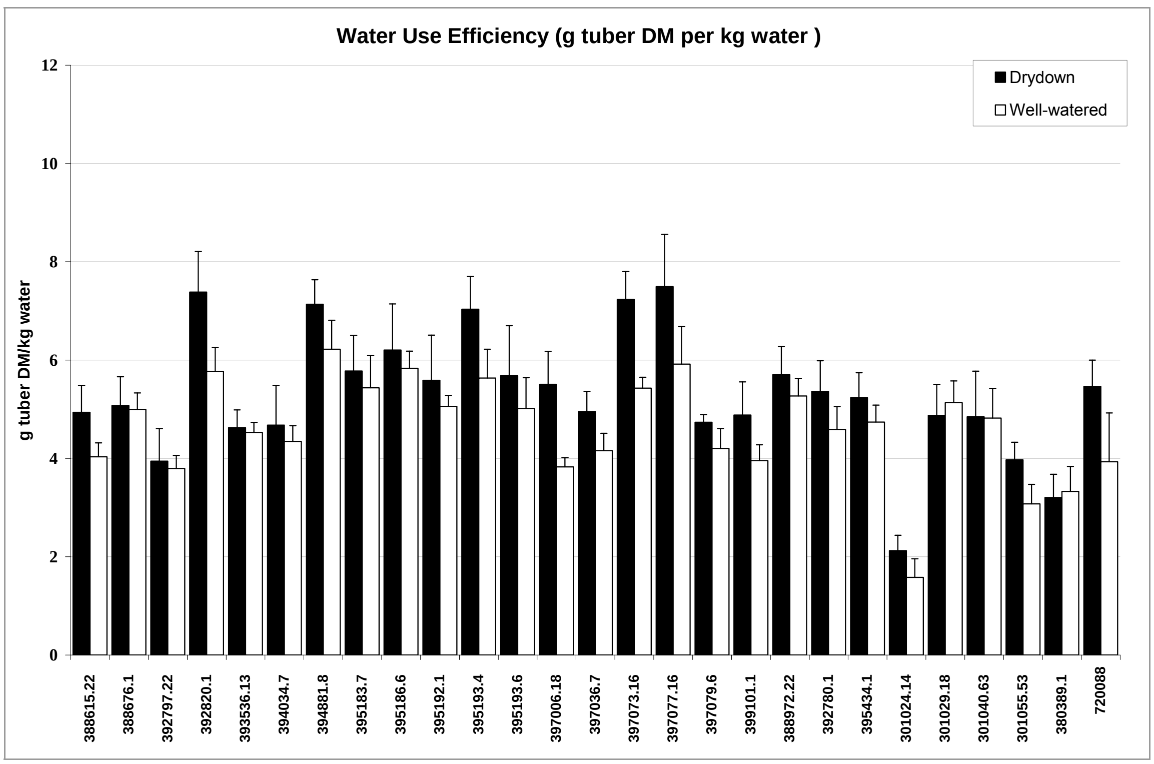

Figure 1. Variation of water use efficiency under well-watered and drought conditions in improved CIP potato clones. Water use efficiency was determined at CIP according to Krishnamurthy et al. (2007). DM: dry matter.

Increased harvest index under drought

Stress might alter carbon allocation to different tissues. Under heat, carbon transport to tubers is restricted; instead, above ground tissues act as sink for sugars, resulting in sugar-mediated reduction of photosynthesis and reduced tuber growth (Lafta and Lorenzen 1995, Timlin et al., 2006, Basu and Minhas, 1991). Similarly drought alters carbon partitioning in potato. Allocation of sugars to tubers varies under drought and both increase and decrease of harvest index is observed in a genotype-dependent manner (Fig. 2). For drought prone areas, genotypes with increasing harvest index under drought would be preferred.

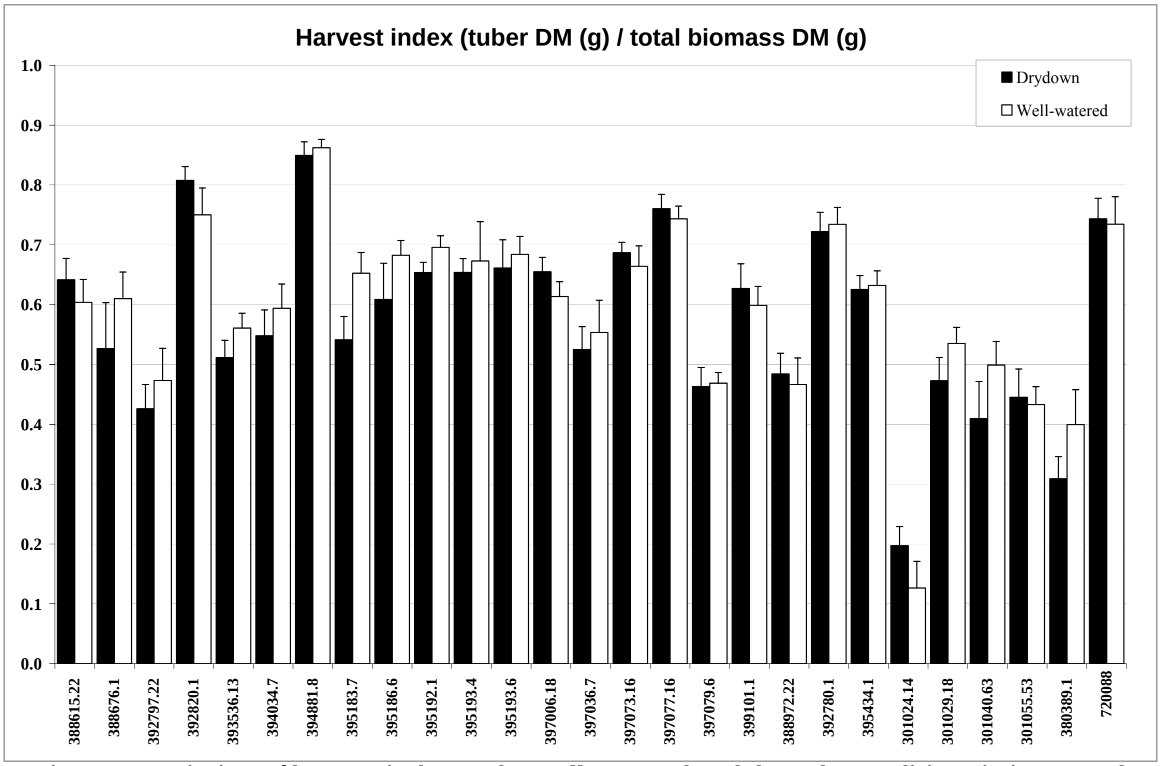

Figure 2. Variation of harvest index under well-watered and drought conditions in improved CIP potato clones under drought and well watered conditions.

Increased root size

Some potato genotypes have the capacity to increase root size under drought. Together with reduction of canopy size under water stress, this might lead to dramatically increased root/shoot size ratios in some genotypes. Genotypes with increased root/shoot size ratios support drought better and generally have less yield loss under water stress than clones that lack the capacity to enlarge their root system under water stress conditions.

Detoxification of reactive oxygen species

Reactive oxygen species are produced by the Mehler reaction and by the antenna pigments, during photorespiration and detoxifying reactions catalyzed by cytochromes, as well as in oxidative processes in mitochondria (Asada and Takahashi 1987). They act as signaling molecules for regulating development and various physiological responses (Miller et al., 2008). Under stress, reactive oxygen species accumulate and can reach toxic levels in the plant. Reactive oxygen scavengers like superoxide dismutase, ascorbate peroxidase, catalase, glutathione peroxidase, peroxiredoxin and others can mitigate the toxic effects of these molecules (Watkinson et al., 2006, Schafleitner et al., 2007, Mane et al., 2008). Under drought, we have observed up-regulation of an array of putative active oxygen scavengers acting in the chloroplast. Moreover, an antiquitin family aldehyde dehydrogenase 7 gene was found induced in drought tolerant potato cultivars only. In model plants this gene is involved in the detoxification of reactive aldehyde species generated by oxidative stress-associated lipid peroxidation (Rodrigues 2006). This gene would be a good candidate for mitigating oxidative stress in mitochondria.

Osmotic adjustment

Decrease of osmotic potential in plant tissues as a consequence of solute accumulation is often observed in potato plants under drought stress. Although the contribution of osmotic adjustment for increased water uptake from drying soils is very limited (Serraj and Sinclair 2002), decrease of osmotic potential is considered as a desirable trait in plant drought tolerance (Levy 1983, Jefferies 1993, Heuer and Nadler 1998). Osmotic adjustment contributes with turgor maintenance under increasing water deficit and the accumulating osmolytes act also as protein and membrane protectors (reviewed by Yancey 2005). Particularly under transient water stress, osmotic adjustment might improve plant survival and regeneration. Many metabolites have been proposed to contribute to osmotic adjustment, including metal ions, organic acids, polyamines, sugars, sugar alcohols, amino acids and their derivates, and proteins (Handa 1983).

Stabilization of proteins and membranes

Protein and membrane-stabilizing properties have been attributed particularly to late embryo abundant (LEA) and dehydrin proteins whose expression is strongly induced under drought stress (Schafleitner et al., 2007). Another protein group probably involved in protein stabilization and re-folding are chaperones such as DnaJ family and heat shock proteins. Genes encoding these proteins are highly expressed under drought stress and could be associated with tolerance (Watkinson et al., 2006, Schafleitner et al., 2007).

Conclusions

The present knowledge on water stress tolerance in potato points towards several candidate traits that could be used for breeding drought tolerant potato varieties. 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 and to better understand the trade-offs such as the yield penalty caused by a tolerance trait, thorough agronomical analysis of genotypes expressing these candidate traits in different drought environments will be required.

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