DEMETER: Journal of Farming and Agriculture
Vol 2, Issue 3, November 2024, Page 189-195
ISSN: 2987-5889 (Media Online)
DOI: https://doi.org/10.58905/demeter.v2i3.424

The Effect of Water Stress on Tuber Formation in Potato Plants

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Abstract. Potato (*Solanum tuberosum* L.) is often considered a drought-sensitive crop, and its sustained production is increasingly threatened by frequent drought events. Drought presents one of the most significant challenges to potato production worldwide. Plants experience water stress when the water they receive is insufficient to meet their actual needs. The effects of drought stress range from disruptions at the molecular and biochemical levels within cells to physiological and morphological impairments at the leaf and whole-plant levels. Potato plants are particularly vulnerable to drought due to their shallow root systems. As a result, climate change is expected to have a considerable impact on global potato production, as limited water availability can significantly reduce tuber yield. Potato plants respond to drought stress through various physiological, biochemical, and molecular strategies. This review compiles research findings to better understand the impact of water stress on tuber formation, the mechanisms through which drought stress affects potato plants, the plant's resistance responses, and strategies to mitigate the effects of drought stress in potatoes.

Keywords: Drought, Potato, Stress, Response, Tuber Formation

1 Introduction

Potato (*Solanum tuberosum* L.) is a horticultural crop with high potential to be developed as an alternative staple food to rice. Amid current unfavorable climatic conditions, concerns over food shortages are inevitable. Therefore, potatoes, as a tuber crop, are increasingly viewed as a promising food source. Potatoes are one of the most dominant food crops globally, with high production rates, especially in subtropical countries such as the United States, the Netherlands, New Zealand, and Japan.

In addition to their high carbohydrate content, potatoes are also rich in other nutrients, including proteins, essential amino acids, sodium, vitamin C, calcium, iron, and vitamin B6. The use of potatoes in the food processing industry is also growing, with potatoes commonly processed into French fries, chips, or other snack products [1]. In terms of production, potato productivity in Indonesia currently stands at around 1.2 million tons per year [2]. Although potatoes are traditionally grown in highland areas, they are now commonly cultivated in mid-altitude regions as well. However, achieving optimal yields requires appropriate agronomic management, particularly adequate water supply throughout the plant's growth cycle.

Agricultural disturbances can pose a significant threat to crop yields. Any form of stress experienced by the plant can lead to reduced productivity, or even complete crop failure. It is therefore essential to address these issues to minimize negative impacts. One of the main abiotic stress factors that affects crops is drought, especially in the context of Indonesia's increasingly unpredictable climate, where prolonged dry seasons can lead to water stress and hinder plant growth. This paper aims to explore the effects of water stress on tuber formation in potato plants (*Solanum tuberosum* L.)

2 Materials and Methods

This study is a literature review, compiling and analyzing several reputable national and international journal articles indexed between 2020 and 2024. The selected articles focus on the effects of water stress or drought on

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tuber formation in potato plants. Sources were chosen based on their relevance to the topic, scientific validity, and data accuracy.

3 Results and Discussion

3.1 Water Stress/Drought Stress on Potato Plants

Stress on plants is a change in environmental conditions that reduces growth and development activity in plants. One of the factors causing stress in plants is water availability. Water availability significantly affects the growth process and average harvest yields. Insufficient water availability is the most limiting factor for plant growth worldwide. Under water drought stress, the water potential in the root zone becomes negative and limits the root's reach for water, thereby affecting plant growth and production.

In plants, stress can be defined as any unfavorable condition or substance that affects or hinders the metabolism, growth, or development of the plant and refers to environmental changes. Stress can be classified into two categories: abiotic and biotic. Abiotic stress refers to environmental factors such as physical or chemical, while biotic stress exposes plants to biological units such as diseases and predators.

Drought is technically a purely meteorological term that describes a long period of little or no rainfall. From a biological perspective, the definition of drought is expanded to include its impact on plant life. Drought in this context is still a period with little or no rain, but it leads to a deficit of soil moisture and, as a result, a reduction in water potential in the affected plant tissues. In agriculture, drought can be considered a period of water shortage that causes a deficit of moisture in the soil and drought stress in plants, preventing them from reaching their maximum genetic yield potential. Drought stress is a plant's response to drought and includes the morphological and physiological adaptations that occur when plants sense the loss of sufficient water to sustain growth before drought.

Drought can be further defined in terms of onset and duration related to the plant life cycle. Intermittent drought describes one or more periods of inadequate water supply for optimal growth that occur at any time during the growing season. After intermittent drought, soil moisture is replenished allowing normal growth to continue. This is different from terminal drought, which also describes a period of inadequate water supply for optimal growth, but there is no replenishment of soil moisture in the plant life cycle. Terminal drought leads to a progressive decrease in soil moisture and, depending on the severity and duration, can result in reduced yields and even early plant death.

Potatoes are one of the most important food crops in the world, alongside wheat, rice, and corn. Cultivated potatoes (Solanum tuberosum L.) are sensitive to moderately sensitive to drought, depending on the criteria used for classification. This sensitivity is related to the plant's growth stages, becoming more sensitive to drought during the early growth period and the tuberization period. Drought stress occurs when soil moisture is low, relative humidity is low, and temperatures are high. If drought persists, the plants will dry out and production will be negatively affected. In potatoes, drought stress slows down plant development and reduces plant mass weight, as well as dramatically decreasing the number, size, and yield of tubers.

Drought stress is one of the main limiting factors in potato plant growth. When water availability is insufficient, the plants undergo various physiological and morphological changes that can affect their ability to grow optimally. Plant growth and development are determined by the plants' ability to perform photosynthesis.

3.2 The Influence of Water Stress on the Tuber Formation of Potato Plants

Potato plants are one of the food crops that are highly susceptible to drought stress. Drought stress is a multidimensional factor that has complex effects on the physiology and growth of plants [3]. Drought can affect various aspects of the growth and development of potato plants, including a decrease in biomass, physiological changes, and a reduction in tuber yield. According to a study by Aliche et al. (2018), drought stress results in a decrease in the rate of photosynthesis and an increase in the production of free radicals, which can damage plant cells [4]. In addition, drought can also affect the distribution and absorption of nutrients, which ultimately impacts the quality and quantity of the harvest.

Potato plants are classified as C3 plants, which perform photosynthesis to produce energy. Photosynthesis works optimally at temperatures of 20-25°C, with a light intensity needed of around 300-500 µmol/m2/s for maximum photosynthesis rate. The growth of potato plants consists of several phases, starting from the vegetative phase which includes the formation of leaves, stems, and roots, to the tuber formation and filling phase where the products of photosynthesis are stored in the form of starch in the tubers [5]. The ideal temperature for tuber formation is 15-20°C, while temperatures above 25°C can inhibit this process.

The absorption of water and nutrients is very important, especially during the tuber formation phase. Drought can impact all growth phases, including disrupting the photosynthesis process and inhibiting tuber initiation, leading to poor tuber formation. The tuber initiation phase is a critical period for plants when they are under

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drought stress. The potato's response to drought varies depending on drought capacity and the type of genotype being cultivated. The physiological response of the plant may include a decrease in (growth rate, internal CO2 concentration, photosynthesis rate, and stomatal conductance), loss of turgor pressure, as well as signals from the roots in the form of abscisic acid (ABA).

Drought can affect various aspects of the growth and development of potato plants, including reduced biomass, physiological changes, and decreased tuber yields. Drought in potatoes not only reduces harvests but also damages the quality of potato tubers, such as scabbing on the tubers, due to the plants absorbing less water [6].

Water stress during the initiation stage of stolons and tubers not only inhibits leaf and plant development but also limits the number of stolons, which leads to a reduction in the number of tubers and decreases the harvest yield and dry weight of the tubers.

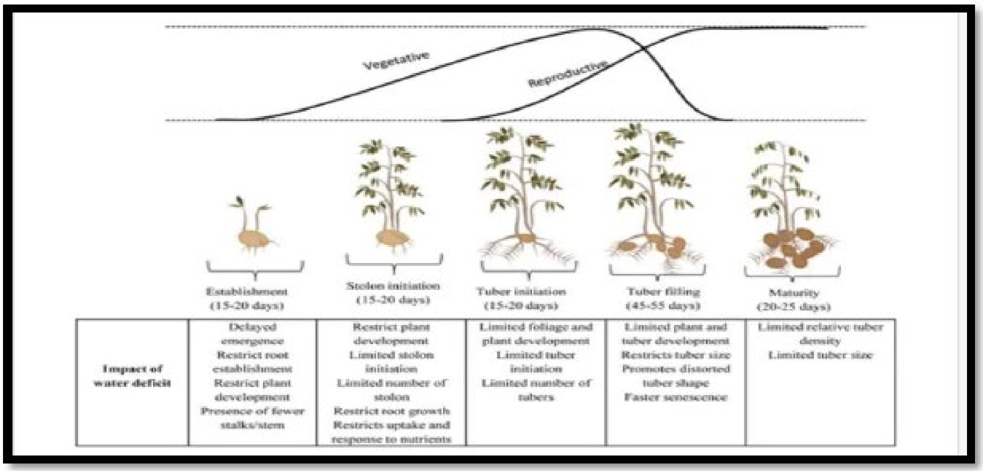

Figure 1. The effect of water stress on various stages of potato growth

From the image above, we can see that at the tuber initiation stage, water stress affects leaf and plant development, tuber initiation is limited, and the number of tubers is limited. At the tuber filling stage, water stress restricts plant and tuber development, limiting tuber size, causing many tubers to be defective, and accelerating cell aging. At the tuber maturity stage, water stress limits tuber density and tuber size is also restricted.

The productivity of potato plants is significantly affected by water availability. Drought during critical phases such as tuber formation can reduce the size and weight of tubers significantly. Research (Kartika and Kurniasih, 2021) shows that drought stress can decrease crop yield compared to crops that receive adequate irrigation [7]. In addition, tubers also decline, with lower starch content and higher moisture content, making them less ideal for consumption and processing. A study by Handayani et al. (2006) found that potato plants exposed to drought showed a decrease in the yield of the number of tubers per plant by 17.54%, the weight of tubers per plant by 70.35%, the length of tubers by 44.45%, and the diameter of tubers by 42.85% [8].

In the research by Gervais et al., 2021, on the treatment of 56 potato genotypes, including 54 commercial cultivars, grown under good irrigation conditions for 5 weeks and subjected to water stress for 6 days followed by re-irrigation until tuber harvest [9]. Under good irrigation conditions, potato genotypes showed differences in tuber yield. Drought stress significantly inhibited tuber yield in all genotypes, however, the reduction in tuber yield varied among genotypes. The percentage of tuber yield and quantity for potato genotypes experiencing drought stress was relatively smaller compared to potato genotypes that were well-irrigated. The reduction in tuber yield caused by drought was associated with a decrease in the total number of tubers for most potato genotypes under drought. However, the genotype's ability to maintain higher tuber yield under drought is not related to its capacity to sustain more tubers. Drought significantly reduces the total number of tubers in all genotypes regardless of their capacity to maintain differential tuber yield under drought conditions [10].

In their research, Chang et al also reported that drought stress during tuber initiation and stolonization limits tuber yield by reducing the number of tubers produced by the plants. This observation is consistent with previous studies that state that the number of tubers produced is most sensitive to drought stress at the tuber initiation stage. On the other hand, some studies have reported an increase in the number of tubers under drought stress. This may be due to the adaptive response of the cultivar to maintain yield under drought pressure or the effects of pre-existing abiotic stress, such as heat stress delaying tuber formation and resulting in more tuber production but smaller in size. Rykaczewska also reported an increase in small-sized tubers (<3cm) under drought stress.

In the writing of Nasir and Toth, 2022, the yield of fresh tubers depends on the allocation of dry matter to the tubers and the moisture content of the tubers, where the moisture content contributes up to 80% of the fresh tuber mass depending on the cultivar [11]. Therefore, the mass of fresh tubers is significantly affected by water

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deficiency. Jefferies and MacKerron reported that long-term water stress can reduce the relative water content of tubers by up to 69% compared to well-irrigated potatoes. However, the response of potatoes to water deficiency highly depends on the cultivar. The cultivars Remarka and Desiree were subjected to similar drought stress conditions in a field study. The results indicated a decrease of 44% and 11% in the yield of fresh tubers for cultivars Remarka and Desiree, respectively. In another study, Boguszewska-Mankowska et al. examined the effects of drought stress on fresh tuber weight, where all cultivars decreased under drought stress varying from 1248 g (in Gwiazada) to 788 g (in Cekin). In this study, the decrease in tuber moisture content has been mentioned to cause a reduction in the yield of fresh tubers.

In addition to the cultivar, the weight of fresh tubers is also influenced by the length and severity of drought stress. Both late drought and early drought significantly affect potato yield. Early stress (from sprout emergence to tuber initiation stage) significantly reduces the weight of fresh tubers from early mature and late mature cultivars. However, late drought (occurring from sprout emergence to tuber bulking stage) affects early mature cultivars more severely than late mature cultivars.

3.3 The Mechanism of Potato Plants Under Stress Due to Drought Conditions

Drought stress will reduce the growth and photosynthesis of plants due to stomatal closure and the effects of metabolism. Water deficit will cause stomatal closure, which will reduce cellular CO2 concentration, while dehydration of mesophyll cells in leaves can cause damage to photosynthetic organs. The adverse effects of drought stress on photosynthesis will be mediated by responses to: (i) respiration systems, electron transport, ATP synthesis in mitochondria, (ii) accumulation of metabolites induced by stress; and (iii) gene expression and protein synthesis.

Plants generally respond to drought stress by closing their stomata to reduce further water loss through evapotranspiration. This response also reduces gas exchange through the stomata, limiting the availability of CO2 for photosynthetic assimilation. Stomatal closure was previously thought to be the primary hydraulic response to the decline in leaf water potential caused by excessive water loss through evapotranspiration, regardless of root water potential or soil moisture. Abscisic acid (ABA) has been identified as a key molecule involved in root-to-shoot signaling of drought stress. Potato root tips have been shown to produce ABA in response to moderate decreases in soil moisture. A linear relationship between xylem-borne ABA, whose concentration is enhanced by ABA production in the roots, and stomatal conductance has been observed in light groundwater deficit on potatoes. This indicates that root-to-shoot chemical signaling plays an important role in stomatal conductance even before a decrease in leaf water potential is detected.

Water deficit will cause the closure of stomata which will reduce the concentration of CO2 in the mesophyll (changes in electron transport and biochemical pathways). Biochemical changes include a decrease in the synthesis of ribulose bisphosphate (RuBP).

At the electron transport level, the decrease in CO2 assimilation leads to a decrease in NADP regeneration, resulting in the formation of reactive oxygen species (ROS) and potential inhibitor damage. The decrease in intercellular CO2 concentration supports the oxygenation of Rubisco (RuBP carboxylation/oxygenation), which also contributes to ROS production.

3.4 The Influence of Water Stress on Hormones in Potato Plants

Drought stress affects biochemical and physiological processes at the cellular level. Plants experiencing drought stress have lower turgor pressure, thereby reducing physiological functions such as photosynthesis activity [12]. Biochemically, drought stress reduces the synthesis of auxins, cytokinins, and gibberellins (GA) and inhibits the activity of the enzyme alpha-amylase. Drought stress also affects the onset of leaf growth and reduces cell division and expansion [13].

Plants cope with water scarcity by reducing water evaporation and increasing water uptake from the soil, such as in succulent plants. Plants reduce water evaporation by closing their stomata. The closure of stomata is related to the activity of the abscisic acid (ABA) hormone. When the soil is dry, hydraulic signals induce the synthesis of ABA in plants. ABA in the roots is transported to the stomatal guard cells, causing the stomata to close and leading to a decrease in photosynthesis and respiration. The decrease in respiration is caused by changes in the permeability of mitochondrial membranes. Changes in the structure of phospholipids or proteins inhibit the oxidation of respiratory substrates. Banzinger et al. (2000) mention that drought stress will affect photosystem II. During drought conditions, electron transfer is hindered, resulting in chlorophyll undergoing photooxidation and a decrease in photosynthetic activity [14].

In response to drought signals, the plant hormone ABA (abscisic acid) increases relative to the severity of stress and is a key signal in the cellular response by activating the expression of various drought-responsive genes.

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Other hormone signals sent to the shoots through transpiration flow along with ABA after drought perception, namely ethylene and gibberellin acid (GA). These hormones trigger young and mature leaves. With the response of ABA in mature leaves, and the response of ethylene and GA in dividing and developing leaf cells. Similarly, jasmonic acid (JA) becomes an important cellular regulator that activates the signaling transduction pathway between stress perception and responses under drought conditions.

3.5 Response of Potato Plant Resilience to Water Stress

When plants experience drought stress, they will initiate mechanisms to cope with it; roots can sense water deficit first, triggering physiological and biochemical responses, and optimizing root morphology and architecture to better deal with subsequent drought stress [15].

Physiological Response:

a. Stomatal Closure
   One of the physiological responses of potato plants subjected to drought stress is an increase in the production of stress hormones, such as abscisic acid (ABA), which triggers stomatal closure. Stomatal closure reduces water loss through transpiration but also limits the entry of carbon dioxide, which may potentially lower the rate of photosynthesis.
b. Accumulation of Osmolytes
   Potato plants also increase the accumulation of osmolytes such as proline and soluble sugars. These osmolytes function to maintain cell turgor pressure so that plant cells can continue to function despite water deficits.
c. Antioxidant Activity
   In facing drought, potato plants increase the activity of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) which help reduce oxidative damage caused by free radicals. Drought stress triggers the accumulation of reactive oxygen species (ROS), and enzymes like SOD and CAT help decompose ROS to prevent damage to plant cells [16]. The mechanisms of drought tolerance are generally controlled by many genes and the expression of each of these genes is very complex. At the cellular level, the cell membrane, like the endomembrane system, undergoes dramatic changes in disposition and limits the function of organelles, just as the integrity of the cell responds to water stress. The cell wall is a physical barrier that also provides protection to a limited extent due to the deformation of its properties. When the cell is subjected to water stress, the rigidity of the cell wall will provide mechanical protection, but this organ is permeable, allowing desiccation to occur if higher stress is applied.

Biochemical Response:

a. Biochemical changes
   The increase of osmoprotectants such as proline helps protect cells from osmotic stress, while antioxidants prevent damage caused by oxidative stress. These biochemical adaptations are important to minimize cell damage and ensure the survival of plants during periods of water stress.
b. Metabolism Settings
   Potato plants can modify their metabolic pathways to improve the efficiency of water and nutrient use. This includes increased synthesis of compounds that help plants withstand drought conditions [17].

Morphological Response:

a. Morphological adjustments of leaves
   Potato plants can reduce leaf area to minimize water loss through transpiration. Smaller and thicker leaves can help reduce water evaporation [18].
   Modification of Root Systems
b. Potato plants, which have a relatively shallow root system, often face difficulties accessing deeper groundwater during periods of drought. Drought forces potato plants to allocate resources to the root system, particularly deeper roots to search for water [17]. Potato plants with deeper roots are more resilient to drought. The photosynthesis results of potatoes (starch) that should be stored and accumulated into potato tubers are channeled to the potato roots to sustain their life cycle; therefore, potatoes experiencing drought stress will produce tubers that are very small compared to potato plants growing in their optimal environment [19].

3.6 How to Overcome Drought Stress on Potato Plants

Agronomic steps are potential measures to reduce the physiological impact of drought on potato plants. Agronomic approaches include a series of actions that can be taken to maximize potato yields. By examining various effective agronomic methods, it is hoped that practical solutions can be found to help farmers improve potato productivity under drought conditions. Agronomic approaches that focus on the use of tolerant varieties, water use efficiency, soil management, and technical cultures that include fertilization, addition of organic matter, use of mulch, determination of plant spacing, and the use of bio-fertilizers and plant growth regulators are expected to have a significant impact on enhancing potato production resilience to drought stress. The following are the steps that can be taken to address drought:

a. Land management, such as weed sanitation, soil loosening, making ridges/beds, adding organic matter or compost, using mulch.
b. The use of tolerant varieties / breeding of resistant varieties, such as black potatoes, porvenir, patagonia, and yaike, shows better resistance to drought.
c. Selection of plant materials, such as disease-free tubers, mini cutting seeds with a shorter lifespan and high disease resistance. Planting asexual propagation plants on a large scale creates possibilities for different genes and, as a result, selection for desired characteristics. Drought tolerance in plants can be improved through traditional breeding or genetic manipulation techniques.
d. The spacing and planting time settings, the ideal planting distance is 70 x 15 cm, the right time to plant potatoes to address drought is at the beginning of the rainy season and after the first rainy season to take advantage of optimal soil moisture.
e. Providing shade, the provision of shade on potatoes causes the soil to become saturated, temperature and humidity become more stable.
f. Irrigation techniques, such as drip irrigation.
g. Pest Organism Control, control using the concept of Integrated Pest Management (IPM)
h. The use of beneficial microorganisms, such as PGPB (Plant Growth Promoting Bacteria), biological control agents like Trichoderma spp.
i. Planting arrangements, cropping patterns, and crop rotation
j. The use of Plant Growth Regulators (PGR), such as Paclobutrazol which can inhibit cell elongation, salicylic acid which can maintain osmotic potential, increase antioxidant enzymes, and secondary metabolites.

4 Conclusion

The presence of drought stress will affect the photosynthesis process, thereby directly impacting potato plant productivity. Potato plants exposed to drought show a decrease in crop yield of 17.54%, tuber weight of 70.35%, tuber length of 44.45%, and tuber diameter of 42.85%.

5 Acknowledgements

Acknowledgments. The author expresses gratitude to all parties who have supported this writing, also to Prof. Dr. Ir. Nurhayati, MP who has guided the author in the preparation of this scientific paper. Thanks also to colleagues who have provided input in the writing.

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