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Review Article

RESPONSE OF POTATO TO HEAT STRESS AND STRATEGIC METHODS TO COPE WITH IT

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ABSTRACT

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. However, low land tropical regions are characterized by high temperatures that limit successful potato cultivation. High temperatures in potato promote haulm growth and suppress tuber production, whereas disbudding and paclobutrazol have the opposite effect, promoting tuber production and reducing the growth of the haulms by inhibiting GA biosynthesis which was increased by high temperature. In addition, the germplasm base for potato is large and assessments of germplasm performance under challenging conditions have revealed new possibilities.

Keywords: Heat, Disbudding, Paclobutrazol, Potato.

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INTRODUCTION

Potato (*Solanum tuberosum* L.) is one of the most valuable crops in the world. In volume of world crops production, it ranks fourth following wheat, maize, and rice and took first rank from root and tuber crops (Douches, 2013). It is a rich source of nutrients about 79% water, 18% starch as a good source of energy, 2% protein and 1% vitamins including Vitamin C, minerals including calcium and magnesium and many trace elements (Ahmad *et al*. 2011).

Potato (*S. tuberosum* L.) is categorized in Solanaceae family and genus Solanum (Thompson and Kelly, 1972). It is believed to be originated and native to continent of South America (Eskin and Michael, 1989). Reports indicated that the introduction of potato to Ethiopia is in the year 1859 (Berga *et al*. 1994b). The cultivation of potato in Ethiopia was not wide and restricted only to homesteads for many years. Ethiopia with diverse agro ecology, suitable environmental and soil condition fits potato production, but the area cverage of production is estimated to be only about 66,926 ha and with national average yield of 13.8 t ha^{-1}, which is very low compared to the world's average yield of 19 t ha^{-1} (CSA, 2017). This low yield of potato is associated with different factors mainly lack of improved varieties, less availability and cost of seed, poor agronomic management, pest attack, poor post-harvest handling, and lack of adequate market facilities (Tekalign and Hammes, 2005).

Potato prefers cool temperature between 16 and 25°C that favor foliage growth, better photosynthesis, and tuberization (Levy, 1992). High temperature is one of the factors affecting the expansion of potato across different parts of the world (Levy, 1986). In Ethiopia, about 35% of semi-arid areas are considered suitable for potato production, but its cultivation is not practiced due to high temperatures across the months of the year. High temperatures in potato crops cause low production of assimilates, delayed tuberization, and low distribution of assimilates to tubers. Due to this, high temperature across tropics is considered the limiting factor in potato production (Menzel 1980; Vandam *et al*. 1996).

Formation of stolon is the prime stage of tuber formation which is the source of tuberization in its sub apical region (Booth, 1963). Environmental factors, mainly temperature and photoperiod are the factors affecting these processes (Slater, 1968). An early tuber growth in potato is associated to low mean temperatures (15–19°C) under a short photoperiod (12 h) (Vandam *et al*. 1996). In these conditions, growth and bulking are early, in addition absolute tuber growth rates and dry matter partitioning higher. Conversely, higher temperatures enhanced leaf growth, less assimilate partitioning, delayed tuber initiation and bulking, decreased absolute growth rate, and net photosynthesis happens in increasing dark respiration (Levy, 1992; Vandam *et al*. 1996). Some cultivars are more sensitive to high temperatures than are others (Khedher and Ewing, 1985). Nevertheless, it seems safe to say that for all genotypes, high temperatures, like long photoperiods, decrease the partitioning of assimilates to tubers, but an increase of partitioning to other parts (Wolf *et al*. 1990).

The inhibition of tuberization by high temperature is considered to be enhanced through the production of high levels of endogenous gibberellins (Menzel, 1983) which is believed to delay or negatively alter tuberization (Vreugdenhil and Sergeeva, 1999). The hormonal activity affecting potato tuberization can be altered by using chloroethylammonium chloride (CCC) (Menzel, 1980), and paclobutrazol (PBZ) (Tekalign and Hammes, 2005b).

Pruning by manual and commercially available chemical agents serve as a useful alternative. Both 2, 3, 5-tri-iodobenzoicacid and maleic hydrazide effectively inhibits bud development (the site of GA biosynthesis) at the lower amount and cause death of the buds at higher concentrations (Sachs and Hackett, 1972). Fatty alcohols such as 1-decanol and the lower alkyl esters such as C_6-C_{10} fatty acids can be used to selectively kill or inhibit bud development without damaging stem or leaf tissue (Cathey *et al*. 1966). These substances are mainly contact phytotoxins, which enter through the cuticle and destroy underlying tissues by rupturing cell membranes. Their selective action is dependent on differences in cuticle structure and susceptibility of the buds (Dicks, 1976).

Cultivars development which have tolerance to high temperatures has been tried and achieved by integrating sources of tolerance in to the cultivated potato through conventional breeding (David and Richard, 2007). Hence, the aim of this review is to determine response of potato to high temperature and measures taken to cope with such stress, which has become highly important in mitigating the impact of global warming.

POTATO RESPONSE TO HEAT STRESS

Sprout development

Smith (1968) described that from the environmental factors affecting plant growth and development, temperature is the single factor which is uncontrolled and seriously affecting growth and yield of potatoes. On a controlled environmental condition, the development of seed tubers above soil surface requires a temperature between 6°C and 18°C to optimum stem elongation (Borah and Milthrope, 1962). The growth of haulm is faster at high temperatures of 27°C in which the ratio of stem to weight of leaves is higher as the temperature is beyond the optimum level for leaf development (12–14°C).

Tuber induction and tuber initiation

Photoperiod has a significant impact on induction and initiation of tuberization in potato plant. Most traditional potato species known worldwide are short day plants for these processes, implies fast tuberization is observed under photoperiods shorter than critical values. Temperature alters the response of potato to photoperiods (Ewing and Struik, 1992; Struik and Ewing, 1995). The impact of higher temperature is higher in impeding, delaying, or inhibiting tuberization than cold temperatures (Ewing and Struik, 1992; Jackson, 1999; Snyder and Ewing, 1989; Wheeler *et al*. 1986). The impact of higher soil temperature is on preventing stolon from forming tubers but not on formation of stolon itself (Ewing and Struik, 1992). According to Kooman *et al*. (1996), duration between emergence and tuber initiation is short if treated by a temperature about 22°C. Whereas, slow development is observed at temperatures above that value (22°C) (Ewing and Struik, 1992). In consequence, the impact of high temperature prolongs the time between emergence and tuber initiation, there by creates larger plant size in start of tuber initiation. Apart from this, even if there is significant genetic variation in response to heat, but heat may completely impede tuber induction and formation (Ben Kheder and Ewing, 1985).

According to Borah and Milthorpe (1962), an optimum temperature for tuber formation is 20°C. Different responses have been recorded as at higher temperatures (25°C) it delayed tuberization by 2 week and at lower temperature (15°C), it delayed by 1 week. The cause for slower tuber formation at the lower temperature (<20°C) could be associated with slow metabolism and growth, and at the higher temperatures (>25°C) it could be the specific kind of inhibitory effect by high temperatures.

Tuber yield

As for research results, tuber yield of potato is very sensitive to changes in temperature. As illustrated in Table 1, the tuber yield of potato decreased with an increase in temperature in the range of 15–27°C. Yandell *et al*. (1988) verified as the optimum temperatures for tuber yield in Russet Burbank and Norland were 17.5°C and 18.7°C, respectively. Burton (1981) reported as the optimum temperature at which higher yield of potato were recorded is at 22°C. As illustrated by different authors, the optimum temperatures usually are in the range of 14–22°C (Marinus and Bodlaender, 1975; Sands *et al*. 1979; Timlin *et al*. 2006).

High temperature can adversely affect potato tuber yield in two distinct ways. The first by its impact on reducing growth of the crop, in much the same manner as its impact on other crops (Gregory, 1965). The effect of heat stress and heat induced moisture stress could be observed at interrelationships among enzymes, hormones, and perhaps membranes, shifting the metabolic balance so that there is less photosynthetic available for growth (Ewing, 1981). The second way is by its impact on reducing the distribution of photosynthates to the tubers (Ewing, 1981).

An increase in either day or night temperatures beyond optimal levels decreases tuber yields, from those the effect of high night temperatures is more deleterious (Gregory, 1956). Both high air temperature and high soil temperature cause yield reduction (Slater, 1968; Gregory, 1965). The effect of high soil temperature on reducing tuber yield is very high, mainly if combined with high ambient air temperatures (30°C day/23°C night).

Photosynthesis and respiration

The impact of temperature on respiration and photosynthesis is also well documented. The research result by Winkler (1971) concluded that the optimum temperature for photosynthesis and respiration is in the range of 16–20°C. As for his verification, the rate of dark respiration is doubled for every increase in 10°C temperature. According to Burton (1981) the optimum temperature for photosynthesis in European potato cultivars is about 20°C, and reducing temperature to 10°C caused a 25% reduction; however, for every 5°C raise above 20°C the photosynthesis rate approximately lowered by 25%. Therefore, he concluded that at temperatures above 30°C, net assimilation amount of potato falls to zero and yield reduction may happen. An experiment was conducted by Wivutvongvana (1979) to compare heat tolerant and heat sensitive clones of *Solanum chacoense* and *Solanum acaule* growing under non-tuberizing long day photoperiod. The result indicated that high rate of dark respiration was recorded by heat sensitive clones but there was significant difference in rate of carbon dioxide uptake during photosynthesis to heat tolerant clones. This result could indicate that tolerance to high temperature is associated to difference in respiration than photosynthesis. Dwelle *et al*. (1981) found that cv Russet Burbank had maximum photosynthetic rates at 24–30°C with a substantial decline in the rate of assimilation at 35°C. In these experiments, stomatal conductance reached its maximum at 24°C and remained at the same level even at 35°C. Hence, they concluded that the reduced carbon assimilation could not be attributed to changes in stomatal conductance but rather to the effect of high temperature on the photosynthetic system. On the other hand, Dwelle (1985) observed differences in the rate of assimilation as well as differences in optimum temperatures among potato clones. Those results could suggest that clones with characteristics of higher temperature for photosynthesis and which can maintain low dark reaction at high temperature is best fit to warm climate. In contrast, Lafta and Lorenzen (1995) reported that high temperatures (31°C day/29°C night) have no effect on rate of photosynthesis for either heat tolerant cv Norchip or heat susceptible cv up to date. But, Prange *et al*. (1990) reported that temperatures of 30/25°C (day/night) reduced net photosynthesis, because of reduction in the activity of photosystem II. Havaux (1993) described that rapid and irreversible loss of photosystem II in potato occurs at about 38°C. However, on plants acclimated at 30–35°C, the activity of photosystem II was maintained without appreciable loss even at 40°C. In heat tolerant cv Sahel the rise in the threshold temperature was as high as 8°C than in the heat sensitive cv Haig. More tolerance to stress tolerance was found for *Solanum juzepczukii* compared to *S. tuberosum* (Havaux, 1995). Hence, incorporation of this acclimation response could have paramount importance in enhancing field performance of cultivated potato in hot seasons.

Partitioning of assimilates

Temperature has a significant effect on determining the partitioning of assimilates to different parts of the potato plant. The effect of high temperature is exhibited in its impact in reducing assimilate partitioning to tubers and in the reverse enhances distribution to haulm (Vandam *et al*. 1996). The metabolic activity inside the plant is also affected by high temperature; it is through its role in determining changes in metabolic balance, presumably through growth regulators, enzymes, and other biochemical processes (Ewing, 1981). Accordingly, Krauss (1978) and Krauss and Marschner (1982) verified that under

Table 1: Effects of temperature on onset of tuber growth, relative tuber growth rate, relative partitioning rate (RPR), final dry matter tuber yield and final tuber number per plant

Cultivar	Average temperature (°C)	OTG (DAP)	RTGR (d^{-1})	RPR (d^{-1})	Yield ($g\ pl^{-1}$)	Number (per plant)
Spunta	15	36	0.38	0.090	213	23
	19	38	0.37	0.090	191	23
	23	42	0.34	0.055	140	22
	27	68	0.32	0.040	31	_
Desiree	15	35	0.38	0.085	205	22
	19	36	0.37	0.060	154	29
	23	40	0.34	0.045	42	42
	27	70	0.32	0.035	0	_

Data are for cvs Spunta and Desiree grown at a photoperiod of 12 h. Temperature regimes had a day-night differential of 6°C. sources: (Vandam et al. 1996; Ingram and McCloud, 1984).

high GA/abscisic acid (ABA) ratio, haulm growth is enhanced and tuber growth is inhibited, whereas at lower ratios the growth of vines is limited and tuber growth is promoted, 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). Higher level of endogenous GA reduced the activity of ADPG-pyrophosphorylase in the tubers, which slowed or stopped tuber growth (Mares *et al*. 1981). This could verify the association between tuber formation and high concentration of soluble sugars in tips of stolon (Slater, 1968). The higher levels of sucrose needed in media for *in vitro* tuber formation (Levy *et al*. 1993a) also agree to this result. The inhibitory impact of high temperature on tuber initiation and growth may arise from higher GA content which could promote and enhance shoot elongation through partitioning of carbohydrates (Mares *et al*. 1981; Booth and Lovell, 1972). Lafta and Lorenzen (1995) found that the reduction of activity of sucrose synthase in tubers of heat susceptible up to date was affected more by heat stress (72% reduction) than in the heat tolerant Norchip (59% reduction). Concomitantly, the reduction in tuber growth was greater under heat stress in up to date than in Norchip, as also reported by Wolf *et al*. (1990b). However, the report by Lafta and Lorenzen (1995) did not explain about the differences in heat susceptibility of cultivars based on enzyme activities. Krauss and Marschner (1984) described that the activities of enzymes have role in starch metabolism which depressed at soil temperatures of 30°C, resulting in an inhibition of sugar conversion into starch.

Tuber number

High temperature stimulates the production of large number of tubers in cost of slowed growth of tubers. In accordance with this, the research result by Borah and Milthorpe (1962) supported the evidence of higher tuber number by high temperature. In contrast, Lafta and Lorenzen (1995) reported reduced tuber number at higher temperatures. Reports also verified that in long days, higher tuber number is recorded at the lower optimum temperatures (Wheeler *et al*. 1986) and there is significant interaction between genotypes and environment (Vandam *et al*. 1996). Such difference were associated with the categorization of tuber in which some may consider the swelling tuber as full tuber.

As indicated in Table 1. For cv. Spunta, at a temperature of 23°C and below, tuber number didn't indicate significant difference. Whereas, in cv. Desiree while the temperature increases from 15 to 23°C, the tuber number also showed an increase in exhibiting factors associated to higher temperature that prolonged stolon formation and enhanced stolon branching.

Tuber quality

Physiological tuber disorders

Heat stress, hot, and dry weather creates physiological disorder in potato tubers (Ahmadi *et al*. 1960). Exposure to high temperature creates internal rust spots or chocolate spots which could show symptom of necrotic brown spots in the tuber parenchyma (Iritani *et al*. 1984). Common features appeared in affected cells are discoloration, then wound phellogen and suberization, and finally aggregate and collapse of cells (Hooker, 1981). Similarly, high soil temperature exhibited heat necrosis, and brown discoloration in the vascular ring (Hooker, 1981). These necrotic symptoms are variable depending on severity of stress, cultivar, tuber developmental stage, and environmental conditions (Henninger *et al*. 2000).

Different types of tuber disorder symptoms by the effect of higher temperature are irregular tuber shape, chain tuberization or secondary tuber formation (often associated with excessive stolon elongation and branching), and sprouted tubers (Marinus and Bodlaender, 1975). Common problems such as tuber malformation and sprouting are associated to high temperature and drought stresses on field conditions (Levy, 1986a).

The impact of high temperature could be also exhibited during tuber maturation and at onset of tuber dormancy; it may shorten their rest period, release the inhibition of tuber buds, which could force the formation of pre-harvest sprouting. It is indicated that such processes are associated with an increase in endogenous content of growth-promoting substances like gibberellins. The dormancy of tubers is reported to be affected by the balance between growth inhibiting and promoting compounds. Burton *et al*. (1992) reported a dramatic decrease in content of ABA and enhanced gibberellin concentrations in potato during end of dormancy and start of sprout growth. After harvest, treatment of tubers by gibberellins breaks dormancy and enhanced the stimulation of sprout growth. On the other hand, treating by thidiazuron showed reduced content of ABA and induced tuber sprouting (Ji and Wang, 1988). The report by Krauss and Marschner (1984) described that at higher temperatures (30°C), higher content of gibberellins and lower ratio of gibberellins to ABA is recorded. Likewise, van den Berg *et al*. (1991) found a lower amount of ABA that enhanced sprouting of tubers produced from leaf cuttings under high temperature (35°C).

On the other hand, exposure of tuber for high temperature even for short time causes tuber cracking (Lugt *et al*. 1964), in which it is associated to formation of high internal turgor pressure on tubers of potato. Potato grown in hot summer and irrigated at such conditions created rotting of tubers while underground (Levy, 1986a). The other impact of high temperature during growth is observed to increase the level of steroidal glycoalkaloids in tubers, which laterally may create bitter taste to the tubers (Dimenstein *et al*. 1997).

Specific gravity and dry matter content

Reports by Lujan and Smith (1964) concluded that specific gravity is an accurate index of mealiness for potatoes. The suitability of potato tubers to different roles such as cooking, canning, or dehydrating is accurately expressed by this factor. Based on different researches conducted on relationship of specific gravity to cooking, it is expressed that tubers with high specific gravity are mealy, contain high starch and slough for cooking (Nelson and Shaw, 1976).

Lower specific gravity was recorded on tubers grown at higher temperature areas; this could be due to reduced available starch content to be transported to leaves and low incorporation of starch in to tuber tissue (Van Es and Hartmans, 1987). In addition, the dry matter content of potato should be well known as it determines weight of processed products. It also determines quality of potato for processing and cooking. Tubers with high dry matter content are suitable for processing and cooking as it contain less sugar and high water content (Nelson and Shaw, 1976).

Due to its characteristics of growing in cooler areas, potato is classified as a "cool season" crop. This indicates that temperature has significant effect on dry matter than any other environmental factor. At high temperatures, it is exhibited that there is high respiration which may cause higher burning of solids accumulated by photosynthesis, and then it creates lower dry matter content. At higher temperatures at night such impact could be even higher (Van Es and Hartmans, 1987). Lower dry matter partitioning to tubers is recorded at areas of higher day and night temperature (40/30°C) ranges (Ben Kheder and Ewing, 1985) and it may cause an increased assimilation levels by other parts of the plant which may be related to high GA levels (Menzel, 1980;Vandam *et al.* 1996). Several other reports also verified quantitative decline of dry matter content by higher growth temperature (Ben Kheder and Ewing, 1985; Marinus and Bodlaender,1975).

METHODS TO COPE WITH HEAT STRESS

Disbudding

The investigation by Chapman (1958) and Hammes and Beyers (1973) verified that tuber initiation can be enhanced by manual disbudding on long days. Other research report by Das Gupta (1972) concluded that decapitation increases the formation of storage roots and higher root/shoot ratio was recorded in *Beta vulgaris* plant.

The inhibition of tuberization in long day conditions is associated with the formation of inhibitor substance (could be gibberellins) from leaves and buds (Chapman, 1958; Hammes and Beyers 1973). The verified impact of vegetative buds in producing gibberellins was reported by Lockhart (1957) who observed the reinitiating of suppressed shoot growth with addition of gibberellins. The result was later confirmed by experiments utilizing the agar diffusion technique in pea (Jones and Lang, 1968), sunflower (Jones and Phillips, 1966), and red clover (Stoddart and Lang, 1967).

The probability of gibberellin production at this site was confirmed by existence of exceeded amount of diffusible gibberellins over time than extractable gibberellins. The experiment by Jones and Phillips (1967) later evidenced such gibberellins synthesis by indicting that CCC significantly reduces the amounts of diffusing gibberellins. It could be indicated that gibberellins produced by buds are on continuous transportation through potato. Gibberellins are known to be part of the sieve tube sap (Hoad and Bowen, 1968) and xylem exudates (Skene, 1967) in different plants and exogenous 14C labeled gibberellins are moved in the plant (Bowen and Wareing, 1969).

Ting and Lockhart (1965) verified that movement of assimilates and gibberellins transport are closely correlated. In *Phaseolus coccineus*, Nash and Crozier (1975) have observed very limited distribution of apically synthesized gibberellins and could only influence immediate sub-apical region. The source to sink relationship on potato plant could be different scenario as the transport of gibberellins could be bud to stolon which is different to Phaseolus (Ting and Lockhart, 1965).

The response of potato to exogenous gibberellins could verify conclusions indicating that tuberization is controlled by this hormone (Menzel, 1980). The reported impact of disbudding depends on reduction of amount of gibberellin reaching to stolons from buds. As for reports, roots possibly play part in tuberization (Krauss and Sattlemacher, 1979). Crozier and Reid (1971, 1972) also indicated gibberellins may be synthesized by leaves of *P. coccineus* and could be transported to roots, which may undergo conversion to other gibberellins, and return to shoot. They concluded that the shoot part is the primary site of gibberellin synthesis.

The impact of high temperature could be in increasing the amount of endogenous gibberellins and inhibiting tuberization (Menzel, 1980). The researcher also indicated that negative impact of high temperatures on tuberization could be controlled by manual or chemical disbudding. In such evidences even if there were no direct measurements of phytochrome levels yet, the verification of such results are consistent in indicating site of synthesis of gibberellin at buds, its transportation to stolon and the inhibitory impact on tuberization. Until the actual gibberellin contents is quantified the mechanism how high temperatures affect gibberellin biosynthesis is not well investigated that could be direct effect on synthesis or/and transport or by influencing meristematic activity.

The removal of buds and younger leaves significantly increased tuber yield, number, dry matter contents and specific gravity. This indicates that bud and younger leaves growth may have a depressing effect on tuber development perhaps due to competition for assimilate between them (Bizuayehu and Tekalign, 2007). The results showed in Table 2 revealed the possibility of improving potato tuber yield by manipulation of the pruning treatments.

Paclobutrazol

The shoot growth of plants is highly regulated by triazoles even in very low amounts. The reported impact of PBZ in suppressing growth at different plants is well recorded in which the treated plants are dark green, short stature, and compact (Sebastian *et al.* 2002). Even if the dose of PBZ which is effective is variable from plant to plant, its growth reduction is well associated to reduce internode length (Davis and Curry, 1991). In potato plant this hormone reduces number of leaves; growth of shoots and the plant become short stature. The research

Table 2: The effect of pruning treatments on total tuber yield, total tuber number, specific gravity and dry matter content of potato

Treatments (manual pruning)	Total tuber yield (ton/ha)	Total tuber number (hill^{-1})	Specific gravity (gcm^{-3})	Dry Matter content (%)
Normal growing plants (control)	18.12^{b}	9.14^{b}	1.0710^{b}	18.03^{b}
Terminal buds removed	20.35^{b}	9.48^{b}	1.0734^{b}	18.42^{b}
Terminal buds and younger leaves removed	21.06^{b}	9.61^{b}	1.0736^{b}	18.49^{b}
Terminal and axillary buds removed	29.23^{a}	11.67^{a}	1.0873^{a}	21.06^{a}
Terminal buds, axillary buds, and younger leaves removed	30.01^{a}	11.86^{a}	1.0881^{a}	21.33^{a}
CV (%)	11.66	11.38	0.19	2.42

Means of the same main effect in a same column followed by the same letters are not significantly different at 5% level of probability. Source: (Bizuayehu and Tekalign, 2007).

report by Haughan *et al*. (1989) indicated that PBZ treatment reduces cell proliferation thereby curtails shoot growth.

Different research studies verified that PBZ enhances the synthesis of chlorophyll in which treated plants markedly showed dark green leaves (Sebastian *et al*. 2002) and/or showed densely packed chloroplasts per unit leaf area (Khalil, 1995). Other researches also reported an increase in chlorophyll a and b contents in PBZ treated plants (Tekalign, 2006). In experiment conducted on potato plant by Bandara and Tanino (1995), higher chlorophyll content was exhibited in PBZ treated leaves. The impact of PBZ in delaying senescence and higher chlorophyll content of leaves could be associated to its impact on content of indigenous cytokinin content. The impact of cytokinin is exhibited by its impact in increased chlorophyl differentiation and chlorophyll biosynthesis which in turn prevents degradation of chlorophyll (Fletcher *et al*. 1982). Inhibitors of GA biosynthesis exhibited an increase in cytokinin content in rice (Izumi *et al*. 1988), soybean (Grossman, 1992), and *Dianthus carophyllus* (Sebastian *et al*. 2002). Other research reports also verified that onset of senescence is delayed by the treatment of triazole (Davis and Curry, 1991).

Treating plants by PBZ enhanced the chlorophyll content of leaves and earlier tuberization which favors higher net leaf photosynthesis (Tekalign, 2006). Such promoted net photosynthesis by treatment of PBZ was reported in soybean (Sankhla *et al*. 1985) and rape (Zhou and Xi, 1993). Other evidences also indicated treating by GA decreases tuberization in potato, whereas GA biosynthesis inhibitors exhibited promoted tuberization (Bandara and Tanino, 1995; Langille and Hepler, 1992). Analyzing rate of photosynthesis as separate event is difficult, but higher demand for sink created higher amount of source output, in which the reverse is also true (Peet and Kramer, 1980). In situation of higher tuber growth, amount of net photosynthesis and translocation of photo assimilates to the tubers is higher (Dwelle *et al*. 1981). Conversely, significant reduction in photosynthesis was exhibited when fast growing tuber is removed which could indicate an imbalance in source and sink relationships (Nosberger and Humphries, 1965).

The effect of PBZ on partitioning of dry matters is also well recorded. This could be related to the impact of PBZ in formation of lower GA level in tuber tissues which may enhance the sink activity of tubers. On long days and higher temperatures, the biosynthesis of GA is higher that could cause fast growth in the top parts (Vreugdenhil and Sergeeva, 1999). The exogenous application of GA in turn causes an inhibition of tuber formation; lower sink activity of tubers and increased growth of shoots and stolon (Menzel, 1980; Mares *et al*. 1981; Vreugdenhil and Struik, 1989). Other research reports indicated that high temperature reduces growth rate of tubers, the partitioning of assimilates, but increased distribution of assimilates to other parts of the plant (Menzel, 1980; Vandam *et al*. 1996).

Due to its impact on increased rate of photosynthesis, earlier tuberization, higher chlorophyll content and reduced senescence of leaves, PBZ treated plants showed increased tuber yield (Tekalign, 2006) (Table 3). Lower tuber numbers could be recorded under lower levels of GA activity which may cause lower stolon number (Kumar and Wareing, 1972). Simko (1994) reported that higher tuber yield was recorded at PBZ treated plants even if it is not clear that it is by increased tuber size or number. Conversely, Bandara and Tanino (1995) verified that the treatment of potato by PBZ nearly doubled number of tubers per plant but didn't affect total fresh weight of the tubers. Such difference could be observed due to the difference in growing conditions mainly, cooler growing conditions, as 23±2°C/18±2°C day/night temperature and length of the day to 16 h.

The characteristics of tubers with higher specific gravity and dry matter content in PBZ treated plants could be due to reduced GA in tuber tissue which may hasten sink strength to attract high assimilates and improve starch synthesis. Booth and Lovell (1972) reported that higher accumulation of GA in tuber tissue creates reduced sink strength. In inductive growing conditions, the activities of enzymes parted in potato tuber starch biosynthesis such as ADPG-pyrophosphorylase, starch phosphorylase and starch synthase increases (Visser *et al*. 1994). Exogenous application of GA_3 on the growing tubers significantly decreases the activity of ADPG-pyrophosphorylase, while the role of starch phosphorylase remained more or less constant (Mares *et al*. 1981). In agreement to this, Booth and Lovell (1972) reported that application of GA_3 to potato shoots reduces movement of photosynthates to the tubers, reduced starch accumulation, increased sugar levels and resulted in reduction of tuber growth.

Tekalign and Asfaw (2002) verified that there is a positive correlation between dry matter content and specific gravity of potato tubers. In production of potato for processing purpose, enhancing the dry matter content by treating with PBZ is important as it increases the specific gravity of tubers.

By its impact of counteracting the activity of GA it is verified that PBZ enhances tuber crude protein content. On the other hand, GA_3 in turn inhibits accumulation of patatin (a glycoprotein associated with tuberization) and other tuber specific proteins (Vreugdenhil and Sergeeva, 1999). There is positive correlation between crude protein content and dry matter content, in which increased dry matter content increases crude protein content. As per report by Paiva *et al*. (1983) the activity of GA in regulating accumulation of starch and patatin was well recorded, on the other hand, close correlation was observed between starch and patatin content.

Different reports have proved that treatment of plants by PBZ significantly extended tuber dormancy (Tekalign, 2006; Bandara and Tanino, 1995; Simko, 1994; Harvey *et al*. 1991). This could be due to the effect of PBZ in inhibition of GA biosynthesis and prevention of ABA catabolism (Rademacher, 1997). This, in turn, could create lower GA and high ABA concentrations in the tubers. The impact of GA_3 in shortening tuber dormancy (Dogonadze *et al*. 2000) and the effect of ABA in inhibiting sprouting by hindering DNA and RNA synthesis is well recorded (Hemberg, 1970). The role of PBZ in prolonging tuber dormancy might have positive impact in potato industry as it prevents sprouting of potato cultivars in short time.

Screening for tolerance to heat stress

Differences in heat stress tolerance have been recorded (Levy *et al*. 1991) mainly in primitive and wild *Solanum* species (Mendoza and Estrada, 1979) and in hybrid clones developed by crosses among various sources of tolerance (Mendoza and Estrada, 1979; Veilleux *et al*. 1997).

Selecting reliable methodology to screen genotypes tolerant to heat stress is the prerequisite in success of breeding. Field trials are mainly suffered by impact of unpredictable weather, soil type, moisture and mineral distribution, disease incidence, etc., hence usually accommodate very limited number of clones (Tai *et al*. 1994). The other factor which prominently affects the use of seed tubers is also identified which is named tuber dormancy. There is variability in length of tuber dormancy across genotypes, which makes it difficult to synchronize the physiological status of seed tubers to a specific planting date. "Young" tubers grow at a slower pace, produce fewer stems and tuberize and mature late, while "older" tubers grow fast, develop more stems and tuberize and mature earlier. Such case may significantly alter the response to stress (Haynes *et al*. 1988). The maturation time of clones and cultivars is also variable in which early maturing ones express greater tolerance to stress than late maturing when grown in summer season (Levy, 1986b). Early maturing clones are known in accumulating yield in short period and late maturing types accumulate yield in long period which may cause exposure to high temperature in late summer. The relative yield ratio to potential yield is higher in late maturing types.

Table 3: Tuber fresh mass, number, specific gravity, dry matter and dormancy period as influenced by rates of PBZ application

PBZ rate (mg a.i. plant -1)	Tuber fresh mass (g pot $^{-1}$)	Tuber number (pot $^{-1}$)	Specific gravity (g cm $^{-3}$)	Dry matter (%)	Dormancy period (days)
0 (control)	71.9^{c}	10.47^{a}	1.048^{b}	13.84^{b}	13.84^{b}
45.0	151.5^{b}	8.05^{b}	1.061^{a}	42.30^{a}	42.30^{a}
67.5	155.6^{a}	7.00^{c}	1.065^{a}	43.92^{a}	43.92^{a}
90.0	141.2^{a}	6.01^{d}	1.061^{a}	44.08^{a}	44.08^{a}
SEM	5.0	0.20	0.001	0.26	0.53

Means within the same column sharing the same letters are not significantly different ($p<0.01$). sources: (Tekalign, 2006)

However, in favorable growing conditions, late maturing cultivars mostly out yield early maturing ones because of their longer growing period.

To select heat tolerant clones, different methods have been tried and used. To select heat tolerant sources in population of *Solanum andigena,* Ewing *et al*. (1983) used method of exposing of tuber for higher temperature. The selection of heat tolerant clones was conducted by two traits: Vigorosity of the shoot (indicates ability to produce high biomass under heat stress), and tuber formation (indicate ability to produce tuber at higher heat stress). This procedure is one of the repeatedly used methodologies for repeated comparison of clones in greenhouse condition (Nagarajan and Minhas, 1995). Use of cutting as research material overcomes problems associated to dormancy in tuber propagated materials. This procedure could easily identify heat tolerant and heat susceptible genotypes which could, in turn, help in identification of parent material (Ewing *et al*. 1983) and in selecting clones before field tests.

Mendoza and Estrada (1979) indicated that there should be a procedure that helps screening of heat tolerant genotypes (numbering in the thousands) in seedlings. Sattelmacher (1983) in turn responded by greenhouse of seedling populations by criteria of their capacity in tuberization under high temperatures treatments. As for his conclusion, tubers subjected to high temperature for 50 days gave high yield, and late tuberized ones gave better yield at the end of the growing season. This result is similar to yield difference recorded in late and early maturing cultivars grown under favorable conditions. Higher yield was recorded in late maturing cultivars than early maturing ones due to the fact that late maturing ones accumulate high yield in their long stay on field. Hence, late maturation and heat tolerance are the factors needed in getting high yield in warm climates. In a study of potato cultivar response to high temperature, to identify those that might be suitable for controlled ecological life support systems, Tibbitts *et al*. (1992) verified that late maturing cultivars had greater yield potential, confirmed by experiment of selecting potato cultivar which is suitable in controlled life support as subjected to high temperature (30°C continuous for 56 days/12 h photoperiod).

In an experiment conducted by Levy *et al*. (1991), their screening of parental materials (grouped according to maturation) under field and controlled greenhouse conditions, early maturation is closely associate to tolerance to high temperatures. Seedlings developed by a cross between heat tolerant and susceptible parents were tested to tolerance of high temperatures under greenhouse (30–35°C day/20–22°C night; 13 h photoperiod) condition. In such cases, 0.4–3.9% of seedlings developed tuber at after 88 days. After this those seedlings were subsequently subjected to lower temperatures (24–25°C day/15–16°C night) to get increased number of selections. Later on, at about 69 additional days, 44–72% reportedly formed tubers and retained for additional tests. This procedure was in resemble to procedure developed by Reynolds and Ewing (1989), who first tested vigorosity of shoot grown cuttings, and then their potential to tuberization at higher temperature ranges. The other factor used in measuring tolerance to high temperature was elongation of stem (Nagarajan and Minhas, 1995). Enhancing the activity of GA in heat tolerant cultivars of Desiree and LT1 exhibited an increase of dry matter partitioning to shoots without altering formation of tubers. But, less tolerant cultivars could not able to tuberize in this condition. Hence, it can be concluded that heat tolerance capacity is dependent on ability to maintain the growth of tuber and haulm by balanced partitioning of assimilates. In different countries like sub-tropical India (Shekhawat and Naik, 1999), the semi-arid Middle East (Levy *et al*. 2001), and the tropics (CIP, 1984) screening by physiological response to heat stress was highly important in development of new heat tolerant cultivars.

Even if it is mainly labor intensive for use in breeding populations, *in vitro* tuber formation, or microtuberization in high temperatures has been suggested as a screening tool for heat tolerance (Nowak and Colborne, 1989). Utilizing system of microtuberization at 28°C followed by radiation treatment of two cultivars of potato, Das *et al*. (2000) selected heat tolerant mutants after the microtubers are planted at field in natural system of heat stress.

CONCLUSION

The inhibitory impact of higher temperature has been mediated by producing GA like chemicals which are effective in inhibition of tuber formation. As per the result of different researches the hormonal impact which alters potato tuberization can be modified through use of GA biosynthesis inhibitors. The associated impact of PBZ in growth regulation is known to be by inhibiting GA biosynthesis and preventing ABA catabolism through its interference with ent-kaurene oxidase activity in the ent-kaurene oxidation pathway. Hence, it increases tuber yield and quality by increasing efficiency of photosynthesis and partitioning of assimilates to tubers.

Pruning by its impact in manipulation of indigenous phytohormone levels is considered as alternative method. The buds at the vegetative parts and younger leaves are main sites of gibberellins synthesis, and their removal substantially modified the phytohormone levels in the plant and results in the increase in yield and quality.

As there is larger germplasm base in potato plant, evaluation of their performance for challenging conditions revealed new possibilities. Combined with advancements in knowledge of molecular biology of the potato and revelation of genes responsible for stress resistance, the system is promising to meet the challenges of enhancing potato yield in non-traditional and stress susceptible conditions.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF DATA AND MATERIALS

Primary data were not used to support this study.

COMPETING INTERESTS

The authors declare that they have no conflicts of interest.

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BDA is the first author of the review article, whereas the co-authors have contributed equally for the literature collection, manuscript documentation, and its revision. All authors read and approved the final manuscript.

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