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Factors Affect to Stolon Formation and Tuberization in Potato: A Review

P.D. Abeytilakarathna
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ABSTRACT

Potato tuber formation is a complex process that is induced by a mobile signal called tuberigen. It involves several genes such as *AtBMI, St 14-3-3s, StBEL, StBELL11, StBELL29, StBMI1-1, StCDF1, StCEN, StCO, StFDL1, StFT, StGA2ox1, StGA3ox2, StMSI1, StSP6A*. This article focuses on important factors such as genetic factors, low temperature, high irradiation, low nitrogen, abscisic acid, chlormequat chloride, auxin, Jasmonic acid, cytokinin and paclobutrazol that induce tuber formation while ethylene, drought, low irradiation, high-temperature that reduce or inhibit tuber initiation.

Key words: Potato, Stolon, Tuber formation, Tuberization.

Potato (*Solanum tuberosum* L.) is one of the major food crops, after rice, wheat and maize which is grown in more than 140 countries worldwide (Horton 1987; Hunsigi and Krishna, 1998). According to Wasilewska-Nascimento *et al.* (2020), potato production and area under cultivation have increased dramatically by more than 100% in most of the countries in tropics and subtropics like India, Indonesia, Kenya, Bangladesh, China, Egypt and Peru while it has declined in temperate countries like France, Germany, Ireland, Italy and Poland during last 50 years. But the productivity of the potatoes is greater (more than 45 t ha^{-1}) in Germany, the Netherlands and the USA like high input usage countries than the other countries (Koch *et al*., 2020). Consequently, reviewing the factors that influencing stolons and tuber formation in potatoes, based on the most important experiments conducted under different climatic condition are very important to get an understanding of yield formation of potato as well as enhance its tuber yield even under extreme conditions especially in the tropical and sub-tropical regions.

Jefferies and Lawson (1991) described the seven growth stages of potato plants: seed germination and emergence, tuber dormancy, tuber sprouting, emergence and shoot expansion, flowering, tuber development and senescence.

Formation of stolons and tubers in potatoes

The formation of underground stolon and tuberization are the two processes of tuber formation of potato (Hunsigi and Krishna, 1998; Jackson, 1999). An early phase of the stolon tip begins to swell is considered as the tuberization. Diageotropically growing underground lateral buds are developed into stolons by elongation and transverse division of its apical cells (Xu *et al.,* 1998). Xylem tissues of stolons that are situated in between inner and outer phloem tissues are called a pre-medullary zone. At the time of tuber formation, the apoplastic phloem unloading pathway of assimilates through the cells is changed into a symplastic pathway through the cytoplasm and start to swelling of stolon

Department of Agriculture, Agricultural Research Station, Seetha Eliya, Nuwara Eliya, Sri Lanka.

Corresponding Author: P.D. Abeytilakarathna, Department of Agriculture, Agricultural Research Station, Seetha Eliya, Nuwara Eliya, Sri Lanka. Email: abeytilaka@yahoo.com

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tip by longitudinally dividing the pith and cortex cells. Cells in the pre-medullary zone are divided further with the enlargement of potato tubers. Finally, the tuber size is increased by dividing and enlarging the storage parenchyma cells in the outer cortex of tubers (Hunsigi and Krishna, 1998; Xu *et al.,* 1998; Viola *et al*., 2001; Akoumianakis *et al*., 2016; Zhang *et al*., 2020). Active numbers of tubers per haulm decrease by resorption or remain as very small tubers. The first three weeks after emergence is the most critical period for tuber formation. If anything happens to slow down the growth of plants, it affects negatively final yield (Cho and Iritani, 1983; Oliveira and Da, 2000; Walworth and Carling, 2002; Thornton *et al.,* 2007). The numbers of tubers per plant are determined by different parameters such as numbers of stolons and stems, varieties grown and status of vegetative growth (Wurr *et al*., 1997; Adhikari, 2005). For instance, stolon length is a varietal character (Kratzke and Palta, 1992). According to Celis-Gamboa (2002) stolons were formed 29 days after planting in all maturity types (very early, early, intermediate, late, or very late) of potatoes. Besides, tuberization was begun 29 days after planting in very early maturity types and 36 days after planting in other maturity types.

Genetical regulation of tuber formation

Tuberization, stolons length, number of tubers per plant, tuber size and uniformity are highly heritable and genetically advance in potatoes. Besides, the number of tubers per plant is positively correlated with the final tuber yield, it is least influenced by the prevailing environmental factors such as day length, light intensity and temperature (Tripura *et al*., 2016; Hulscher *et al*., 2013; Bahram *et al*., 2020). Tuber formation of potato is induced by the mobile signal initiated in leaves called tuberigen and it involves *FLOWERING LOCUS T* (*FT*) protein (Rodriguez-Falcon *et al.,* 2006; Abelenda *et al.,* 2011). The authors revealed that several genes are responsible for tuber formation in potatoes. A transcription factor *StBEL5* mRNA that is produced in leaves mobilizes to the stolon tips through the phloem tissue to initiate tubers under a favourable condition with a short-day photoperiod. Potato varieties having overexpression of *StBELL5* produce higher yields due to early tuberization. Full-length mRNA *StBELL11* and *StBELL29* affect to tuberization of potatoes (Chen *et al*., 2003; Banerjee *et al.,* 2006; Kloosterman *et al*., 2013; Lin *et al*., 2013; Sharma *et al*., 2016; Hannapel and Banerjee, 2017; Hannapel *et al.,* 2017). The gene *StBELL5* induces the activity of *SELF-PRUNING 6A* (*StSP6A*) which interacts with *FLOWERING LOCUS D* (*FD*)-like protein in stolons during the tuber initiation. *CYCLING DOF FACTOR1* (*StCDF1*) or overexpression of *StSP6A* and its interaction with *St 14-3-3s* induce early tuber initiation while *StFDL1* delays tuber formation. Besides, overexpression of *CONSTANS* (*CO*)-like gene *StCO* cause to delay the tuber initiation under non-inductive conditions either during short days or long days. *StCO* also affects the level of *StBEL5* mRNA level. *FT*-like protein, *StFT/ StSP6A* transcript level is also induced initiation of tuber formation in wild-type potato plants. Tuberization signal of *StSP6A* is co-expressed with *TERMINAL FLOWER1/ CENTRORADIALIS* genes (*StCEN*) and it is suppressed by *StFDL1* (Rodriguez-Falcon *et al.,* 2006; Navarro *et al.,* 2011; Gonzalez-Sachain *et al*., 2012; Sharma *et al.,* 2016; Hannapel *et al.,* 2017; Teo *et al*., 2017; Zhang *et al*., 2020). *StMSI1* which belongs to the group of *POLYCOM REPRESSIVE COMPLEXES* (*PRC*) protein and micro RNA 156 (*miR156*) increases the stolon formation while *PRC* protein: *StBMI1-1* decreases the number of stolons under short-day photoperiod conditions. Overexpression of *PRC* protein *AtBMI1* stimulates the formation of aerial tubers that causes to reduce the underground tuber yield under short-day conditions. Micro RNA 172 (*miR172*) also influences tuber formation in potatoes (Martin *et al*., 2009: Kumar *et al*., 2020). Lipoxygenases (*LOX1*) transcription factor restricts the development of root and stolons and it regulates the tuber enlargement by accumulating in the apical part of small tubers. The genes; *GA2-oxidase* (*StGA2ox1)* and *GA3-oxidase* (*StGA3ox2*) are induced in stolons under the short-day condition and overexpression of *StGA2ox1* and *StGA3ox2* genes induce early tuberization by control the gibberellins (GA) level in stolons (Kolomiets *et al.,* 2001; Kloosterman *et al*., 2007; Bou-Torrant *et al*., 2011). The cDNA fragments that express during the tuber initiation period are very important as genetic markers for selection phenotypic variation in the potato breeding programs (Strunik *et al*., 1999).

Effect of growth regulators on tuber formation

Several growth regulators affect to stolons and tuber formation of potatoes. Among these, gibberellins (GA) is one of the most important growth regulators and it involves stolon elongation and inhibition of tuber formation in potatoes by affecting starch hydrolase activity or starch synthesis enzymes. GA-oxidase genes are involved to change GA content in the stolon tip before the onset of tubers. GA_1 and GA_3 present in stolon at tuber initiation and active GA decrease with swelling of stolon tip under inducing condition (Smith and Palmer, 1970; Xu *et al*., 1998; Abdala *et al*., 2002; Kloosterman *et al*., 2007; Roumeliotis *et al.,* 2012). Degebasa (2020) pointed out that the dipping of tubers in GA_3 at a rate of 50 ppm for 24 hrs just after harvest, increased the average number of tubers per plant along with the increasing total and marketable tuber yields. But contradictory results were reported by Kumar *et al*., (1981) using a low concentration of GA_3 at a rate of 1, 5 and 10 ppm for 24 hrs. It reduced dry matter yield with a significantly increasing number of tubers without changing the numbers of stolons per plant. According to Wang *et al.* (2018), GA_3 treatment with calcium nitrate improved the number of tuber per plant as well as tuber weight in aeroponic grown potatoes. A study conducted five decades ago by Dyson (1965) confirmed that there was no yield reduction with GA_3 applied to tuber pieces even delays the tuber growth. According to the studies of Struik *et al*. (1989), foliar application of GA_3 at the rate of 25 ppm at an early stage or 60 days after planting reduced dry matter yield but increased fresh yield and number of tubers per plant by applying 40 days after planting. Menzel (1983) pointed out that tuberization was inhibited by gibberellins produced in buds under warm temperatures. Therefore, further researches are needed to confirm the effects of tuber treating with GA_3 or foliar application of gibberellin inhibitors on the total and marketable yields under warm temperature.

The stable concentration of abscisic acid (ABA) is found in the apex portion of the tuber under inducing and non-inducing conditions while GA distributes throughout the tuber tissues. Even though ABA can decrease the formation of tubers and stolons, its exogenous application induces tuber formation by counteracting with gibberellins (Krauss *et al*., 1981; Xu *et al*., 1998).

The most popular GA biosynthesis inhibitor used for commercial potato cultivation is chlormequat chloride (CCC). Foliar application of CCC improves the number of tubers formed and yield of small tubers in both fields grown and hydroponic grown potatoes. Soil application of CCC at emergence is also possible as it induces early tuberization by decreasing stolon growth (Dayson, 1965; Rex, 1992; Wijaya *et al*., 2017). Dahyabhai (2004) observed a significantly higher total tuber yield (79.9%) and a greater number of tubers per plant (32%) than control by a single application of CCC at the rate of 800 ppm at 45 days after planting. But further studies need to confirm the effect of CCC on the yield performance of potatoes due to it may interact with the fertilizer rates, especially the rate of nitrogen and with the different maturity groups.

Some authors did experiments using paclobutrazol which is another GA biosynthesis inhibitor and growth retardant. It also enhanced the number of tubers per plant when applying before tuberization but its high concentration (250 mg L^{-1}) reduced the yield (Lopez *et al.,* 2011; Ellis *et al.,* 2020). Uniconazole and Prohexadione-calcium can also inhibit the GA biosynthesis but their foliar application does not affect the number of tubers formed or the final yield. (Lopez *et al.,* 2011; Ellis *et al*., 2020).

Kinetin which is one of the adenine-type of cytokinins can inhibit tuberization when adding to the culture medium, but it induces tuber formation with a 6% or higher concentration of sucrose in *in-vitro* media. Thidiazuron which belongs to the phenyluron-type of cytokinin and kinetin induce early tuberization, rapid stolon growth and enhance the number of tubers by stimulating basal acid invertase activity (Palmer and Smith, 1970; Pelacho and Mingo-Castel, 1991; Kefi *et al*., 2000; Aksenova *et al*., 2009). Another adenine type of cytokinins: 6-benzyl amino purine (BAP) and zeatin riboside promote tuber formation by increasing glycolysis and ATP synthesis activity (Mauk and Langille, 1978; Cheng *et al*., 2019).

Auxin plays a vital role in tuber formation by inducing tuberization at higher concentrations in stolon before swelling of tubers. Low concentration (2 ppm) of Indole acetic acid (IAA) improves tuberization while its higher concentration (4 ppm) inhibits both stolon elongation and tuberization (Roumeliotis *et al*., 2012a; Roumeliotis *et al.,* 2012 b; Wang *et al.,* 2018; Xu *et al*., 1998).

Jasmonic acid (JA) is also one of the important growth regulators in point of tuberization. It accumulates in the root during the tuber formation stage by improving tuber formation and the number of tubers per plant. The exogenous application of JA on the stolon tip causes to initiate the tuberization. Authors revealed that JA synthesis is stimulated by theobromine which is extracted from *Lasiodiplodia theobromae* fungus (Pelacho and Mingo-Castel, 1991; Abdala *et al*., 2002; Cenzano *et al*., 2003; Gao *et al*., 2003). Jackson and Willmitzer (1994) revealed that the tuber did not form by spraying JA up to 100 μM on *Solanum andigena* (Jus. and Buk.) and *S. demissum* (Lindl.) potatoes under non inducing condition.

Ethylene is also crucial in tuber formation. It inhibits tuber formation, stolon and root elongation by counteracting with kinetin. Foliar application of ethephone promotes tuber formation but it reduced the weight of marketable tubers (Mingo-Castel *et al.,* 1974; Vreugdnhil and Dijk, 1989; Rex, 1992).

Effect of nitrogen on tuber formation

There is no doubt of the importance of soil nitrogen management for achieving a greater yield. Nitrogen absorbs by plants through the root system as nitrate-nitrogen (NO_3-N) or ammonium-nitrogen (NH_4-N). Lower optimum level (22 mg kg^{-1}) of soil NO_3-N is required for obtaining maximum yield (Nurmanov *et al.,* 2019). NO_3-N increases the number of stolons and tubers per plant when applied during the tuber initiation stage. NH_4-N promotes early tuberization but a low number of stolons and tubers per plant (Gao *et al*., 2014; Qiqige *et al*., 2017). According to Dingenen *et al*. (2019), under a limited supply of nitrogen; the number of tubers per plant was reduced in potato varieties Andigena, Desiree, Saturna, Milva and Alegria by 71.4%, 66.7%, 75%, 75% and 40% respectively. Olivera and Da (2000) revealed that the tuber number per plant was increased by 55.3% with increasing nitrogen from 40 kg ha^{-1} to 200 kg ha^{-1}. Tuber formation is delayed when applying a total amount of nitrogen for basal dressing (Kleinkopf *et al.,* 1981; Olivera and Da, 2000) and tuber formation is inhibited by the higher amount of available nitrogen or continuous supply of nitrogen through roots (Sattlemacher and Marschner, 1979; Krauss and Marschner, 1982; Sarkar and Naik, 1998). On the other hand, De la Morena *et al*. (1994) confirmed that there was no direct effect on the final tuber yield or the number of tubers per plant by split application of nitrogen at different rates. This may be due to the leaching of applied nitrogen as mentioned by Errebhi *et al*. (1998). They examined that leaching of NO_3-N was increased with increasing nitrogen rates in basal fertilizers. Consequently, it is important to do further researches to find out clearly whether or not tuberization affect by high-dose soil-applied nitrogen of field-grown potatoes.

Effect of temperature on tuber formation

The optimum temperature for tuber initiation in potatoes is in the range of 15 to 25°C temperature. High temperature 30/25°C (day/night temperature) or high temperature with low irradiation (3.4 MJ m^{-2} d^{-1}) reduce stolons and tuber formation by decreasing photosynthetic efficiency and increasing production of GA in the buds. By increasing temperature in stolons and roots is caused to promote early senesce of plants (Menzel, 1983; Menzel, 1985; Struik *et al.,* 1989; Prange *et al*., 1990; Lafta and Lorenzen, 1995). Li and Zhang (2020) proved that potato yield was decreased by 583 kg ha^{-1} for every increment of temperature by 1°C in china. According to Dam *et al.* (1996), tuber formation is delayed under higher temperatures on long days. Wheeler *et al.* (1986) observed that tuberization did not occur at 28°C either photoperiods of 24 hrs or 12 hrs or 24°C at 24 hrs photoperiod of 400 μmol m^{-2} S^{-1} PPF. The high-temperature effect of potatoes can be mitigated by incorporating organic matter into the soil and mulching with straw-like materials (Paul *et al*., 2017). Zhang *et al.* (2020) found that late-maturing cultivars are highly affected by heat than early cultivars.

Effect of photoperiod and light intensity for tuber formation

It is a well-known fact that the light intensity and duration decide the final yield by controlling photosynthesis and dry matter partitioning to the tubers. Likewise, light intensity and duration affect to tuberization of potatoes. For instance, tuber formation is delayed and reduced when exposed to long photoperiods or shading while tuber initiates early when exposed to far-red light. Tuberization also can take place without a dark period if the temperature is low (Wheeler *et al.,* 1986; Demagante and Zaag, 1988; Marwaha and Sandhu, 2002; Plantenga *et al*., 2016). Cristina *et al*. (2014) found that the number of daylight hours affects the number of stolons formed in early and intermediated maturing varieties. Presently, most of the commercially cultivated potato varieties do not affect tuberization by the length of the photoperiod (Mackerron and Haverkort, 2004; Kloosterman *et al*., 2013). After considering these facts, it is crucial to study CCC-like growth regulators to promote tuberization under low irradiation levels with warm environmental conditions. In warmer areas, it may be suitable for growing potatoes during a cloud-free season with abundant sunlight or provide extra light to promote early tuberization and to initiate more tubers. In the cooler area, additional light may be required to enhance yield, especially during the bulking phase. It is important to consider light intensity when conducting experiments on potatoes to draw valid conclusions.

Effect of drought and irrigation on tuber formation

One of the major limiting factors for the production of potatoes is the limited availability of irrigation water in the tropics and subtropics. Even though water is absorbed by the root system, it can also absorb through the roots of stolons and tubers (Kratzke and Palta, 1985). During water stress, photosynthesis inhibits or reduces due to the closing of stomata (Schapendonk *et al.,* 1989). According to Aliche *et al*. (2020), stolon and tuber formation are inhibited or reduced under drought conditions by reducing carbon partitioning. Wang *et al.* (2013) observed that mulch with trickle irrigation is secured more tubers under water deficit conditions. Li and Zhang (2020) revealed that potato yield was increased with every 100 mm increasing of precipitation in the rainfed area of China. According to Jama-Rodzenska *et al.* (2020), stolons' weights were higher in cv. Denar and Julinka are under low or optimum water levels than higher water. Tuber yield is reduced by early and midseason moisture stress (Lynch *et al.,* 1995).

CONCLUSION

Tuber formation in potatoes is a complex process that consists of two processes: stolon formation and tuberization. It is induced by a mobile signal called tuberigen under an inducive condition by involving several genes. Low temperature, high irradiation and some growth hormones: ABA, CCC, kinetin, BAP, Jasmonic acid, low concentration of IAA and paclobutrazol promote tuber formation while Ethelene, high concentration of IAA, drought, low irradiation, high temperature reduce or inhibit tuber formation. Further studies need to clarify the effects of tuber formation by higher soil nitrogen, CCC with different rates of fertilizers and mitigation of high temperature for field-grown potatoes.

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