

1 Review Paper

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

4
5 Abstract

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

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

17
18 Introduction

19 Potato, *Solanum tuberosum* L. ($2n=4x=48$) is an important and fourth most important
20 food crop in the world, globally grown under different climatic conditions. Potato has its
21 origin in the Andean region of Peru and Bolivia in South America of the New World. The
22 productivity of potato in India came down from 23.13 t/ha (NHRDF Nasik, 2013-14) to 23.07
23 t/ha (NHRDF Nasik, 2015-16), and the possible reasons behind this reduction maybe due to
24 more impact of biotic and abiotic stress. Analysis of recent climate trend suggests that
25 temperature in potato production areas worldwide are increasing and the severity of episodes

26 of above optimal temperature will increase in the coming decades. It is a cool-season crop
27 and the highest yields are obtained in regions with an optimal growth temperature of
28 approximately 20°C. Using simulation model-based predictions of global warming over the
29 next 60 years, Hijmans (2003) predicted potato yield losses in the range of 18 to 32%. The
30 increasing threat of changing environment is predicted to have a catastrophic loss of crop
31 productivity that will result in a wide spread famine.

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

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

51 **Physiological consequence of heat stress on potato:**

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

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

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

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

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

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

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

99 **The concept and mechanism of heat tolerance:** To overcome heat stress the following
100 measures are adopted during growing period-

- 101 i. **Heat escape-** The ability of a crop plant to complete its life cycle before development
102 of serious soil and plant water deficits is called as heat escape. This mechanism
103 involves rapid phenological development i.e. early flowering and maturing, variation
104 in the duration of growth period depending on the extent of water scarcity.
- 105 ii. **Heat avoidance-** Heat avoidance is the ability of plants to maintain relatively high
106 tissue water potential despite a shortage of soil moisture. The heat stress avoidance
107 mechanisms are associated with physiological whole plant mechanisms such as
108 canopy tolerance and leaf area reduction (which decrease radiation, adsorption and
109 transpiration), stomatal closure and cuticular wax formation, adjustments of sink-
110 source relationships through altering root depth and density, root hair development
111 and root hydraulic conductance (Rivero *et al.*, 2007).
- 112 iii. **Heat tolerance-** Plants alter their metabolism in various ways in response to heat
113 stress, especially by producing compatible solutes that are able to organize proteins
114 and cellular structures, maintain cell turgor by osmotic adjustment, and modify the
115 antioxidant system to re-establish the cellular redox balance and homeostasis
116 (Valliyodan and Nguyen, 2006; Munns and Tester, 2008; Janska *et al.*, 2012). Minha
117 *et al.*, (2006) has reported that Kufri Surya is expected to be the most popular variety
118 for early planting in north western plains as well as in rabi and kharif crops in
119 peninsular India. It germinated well under high relative humidity (>90%) and
120 established a vigorous crop canopy when compared with control.

121 **Genetic mechanism for heat tolerance in potato:**

122 Heat tolerance is a complex character, expression of which depends on accomplishment
123 and interaction of various morphological traits viz. earliness, reduced leaf area, leaf molding,
124 wax content, efficient rooting system, stability in yield and number of branches; physiological
125 traits i.e. transpiration, water-use efficiency, stomatal activity and osmotic adjustment and

126 biochemical traits i.e. accumulation of proline, polyamine, trehalose etc., increasing of nitrate
127 reductase activity and storage of carbohydrate. Besides morphological and physiological
128 changes, biochemical changes involving biosynthesis of compatible solutes (fructan,
129 trehalose, polyols, glycine betaine, proline and polyamines) is another way to impart heat
130 stress (Mitra, 2001). Heat stress at relevantly high temperatures produces ROS (superoxide
131 radicals, hydroxyl radicals, and hydrogen peroxide). Tolerant plants generally protect
132 themselves from the damaging effects of ROS with the synthesis of various antioxidant
133 components which control gene expression and influence essential processes such as growth,
134 abiotic stress responses, and pathogen defense (Abiko *et al.*, 2005).

135 **Conventional breeding methods for heat tolerance in potato:**

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

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

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

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

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

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

170 Genetic enhancement using molecular marker technology has revolutionized plant
171 breeding (Collins *et al.*, 2008; Lei *et al.*, 2011). Various ingredients of resistance, handled by
172 various sets of genes are vital for heat resistance at various steps of crop growth or in diverse
173 tissues (Bohnert *et al.*, 2006). Therefore, the use of genetic stocks with diverse levels of heat
174 resistance, cosegregation and correlation analyses, molecular biology methods, molecular
175 markers and quantitative trait loci (QTLs) are promising attributes to detect the genetic source

176 of thermo-resistance (Maestri *et al.*, 2002). Recent widely studied molecular approaches have
177 included omics techniques and the development of transgenic plants through manipulation of
178 target genes (Kosova *et al.*, 2011; Duque *et al.*, 2013). Investigation of these underlying
179 molecular processes may provide ways to develop stress tolerant varieties and to grow them
180 under heat stress conditions. Molecular marker analysis for stress tolerance in vegetables is
181 limited but an effort is underway to identify QTLs underlying tolerance to abiotic stresses.

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

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

193 **Conclusion:**

194 Environmental constraints and the threat of global warming challenge the scientific
195 community to use its understanding of potato physiology and genetics to develop new
196 cultivars that resist both the stress of growing under high temperatures. Because of its
197 importance in the human diet, potato growth and development have received considerable
198 scientific attention, especially the regulation of tuber development. The trend of potato
199 production has been toward greater acreage in warm climates using cultivars that were
200 developed for production in cool climates. Major limitations for potato production in these

201 regions are high temperatures and the scarcity of fresh water resources for irrigation. Hence,
202 the study of abiotic stress on the potato crop has assumed substantial importance. Fortunately,
203 the germplasm base for potato is large and assessments of germplasm performance under
204 challenging conditions have revealed new possibilities. Taken together with the increased
205 knowledge of molecular biology of the potato and of genes responsible for stress resistance,
206 the outlook is promising for our ability to meet the challenge of improving potato yield in
207 nontraditional and stress-prone environments. In the view of the predicted population growth
208 and the resulting increasing requirement for food security, it is up to the scientific community
209 to adapt crop species for high tolerance to abiotic stresses and in particular high temperature
210 stress. A more complete insight of the biological processes behind the heat stress response
211 combined with classical and emerging technologies in plant breeding and genetic engineering
212 is likely to make a significant contribution to improved crops.

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