Review Paper

Breeding for tolerance to heat stress and on changing environment: A case study on Potato

Abstract

Potato crop is the fourth leading food crops in the world after maize, rice, and wheat. It is characterized by specific temperature requirements and develops best at about 20°C. Temperature is one of the essential uncontrollable factors affecting crop yield and heat stress has become a serious concern in many areas of the world. As most commercial potato cultivars are developed in temperate regions, therefore producing the greatest yield under long photoperiods and high temperatures is a serious problem. Thus our need increases for developing potato germplasm that can tolerate these adverse conditions. However, the development of new methodology, such as association genetics in conjunction with marker-assisted selection, offers promise that stress-tolerant germplasm can be developed as our need increases.

Keyword: Potato (*Solanum tuberosum* L.); heat stress; growth; development; tuber yield.

Introduction

Potato, *Solanum tuberosum* L. (2n=4x=48) is an essential and fourth most important food crop in the world, globally grown under different climatic conditions. Potato has its origin in the Andean region of Peru and Bolivia in South America of the New World. The productivity of potato in India came down from 23.13 t/ha (NHRDF Nasik, 2013-14) to 23.07 t/ha (NHRDF Nasik, 2015-16), and the possible reasons behind this reduction perhaps due to more impact of biotic and abiotic stress. Analysis of recent climate trend suggests that temperature in potato production areas worldwide are increasing and the severity of episodes of above optimal temperature will increase in the coming decades. It is a cool-season crop, and the highest yields are obtained in regions with an optimal growth temperature of approximately 20°C. Using simulation model-based predictions of global warming over the next 60 years, Hijmans (2003) predicted potato yield losses in the range of 18 to 32%. The increasing threat of changing environment is anticipated to have a catastrophic loss of crop productivity that will result in a widespread famine.

Temperature is one of the most essential uncontrollable factors affecting crop yield and heat stress is an agricultural problem in many areas in the world. According to Wahid *et al.*, (2007) 'transitory' or constantly high temperatures cause an array of morpho-anatomical, physiological and biochemical changes in plants which affects plant growth and development and may lead to a drastic reduction in economic yield. The acceleration of stem growth with assimilate partitioned more toward the stem; the reduction of photosynthesis and increase of respiration; reduction of root growth; inhibition of tuber initiation and growth; frequent tuber disorders; reduction of tuber dry matter and increase of glycoalkaloid level is the adverse effects of high temperatures on potato (Struik, 2007). Generally, a transient elevation in temperature, usually 10-15°C above ambient, is considered to be the heat stress.

Heat and drought are most prevailing abiotic stresses affecting crop production, so this situation necessitates orientation of a research programme for the development of varieties tolerant to high-temperature stress. Traditionally, plant breeders have addressed the problem of environmental stress by selecting for suitability of performance over a series of environmental conditions using extensive testing and biometrical approaches. The inheritance of abiotic stress resistance is likely to be multigenic, a factor that may limit the utility of transgenic approaches to stress tolerance. However, the development of new methodologies, such as association genetics in conjunction with marker-assisted selection, offers promise that stress-tolerant germplasm which can be developed as our need increases.

The physiological consequence of heat stress on potato:

a) **Effect on tuber initiation:** The optimal temperature for tuber formation is 20°C. The slower tuberization at temperatures lower than 20°C probably results from slowed metabolism and growth, whereas the delayed tuberization at 25°C, when metabolism and growth are accelerated, is due to the specific inhibitory effects of the high temperature on the tuberization process.

b) **Effect on Yield:** Low temperatures, especially low night temperatures increase the number of tubers per plant. At higher temperatures when fewer tubers per plant are formed larger tubers are obtained. Although increases in either day or night temperatures above optimal levels reduce tuber yields, high night temperatures seem to be more deleterious. Higher soil temperatures decreased tuber yields, especially when combined with high ambient air temperatures (30°C day/23°C night).

c) **Effect on bulking rate:** After tuber initiation, both the weight and volume of the tubers increase almost linearly, a process referred to as tuber bulking. Although many tubers may be initiated during the first four to six weeks of growth, only a fraction of these tubers achieves commercial size (greater than 30 mm diameter). Bulking rate is greater for short days and moderate temperatures. Long days and higher temperatures favor dry matter partitioning to the haulm, promote haulm and root growth and delay tuber growth.

d) **Production of hormones:** Growth substances are involved in the plant response to environmental factors. Gibberellic acid (GA), endogenously increased under long days, generally inhibits tuber formation, whereas cytokinins and abscisic acid (ABA) have been shown to promote tuber formation. Jasmonic acid and related compounds (tuberonic acid and its glucoside) have also been reported as tuber-inducing under in vitro conditions (Koda, 2002).

e) **Partitioning of Assimilates:** Temperature has a prominent effect on the partitioning of assimilates to the different parts of the potato plant. High temperature reduces partitioning of assimilates to the tubers and enhance partitioning to the haulm. A high ratio of GA/ABA promotes haulm growth and inhibits tuber growth, whereas a relatively low ratio limits vine growth and promotes tuber growth, a finding that has recently been confirmed by the construction of transgenic potato plants expressing a transcription factor (POTH1) that reduces GA expression and enhances tuberization (Hannapel *et al.,* 2004).

f) **Physiological disorders:** Some physiological tuber disorders that are closely associated with heat stress are- Internal brown spots, also known as internal rust spots or chocolate spots are manifested as necrotic brown spots in the tuber parenchyma in response to high temperature (Iritani *et al.,* 1984). Heat necrosis, a brown discoloration of the vascular ring occurs at high soil temperatures. This necrosis varies with the severity of stress, tuber developmental stage, cultivar and environmental conditions (Henninger *et al.,* 2000; Sterrett *et al.,* 2003). High temperatures also cause irregular tuber shape, chain tuberization or secondary tuber formation (often associated with excessive stolon elongation and branching), sprouted tubers and reduced dry matter content (Marinus and Bodlaender 1975).

g) **Tuber dormancy:** High temperatures during tuber maturation may interfere with the onset of tuber dormancy, shorten their rest period, or even release the inhibition of tuber buds, resulting in pre-harvest sprouting. This is likely associated with an increase of the endogenous content of growth-promoting substances such as gibberellins.

The concept and mechanism of heat tolerance: To overcome heat stress the following measures are adopted during growing period.

Heat escape: The ability of a crop plant to complete its life cycle before development of serious soil and plant water deficits is called as heat escape. This mechanism involves rapid phenological development i.e. early flowering and maturing, variation in the duration of growth period depending on the extent of water scarcity.

Heat avoidance: Heat avoidance is the ability of plants to maintain relatively high tissue water potential despite a shortage of soil moisture. The heat stress avoidance mechanisms are associated with physiological whole plant mechanisms such as canopy tolerance and leaf area reduction (which decrease radiation, adsorption and transpiration), stomatal closure and cuticular wax formation, adjustments of sink-source relationships through altering root depth and density, root hair development and root hydraulic conductance (Rivero *et al.,* 2007).

Heat tolerance: Plants alter their metabolism in various ways in response to heat stress, especially by producing compatible solutes that are able to organize proteins and cellular structures, maintain cell turgor by osmotic adjustment, and modify the antioxidant system to re-establish the cellular redox balance and homeostasis (Valliyodan and Nguyen, 2006; Munns and Tester, 2008; Janska *et al.,* 2012). Minha *et al.,* (2006) has reported that Kufri Surya is expected to be the most popular variety for early planting in north western plains as well as in rabi and kharif crops in peninsular India. It germinated well under high relative humidity (>90%) and established a vigorous crop canopy when compared with control.

Genetic mechanism for heat tolerance in potato:

Heat tolerance is a complex character, expression of which depends on accomplishment and interaction of various morphological traits viz. earliness, reduced leaf area, leaf molding, wax content, efficient rooting system, stability in yield and number of branches;physiological traits i.e. transpiration, water-use efficiency, stomatal activity and osmotic adjustment and biochemical traits i.e. accumulation of proline, polyamine, trehalose etc., increasing of nitrate reductase activity and storage of carbohydrate. Besides morphological and physiological changes, biochemical changes involving biosynthesis of compatible solutes (fructan, trehalose, polyols, glycine betaine, proline and polyamines) is another way to impart heat stress (Mitra, 2001). Heat stress at relevantly high temperatures produces ROS (superoxide radicals, hydroxyl radicals, and hydrogen peroxide). Tolerant plants protect themselves from the damaging effects of ROS with the synthesis of various antioxidant components which control gene expression and influence essential processes such as growth, abiotic stress responses, and pathogen defense (Abiko *et al.,* 2005).

Conventional breeding methods for heat tolerance in potato:

When breeding for stress tolerance, often it is necessary that the derived lines/cultivars be able to perform well under both stress and non-stress conditions. The upper limit of heat tolerance in heat-tolerant lines should be fully characterized before using them in combination breeding programmes. However, the desirable traits which should be included in the heat-tolerance breeding programmes are high water-use efficiency, increased root and early maturity to escape heat and disease resistance. The heat stress tolerance in potato is controlled by multigenes.

The use of seed tubers introduces yetanother confounding effect, namely tuber dormancy. Genotypes vary for length of tuber dormancy, making it difficult to synchronize the physiological status of seed tubers to a specific planting date. Youngtubers emerge at a slower pace, tend to produce fewer stems and tuberize and mature late, while older tubers emerge rapidly, develop more stems and tuberize and mature earlier which may alter the response to stress.

The Role of Heat Shock Proteins and other Candidate Genes in Heat Tolerance:

Plants have evolved a number of adaptive mechanisms that enable them to alleviate the negative effects of high temperature stress or heat stress (HS) (Larkindale *et al.,* 2005; Wahid *et al.,* 2007). One such mechanism is the synthesis of heat shock proteins (HSPs). HSPs play a central role in plant heat tolerance by acting as molecular chaperones; i.e., they promote the refolding of heat-denatured proteins or form complexes with denatured proteins and protect them from irreversible thermal aggregation (Basha *et al.,* 2004). The role of HSPs during heat stress involves the formation of complexes with heat-denatured proteins. Small HSPs could be used as markers for detecting HT genotypes. Based on differential expression observed in heat-tolerant and heat-sensitive cultivars, the employment of HSPs as potential heat tolerance markers has been proposed, so far, for barley and wheat.

To assess the heat tolerance in nine commercial potato cultivars (Savic *et al.,* 2012) used electrolyte leakage assay and reported that ELA combined with immunoblot analysis of HSPs accumulation under HS conditions could be considered as a reliable procedure in screening potato genotypes for heat tolerance and for the identification of heat tolerantpotato cultivars. In addition, HSP18 and HSP21 expression under HS present similar patterns in potato plants grown in vitro compared to ex-vitro grown plants, opening up the possibility for the use of an in-vitro culture for heat tolerance screening.

Molecular and biotechnological steps for development of material for heat tolerance:

Genetic enhancement using molecular marker technology has revolutionized plant breeding (Collins *el al.,* 2008; Lei *et al.,* 2011). Various ingredients of resistance, handled by various sets ofgenes are vital for heat resistance at various steps ofcrop growth or in diverse tissues (Bohnert *et al.,* 2006). Therefore, the use of geneticstocks with diverse levels of heat resistance, cosegregation and correlation analyses, molecular biology methods, molecular markers and quantitativetrait loci (QTLs) are promising attributes to detect thegenetic source of thermo-resistance (Maestri *et al.,* 2002). Recent widely studied molecular approaches have included omics techniques and the development of transgenic plants throughmanipulation of target genes (Kosova *et al.,* 2011; Duque *et al.,* 2013). Investigationof these underlying molecular processes mayprovide ways to develop stress tolerant varieties andto grow them under heat stress conditions. Molecular marker analysis for stress tolerance in vegetables is limited but an effort is underway to identify QTLsunderlying tolerance to abiotic stresses.

The key benefit of QTL based approaches is that they allow loci to be identified that are linked to heat tolerance. The identification of markers linked to QTLs enables breeding of stress-tolerant crops by combining or "pyramiding" QTLs for tolerance to various stresses. Several QTL studies relating to various abiotic stress tolerances have already been reported (Hirayama and Shinozaki, 2010).

An effective set of thermo tolerance markers can also be used to further implement heat tolerance into various crop species**.** Molecular genetic markers are an example of how an effective tool is used to analyze plant genomes and how heritable traits associate to their underlying genetic variation. Sequence-based (microarrays) or anonymous molecular marker systems [amplified fragment length polymorphism (AFLP), ISSR, SSR and other equal effectives] are often employed in applications of modern plant genetic analysis.

Conclusion:

Environmental constraints and the threat of global warming challenge the scientific community to use its understanding of potato physiology and genetics to develop new cultivars that resist both the stress of growing under high temperatures. Because of its importance in the human diet, potato growth and development have received considerable scientific attention, especially the regulation of tuber development. The trend of potato production has been toward greater acreage in warm climates using cultivars that were developed for production in cool climates. Major limitations for potato production in these regions are high temperatures and the scarcity of fresh water resources for irrigation. Hence, the study of abiotic stress on the potato crop has assumed substantial importance. Fortunately, the germplasm base for potato is large and assessments of germplasm performance under challenging conditions have revealed new possibilities.Taken together with the increased knowledge of molecular biology of the potato and of genes responsible for stress resistance, the outlook is promising for our ability to meet the challenge of improving potato yield in nontraditional and stress-prone environments.In the view of the predicted population growth and the resulting increasing requirement for food security, it is up to the scientific community to adapt crop species for high tolerance to abiotic stresses and in particular high temperature stress. A more complete insight of the biological processes behind the heat stress response combined with classical and emerging technologies in plant breeding and genetic engineering is likely to make a significant contribution to improved crops.

References:

Abiko, M., Akibayashi, K., Sakata, T., Kimura, M., Kihara, M. and Itoh, K. 2005. High-temperature induction of male sterility during barley (*Hordeum vulgare* L.) anther development is mediated by transcriptional inhibition. *Sex Plant. Reprod*. **18**: 91-100.

Ahn, Y. J.,Claussen, K. and Zimmerman, J. L. 2004. Genotypic differences in the heat-shock response and thermotolerance in four potato cultivars. *Plant Sci*. **166**: 901-911.

Basha, E., Lee, G.J., Demeler, B. and Vierling, E. 2004. Chaperone activity of cytosolic small heat shock proteins from wheat. *Eur. J. Biochem*. **271**: 1426-1436.

Bohnert, H. J., Gong, Q., Li, P. and Ma, S. 2006. Unraveling Abiotic Stress Tolerance Mechanisms-Getting Genomics Going. *Curr. Opin. Plant Biol*. **9**: 180-188.

Collins, N. C., Tardieu, F. and Tuberosa, R. 2008. Quantitative Trait Loci and Crop Performance under Abiotic Stress: Where do we Stand?, *Plant Physiol*. **147**: 469-486.

Duque, A. S., De, A. M., Da Silva, A. B., Da Silva,J. M., Farinha, A. P., Santos, D., Fevereiro, P. and De Sousa, A. S. 2013. Abiotic Stress Responses in Plants: Unravelling the Complexity of Genes and Networks to Survive in Abiotic Stress-Plant Responses and Applications inAgriculture, *Vahdati K, Leslie C (eds). In Tech., Rijeka, Croatia*. p. 3–23.

Hannapel, D. J., Chen, H., Rosin, F. M., Banerjee, A. K. and Davies, P. J. 2004. Molecular controls of tuberization. *American J. Potato Res.* **81**: 263-274.

Henninger, M. R., Sterrett, S. B. and Haynes, K. G. 2000. Broad-sense heritability and stability of internal heat necrosis and specific gravity in tetraploid potatoes. *Crop Sci*. **40**: 977-984.

Hijmans, R. J. 2003. The effect of climate change on global potato production. *Am. J. Potato Res.* **80**: 271-280.

Hirayama, T. and Shinozaki, K. 2010. Research on plant abiotic stress responses in the post-genome era: past, present and future. *Plant J.* **61**: 1041-1052.

Iba, K. 2002. Acclimative response to temperature stress in higherplants: Approaches of gene engineering for temperature tolerance. *Annu. Rev. Plant Biol.* **53**:225-245.

Iritani, W. M., Weller, L. D. and Knowles, N. R. 1984. Factors influencing incidence of internal brown spot in Russet Burbank potatoes.*American Potato J.* **61**:335-343.

Janska, A., Marsik, P., Zelenkova, S. and Ovesna, J. 2012. Cold Stress and Acclimation: What is Important for Metabolic Adjustment? *Plant Biol*. **12**: 395-405.

Koda, Y. 2002. Involvement of jasmonic acid and related compounds in various morphogenic events of crops. *Jpn. J. Crop Sci.*__71__:1-10.

Kosova, K., Vitamvas, P., Prasil, I. T. and Renaut, J. 2011. Plant Proteome Changes under AbioticStress-Contribution of Proteomics Studies toUnderstanding Plant Stress Response.*J. Proteom.*__74__: 1301-1322.

Larkindale, J., Mishkind, M. and Vierling,E. 2005. Plant responses to high temperature.*In: Plant Abiotic Stress* (Eds. M. Jenks, and P. Hasegawa).100-144. Blackwell, Oxford.

Lei, L., Yan, S. and Jun-Ming, L. I. 2011. Mapping ofQTLs for Drought Tolerance during Seedling Stageusing Introgression Line Populations in Tomato. *Acta Hort. Sin*. **38**: 1921-1928.

Maestri, E., Klueva, N., Perrotta, C., Gulli, M., Nguyen, H. T. and Marmiroli, N. 2002. Molecular Geneticsof Heat Tolerance and Heat Shock Proteins in Cereals.*Plant Mol. Biol*. **48**: 667-681.

Marinus, J. and Bodlaender, K. B. A. 1975. Response of some potato varieties to temperature. *Potato Res*. **18**:189-20.

Minha, J. S., Kumar.,D., Joseph, T. A., Pandey, S. K., Raj, B. T., Singh, S.V., Singh, B. P, and Naik, P. S. 2006. Kufri Surya: A new heat tolerant potato variety suitable for early planting inNorth-Western plains, Peninsular India and Processing into French fries and chips. *Potato J.* **33**: 35-43.

Mitra, J. 2001. Genetics and genetic improvement of drought resistance in crop plants.*Curr. Sci.* **80**(6): 758-763.

Munns, R. and Tester, M. 2008. Mechanisms of Salinity Tolerance.*Ann. Rev. Plant Biol*.**59**: 651-681.

National Horticultural Research And Development Foundation: Area and production data for potato, http://nhrdf.org/en-us/AreaAndProductiionReport.

Rivero, R. M., Kojima, M., Gepstein, A., Sakakibara, H., Mittler, R., Gepstein, S. and Blumwald, E. 2007. Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proc. Natl. Acad. Sci. U.S.A*. **104**:19631-19636.

Savic.J., Dragicevic, I. C. and Pantelic, D. 2012. Expression of small heat shock proteins and heat tolerance in potato (*Solanum tuberosum* L.) *Archives of Biological Sci*. **64**: 135-144.

Sterrett, S. B., Henninger, M. R., Yencho, G. C. and Haynes, K. G. 2003. Stability of internal heat necrosis and specific gravity in tetraploid x diploid potatoes. *Crop Sci.***43**:790-796.

Struik, P.C. 2007. Responses of the potato plant to temperature In: Plant Biology and Biotechnology: *Advances and Perspective (Ed. D. Vreugdenhil)*.367-393. Elsevier, Amsterdam.

Valliyodan, B. and Nguyen, H. T. 2006. Understanding Regulatory Networks and Engineering for Enhanced Drought Tolerance in Plants. *Current Opin. Plant Biol*. **9**: 189-195.

Wahid, A., Gelani, S., Ashraf, M. and Foolad, M.R. 2007. Heat Tolerance in Plants: An Overview.*Environ. Expt. Bot*. **61**: 199-223.

Wang, W.X., Vmocur, B., Shoseyov, O. and Altman, A. 2004. Role of plant heat-shock proteins and molecular chaperones in the abioticstress response. *Trends Plant Sci*.**9**:244-252.

Craita E. Bita, Tom Gerats, Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front. Plant Sci., 31 July 2013 | https://doi.org/10.3389/fpls.2013.00273