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Effects of heat stress on potato productivity and nutritive quality

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Abstract

Potato, Solanum tuberosum L., is the most important non-grain food crop in the world, and a major vegetable crop in Serbia. It is generally considered a cool-season crop and highly susceptible to high temperatures. Elevated temperatures in the environment affect potato plants' growth and development by slowing the sprout emergence, reducing the number of stolons, impeding tuber initiation, reducing tuber bulking and interfering the onset of tuber dormancy. Tuberization is optimal at average daily temperatures in the 15-20 °C range and above this range declines, although moderately elevated temperatures of 20-25 °C may enhance potato foliage growth and the net photosynthesis. Besides reducing the number and mass of tubers, high-temperature stress affects the total and marketable yield of potato by causing tuber disorders and altering tuber processing and nutritive quality. The problem of potato heat-susceptibility is gaining more interest in the last decades due to occurring global climate change. The breeders' efforts have been intensified for selection of new, tolerant potato genotypes, as well as genomics', proteomics', and metabolomics' investigations of potato heat response.

Keywords*: potato, Solanum tuberosum, heat stress, food.*

INTRODUCTION

Potato, *Solanum tuberosum* L., is the most important non-grain food crop in the world, and a major vegetable crop in Serbia with an annual production of 374.000.000 and 590.000 tons, respectively [1]. It is grown in 158 countries and daily consumed by more than a billion people. The major producers of potato are China and India, which are currently responsible for over a third of the total world potato production [1]. Since potato produces more food per unit of production area than any other crop, it is not surprising that its global production has been expanding rapidly, especially in developing countries. It is cultivated by large-scale commercial companies, as well as farmers in remote, resource-poor communities where it contributes greatly to daily, dietary energy intake. Since potato is mostly traded and consumed locally, it is highly recommended by FAO as a food security crop for the 21st century [2].

Potato is generally considered a cool-season crop. It was domesticated over 7000 years ago in Andes of South America, regions with cool temperatures, short daylight, high light intensity, and high humidity. Upon introduction to Europe in the late 16th century, the potato was mostly bred and selected for greater tuber yields under longer daylight. From Europe, potato varieties spread to the world during the 18th and 19th centuries, without improving their heat tolerance. Compared to other crops, potato is highly susceptible to high temperatures [3,4] which can cause heat stress – 'an array of morpho-anatomical, physiological and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield' [5]. Even mildly elevated temperatures (30/20 °C day/night) during tuberization can significantly reduce potato yield [6]. In plenty of places, it is grown under supra-optimal temperature conditions. For instance, cultivation in North Africa is limited to the cooler spring and autumn/winter season with a relatively short production period due to high temperatures [7]. In the last decade, warm summers and frequent heatwaves are not unusual for countries in temperate climate regions which are encountering great problem because of heat susceptibility of favored and most commonly grown potato varieties.

EFFECTS ON GROWTH, DEVELOPMENT AND YIELD

The growth and development of the potato plant, propagated from the tuber, can be divided into five stages: sprout development, vegetative growth, tuber initiation, tuber bulking and maturation. High temperatures significantly affect potato plants at each of particular stages.

Investigation of the potato sprout emergence has shown that optimal environmental temperature for sprout growth is 23 °C, and even moderately elevated temperatures of 25 °C and 28 °C cause a decrease in the rate of sprout elongation [8]. Stage of vegetative growth comprises the formation of all vegetative parts of the plants, including the formation of stolons, modified, underground stems that will later give rise to tubers (**Figure 1**). During vegetative growth, temperatures higher than 25 °C can enhance stem growth and branching, increase the leaf number, but cause a reduction in leaf size and total leaf area [9]. The estimated optimal temperature for stolon initiation, growth and branching is 25 °C [9]. Nevertheless, temperatures ≥ 28 °C may partly or entirely suppress the stolon formation [10,11]. Temperature treatment at 30/24 °C, day/night, caused the 3-fold decline in the number of stolons formed by potato cultivar Désirée [11].

The most heat-vulnerable stages of potato growth and development are tuber initiation and tuber bulking (**Figure 1**). Tuber initiation stage starts with inhibition of the longitudinal growth of the stolons and swelling of the first internode behind the stolon apical bud to form tuber initial. The estimated optimal temperature for tuber initiation is below 20 °C and higher temperatures delay, impede or even inhibit tuber formation [9]. Recent breakthroughs have revealed that elevated temperature probably hinders tuber initiation by suppressing the expression of tuberization signal protein, named StSP6A [6]. This mobile "tuberigen" signal is produced in leaves and moves to the stolon tip where tuberization is initiated [12]. At mildly elevated temperature regime (30/20 °C, day/night), StSP6A transcript levels in leaves decreased by up to 50% at most time points during the 24 h-cycle [6]. Tubers bulking (enlarging) starts approximately two weeks after initials are formed. If conditions are optimal, tubers increase the weight and volume in an almost linear fashion and become a dominant site for the deposition of starch and other nutrients. However, heat stress can affect the source-sink relationships between foliage and tubers and shift assimilate partitioning to the above-ground plant parts with less assimilated carbon incorporated into starch in the tuber [13]. Potato plants exposed to mild heat stress (30/20 °C day/night, 5 weeks) exhibited a shift in assimilate partitioning implied by the significantly increased leaf dry matter and reduced tuber fresh and dry weight, dry matter and harvest index [6]. Also, plants were producing a greater number of smaller tubers. High temperatures during the maturation stage 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 [14]. This interference is probably related to an increase of

Figure 1. Underground parts of potato plants during bulking stage. Note that tuber initiation is not entirely synchronized; some stolons are still forming initials at early bulking stage. s - stolon, si - stolon with tuber initial, tb - tuber at the beginning of bulking, t- tuber. Bar = 1 cm. (unpublished results)

the endogenous content of plant growth regulators such as gibberellins.

In general, tuberization is optimal at daily average temperatures in the 15-20 °C range and above this range declines, although moderately elevated temperatures of 20-25 °C may enhance potato foliage growth and the net photosynthesis. Besides daytime temperatures, tuberization depends on usually lower nocturnal temperatures which enable metabolites produced during daytime to accumulate in the tuber during night. In temperate climate regions of the northern hemisphere, including the territory of Serbia, potato is summer crop and first heat stress events usually occur in June during tuber bulking stage. An investigation conducted on six potato cultivars has shown that heat stress (35/25 °C day/night, 15 days) imposed in the second half of June under favorable soil moisture conditions caused 12% decrease in the total yield [15]. When the time of high-temperature treatment was shifted in the second half of July, beginning of maturation stage, the heat stress effects on the total tuber yield were minor but caused 13% decline in marketable yield due to tuber pre-harvest sprouting in the soil [15]. In Ontario, Canada, the potato yield decreased by 17.2% in 2016 compared with the production in 2015 as a result of extreme heat stress in summer [16]. Later investigation revealed that the primary planted and most popular cultivar Russet Burbank is exceptionally heat-vulnerable [16]. In Serbia, a drastic decline in the potato yield of 24-26% was recorded in the warm year 2011 and the warm and dry year 2012 compared to the moderate year 2013 [1]. Besides the adverse effect on total potato yield, heat stress causes tuber physiological disorders and alters tuber processing and nutritive quality which reduces the proportion of marketable tubers. Marketable yield defines potato profitability, and salable tubers must possess appropriate size, aesthetic, processing and nutritive qualities.

TUBER DISORDERS

Heat stress causes an irregular shape of the tubers by interrupting both their longitudinal and diametric growth during bulking stage. Depending on the occurrence of the high-temperature events, tuber growth can be hindered at the beginning of bulking (causing a constriction at the tuber basal end – pear-shaped or bottleneck tubers, **Figure 2** A, B), in the middle of tuber formation (dumbbell-shaped tuber, **Figure 2** C), or at the end of tuberization when protuberances develop at the apical or rose-end (knobby tuber). High temperatures may also trigger excessive stolon elongation and branching which leads to chain tuberization (**Figure 2** D), as well as resurgence of stolon growth from the tuber in a process known as heat sprouting. If the temperature declines after heat sprouting, a new, secondary tuber will start to form at the stolon tip (**Figure 2** F). Sometimes, secondary tuber develops directly from the node (eye) bud (**Figure 2** E). Some potato cultivars are prone to pre-harvest sprouting due to high temperatures at the end of the growing season (**Figure 2** G). High soil temperatures induce heat stress russeting (roughness) and netting of potato skin (**Figure 2** H, I). Microscopic observation of microtubers exposed to high temperatures revealed heat-enhanced development and accumulation of suberized skin-cell layers to create a thick protective cover [17]. Skin russeting probably results from continued expansion of the tuber and cracking of the inflexible skin as new layers are produced below it.

Symptoms of some physiological disorders may not be externally visible. One of such disorders is internal heat necrosis (IHN). IHN can be described as brownish-red necrotic patches of parenchymal tissue that occur along and inside the vascular ring of harvested tubers. The causes of IHN are still under debate; however, the combination of environmental, nutritional and genetic factors seems to have a significant role in the appearance of symptoms [18]. One of the combinations is a shortage of calcium in the tuber cells under heat stress which leads to the loss of membrane integrity and, subsequently, causes necrosis [19]. Heat stress accompanied by water deficit may cause the tuber disorder named sugar ends, also known as translucent ends, glassy ends or jelly ends. It is characterized by relatively low starch and high sugar content usually in the basal end of the tuber, which results in more translucent appearance and, in more advance stage, jelly-like composition of parenchyma [20]. Accumulation of reducing sugars, mainly glucose, is due to heat-induced changes in the activities of particular key carbohydrate metabolizing enzymes [20]. Although heat-stressed plants pro-

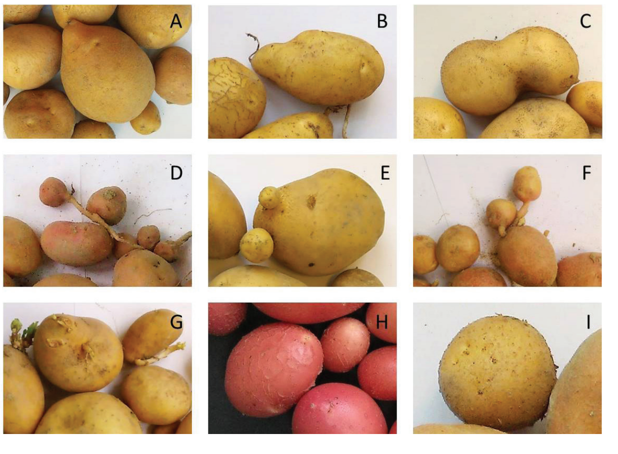

Figure 2. Potato tuber physiological disorders associated with heat stress: pear-shaped or bottleneck tubers (A, B), dumbbell-shaped tuber (C), chained tubers (D), secondary tubers on tuber eye (E) or stolons (F), pre-harvest sprouting of tubers (G), and skin netting and russeting (H, I). (unpublished results)

duce sufficient amounts of assimilate to support starch deposition and tuber growth, tuber cells shift from a starch synthesizes to starch mobilization. Internal physiological disorders can affect large portions of parenchymal tissues, compromising appearance and taste, altering processing-relevant characteristics (specific gravity, frying quality) and increasing susceptibility of tubers to infection by fungi and bacteria.

EFFECTS ON NUTRITIVE QUALITY OF TUBERS

Potato tubers are one of the most important dietary sources of carbohydrates. Though protein content is not high (1-2% on a fresh weight basis), potato proteins are of relatively high 'biological value' (90), compared with other with other major plant protein sources, and with an amino-acid composition that is well matched to human requirements [21]. Potato tubers are good source of vitamins and minerals, such as vitamins C and B6, potassium, magnesium, and iron. Potatoes also contain B vitamins riboflavin, thiamin, folate and niacin, as well as phosphorus and zinc [21]. A common misconception, due to fried products, is that potatoes are high in calories. Tuber has insignificant amount of fat and a low energy density similar to legumes [22]; the energy value of backed or boiled potato is around 75 kcal per 100 g [23].

Most previous studies on the effect of heat stress on tuber nutrients have focused on carbohydrates, which make up about 75% of its total dry matter [23]. Starch or amylum is the dominant carbohydrate in tubers which serves as an energy reserve for the plant. It is composed of two types of polysaccharides, amylose (straight chain α-D-glucose polymer) and amylopectin (branched chain α-D-glucose polymer). Starch is densely packed in granules that typically contain amylose and amylopectin in a ratio of 1:3 and granules are located in cellular organelles – amyloplasts. Sucrose is the major disaccharide of tubers while glucose and fructose (reducing sugars) are the major monosaccharides. Heat stress may shift carbohydrate metabolism away from starch synthesis towards starch mobilization and accumulation of sucrose and reducing sugars, causing the "sweetening" of the tubers, mostly in basal ends (sugar ends). A recent study reported a reduction in total starch, amylopectin and amylose content of tubers by 33.70%, 7.85% and 35.88%, respectively, after exposure of potato plants to 35 °C during tuberization [24]. This reduction was caused by the decline in the activity of key enzymes of starch biosynthesis in tuber cells, ADP-glucose pyrophosphorylase, granule-bound starch synthase and soluble starch synthases, as well as starch branching enzyme [24]. On the other hand, accumulation of reducing sugars is probably due to an increase in sucrose breakdown by vacuolar acid invertase [25]. During frying of tuber stripes, reducing sugars react with amino acids and other cellular substrates in the Maillard reaction. Dark-colored, Maillard reaction products give 'burned' appearance and altered flavor to sugar ends which may be considered as a serious defect of fried potato products. More importantly, reaction of reducing sugars with free amino acid asparagine produces acrylamide, a suspected carcinogen in humans [25].

Potato tubers also contain secondary metabolites significant for human health, such as carotenoids and anthocyanins, as well as toxic steroidal glycoalkaloids [26]. Anthocyanins are mainly present in the cell layers bellow the tuber skin, phelloderm, of the red potatoes. The carotenoids predominantly accumulate in the tuber flesh; yellow flesh results from prevalent lutein accumulation, while rare orange-fleshed tuber cultivars mostly accumulate zeaxanthin. High temperatures do not affect total carotenoid content in tubers, but their composition. In three potato cultivars, Desirée, Melrose and Daifla, 10-day long heat treatment caused alteration of the carotenoid profile, causing increase in the level of zeaxanthin, while reducing the levels of violaxanthin and antheraxanthin [26]. However, the levels of anthocyanins pelargonidin and peonidin remained unchanged by the heat treatment in red potato cultivar Desirée.

The major steroidal glycoalkaloids (SGAs) in commercial potato cultivars are α-chaconine and α-solanine. These secondary metabolites are important for plant resistance to pests and pathogens, but toxic to humans at high levels. Since potato cultivars were bred to contain low levels of SGAs, their content in tubers usually does not exceed 20 mg per 100 g fresh weight [27]. The richest in SGAs is the periderm, a protective tissue which includes tuber skin and several underlying cell strata. Environmental cues, including high temperature, can alter the SGA content of the tubers. Previously, accumulation of SGAs was reported in response to heat stress [28,29], which raised concern related to human consumption. However, recent findings indicate a reduced level of solanine and chaconine in the tuber skin, and downregulation of the SGA biosynthesis pathway after 7-10 days of high-temperature treatment at 33–35 °C [26].

PERSPECTIVES

Heat stress affects the total and marketable yield of potato by reducing the number and mass of tubers, causing tuber disorders, and altering tuber processing and nutritive quality. The problem of potato heat-susceptibility is gaining more interest in the last decades due to occurring global climate change. Thus far, a relatively small number of heat-tolerant potato cultivars is recognized. Given that these cultivars are usually bred for specific hydro-edaphic conditions, the conventional breeding endeavors have been intensified for greater variability of new, tolerant genotypes. Because of limitation in the cultivated-potato gene pool for heat tolerance trait, an effort has been made for identification and utilization of genes/alleles from the germplasm landraces of Andean potato species and wild potatoes occurring in the Americas which are better adapted to abiotic stress. Besides, results of ongoing genomics, proteomics, and metabolomics' research on potato heat response may greatly help conventional breeding strategies, while bioengineering efforts may give an alternative route towards the development of heat stress-tolerant potato.

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Uticaj toplotnog stresa na produktivnost i nutritivni kvalitet krompira

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Kratak sadržaj

Krompir, Solanum tuberosum L., je najvažnija povrtarska kultura gajena za potrebe ljudske ishrane u svetu i dominantna povrtarska vrsta u Srbiji. Generalno se smatra biljkom „hladnijih predela" i izuzetno je osetljiv na visoke temperature. Visoke temperature vazduha i zemljišta utiču na rastenje i razviće biljaka krompira tako što usporavaju pojavu i rast klica, smanjuju broj stolona, usporavaju i redukuju inicijaciju krtola, redukuju nalivanje krtola i ometaju period mirovanja. Za proces tuberizacije, tj. formiranje i rast krtola, optimalne prosečne dnevne temperature su u opsegu 15-20 °C, mada nešto više temperature od 20-25 °C mogu pospešiti rast nadzemnog dela biljke i neto fotosintezu. Pored smanjenja broja i mase krtola, toplotni stres utiče na ukupan i tržišni prinos krompira tako što izaziva i fiziološke poremećaje i deformitet krtola, kao i promenu njihovog nutritivnog kvaliteta i osobina važnih za preradu. U toku prethodne dekade, problem osetljivosti krompira na delovanje visokih temperatura dobio je na značaju usled globalnih klimatskih promena. Pojačan je napor u selekciji novih, toplotno-tolerantnih genotipova krompira, kao i genomska, proteomska i metabolomska istraživanja odgovora biljaka krompira na visoke temperature.

Ključne reči: *krompir, Solanum tuberosum, toplotni stres, hrana.*