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(MATE)

Water Shortage Induced Response of Two Hungarian Potato (*Solanum tuberosum* L.) Genotypes

Doctoral (PhD) dissertation

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LIST OF LEGENDS AND ABBREVIATIONS

ANOVA	Analysis of variance
CAT	Catalase
CV	Coefficient of variation
DAS	Days after sowing
df	Degree of freedom
LAD	Leaf area duration
LAI	Leaf area index
LAR	Leaf area ratio
LW	Leaf weight
MS	Means of squares
N%	Nitrogen content in foliage (%)
NL	Number of leaflets
NT	Number of tubers
p	Probability
PVA	Potato virus A
PVY	Potato virus Y
RDW	Root dry weight
RFW	Root fresh weight
RL	Root length
ROS	Reactive oxygen species
RuBP	Ribulose bisphosphate
RWC	Relative water content
SL	Shoot length
SLA	Specific leaf area
SLW	Specific leaf weight
SOD	Superoxide dismutase
SPAD	Soil plant analysis development
SS	Sum of squares
STDEV	Standard deviation
TDM	Total dry matter
TY	Tuber yield

1. INTRODUCTION

Potato (*Solanum tuberosum* L.) is the fifth most produced main crop in the world after sugar cane (*Saccharum officinarum* L.), wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.). Potato is being cultivated around the globe (Fig. 1). Potato cultivation originated in the New World, where its wild relatives can still be found (Spooner et al. 2004). In South America, potato cultivation began around 8000 years ago, and Spanish conquistadors during the Columbian exchange introduced potatoes to Europe (Lutaladio and Castaldi 2009). By the end of the 16th century, potatoes had been introduced into Ireland and the United Kingdom (Bradshaw and Ramsay 2009). In Europe, its cultivation started almost 100 years later (Bradshaw and Ramsay 2009), but monocultural practices led to the destruction of Irish potatoes on a large scale by late blight (Lutaladio and Castaldi 2009). Therefore, breeders directed their efforts towards producing resistant and high-yielding cultivars (Lutaladio and Castaldi 2009).

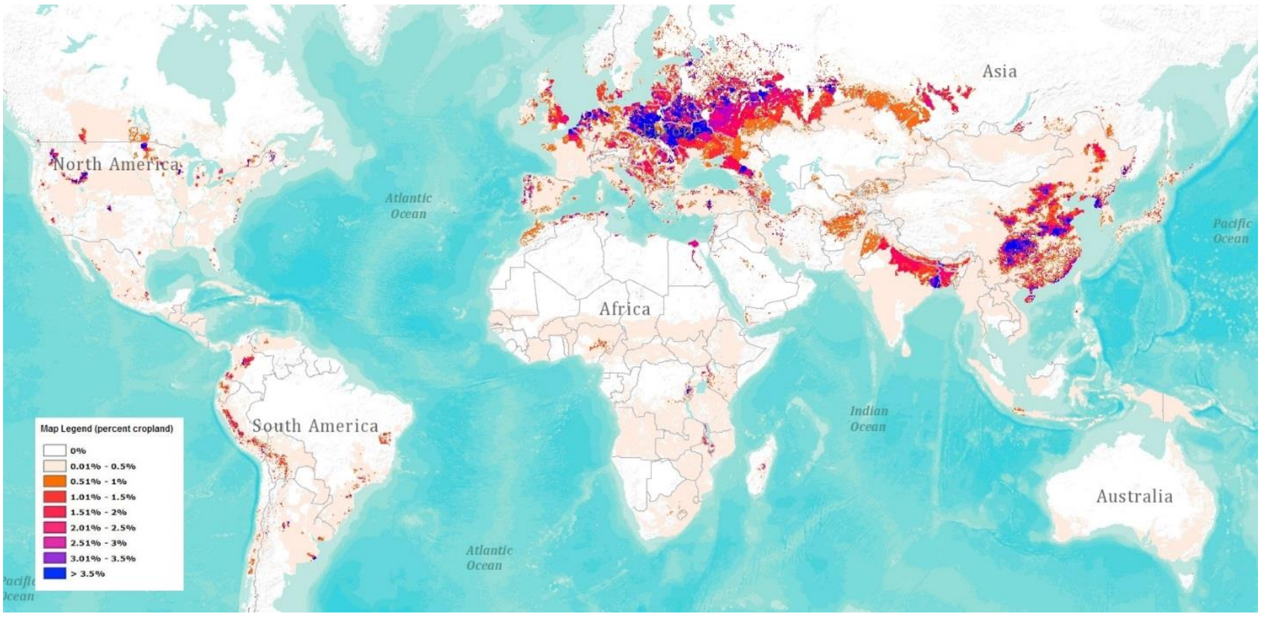


Figure 1 World potato growing regions (Anon. 2022)

Potato production in the world has increased from 270 million tons in 1961 to 370 million tons in 2019. The increase in production is primarily because of a consistent increase in yield potential of potato cultivars, as the area harvested for potato production decreased from 22.14 million hectares to 17.34 million hectares in the same period. The yield potential of potato cultivars has increased by 58.7% in the last half-century (Fig. 2). China, India, Russia, the USA, and Ukraine are the largest potato-producing countries, followed by Poland, Germany, Belarus, Netherlands, and

France (Fig. 3). Europe is the second-largest potato-producing region (125.43 million tons) after Asia (140.6 million tons) (Fig. 4) (Anon. 2021a).

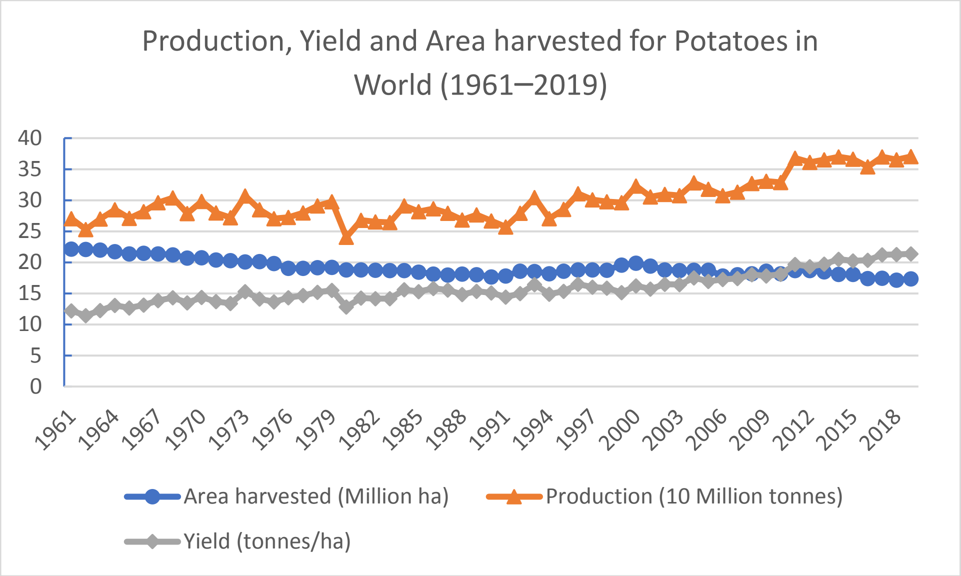


Figure 2 World potato production, yield, and area harvested during 1961-2019 (Anon. 2021a)

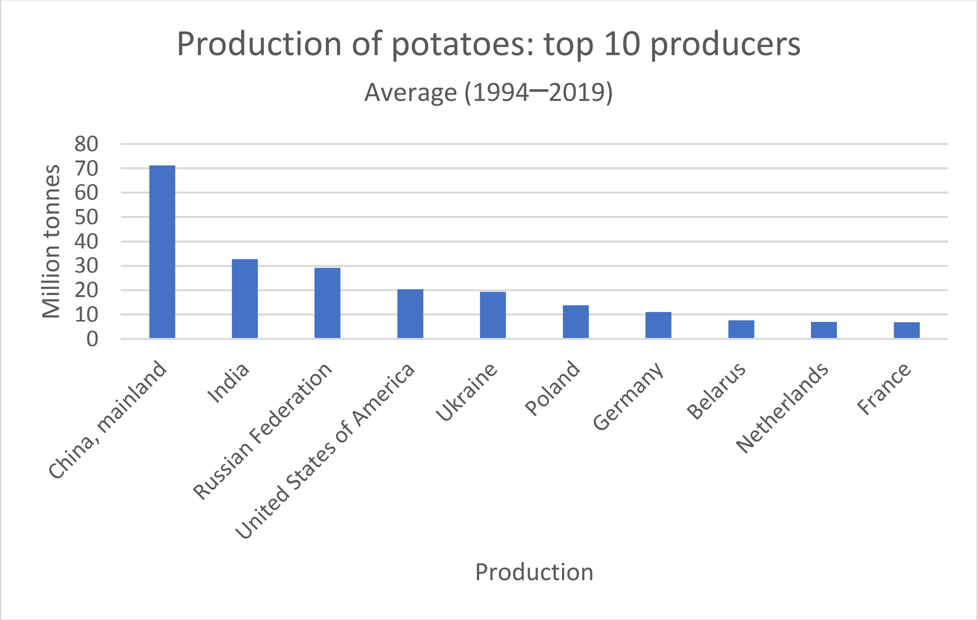


Figure 3 Top 10 potato producers in the world during 1994-2019 (Anon. 2021a)

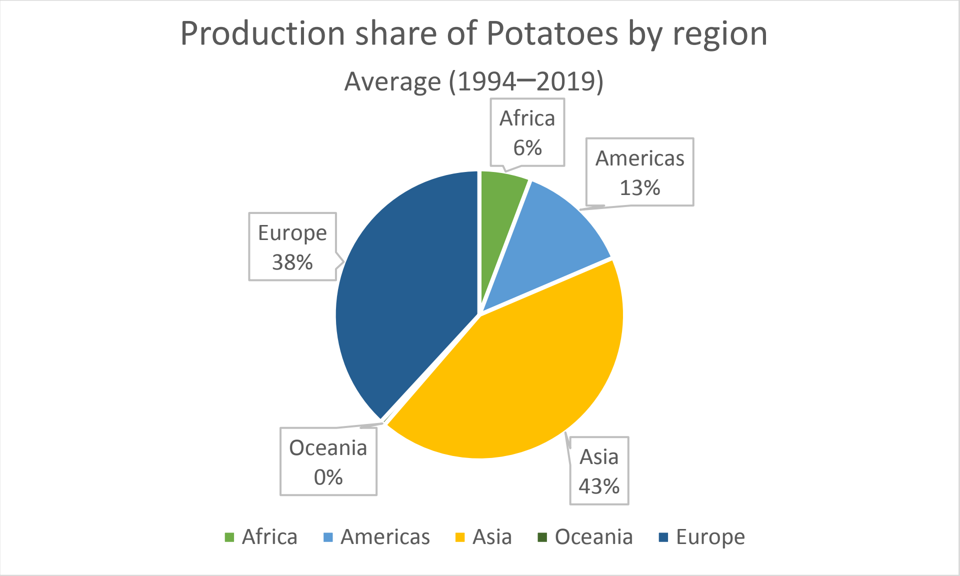


Figure 4 Regional share in potato production during 1994-2019 (Anon. 2021a)

In Europe, potato production has reduced from 137.1 million tons in 1994 to 107.26 million tons in 2019. The highest potato production in Europe was observed during 1996 and has been declining ever since. The main reason for the decrease in tuber production in Europe is the reduction in the harvested area by 51.7% between 1994-2019. In 1994, potatoes were harvested on 9.7 million ha of European land; however, in 2019, only 4.69 million ha of land was used for potato production (Fig. 5). Recent FAO stats show that most of the potato production in Europe comes from Eastern Europe (55%-61%), followed by Northern Europe (25%-29%). Southern Europe and Western Europe contribute only 6% and 10%, respectively (Fig. 6).

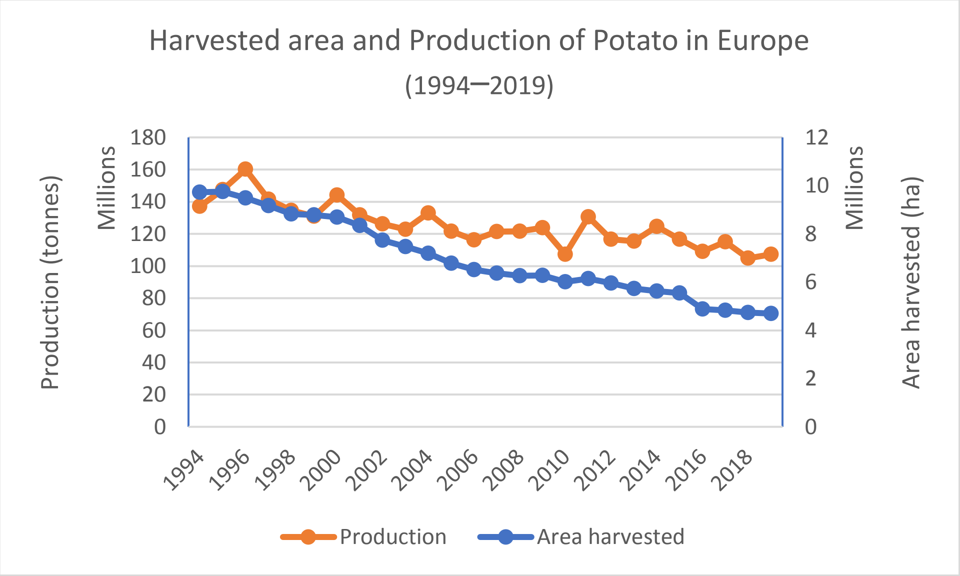


Figure 5 Potato production and area allocated for potato harvest in Europe during 1994-2019 (Anon. 2021a)

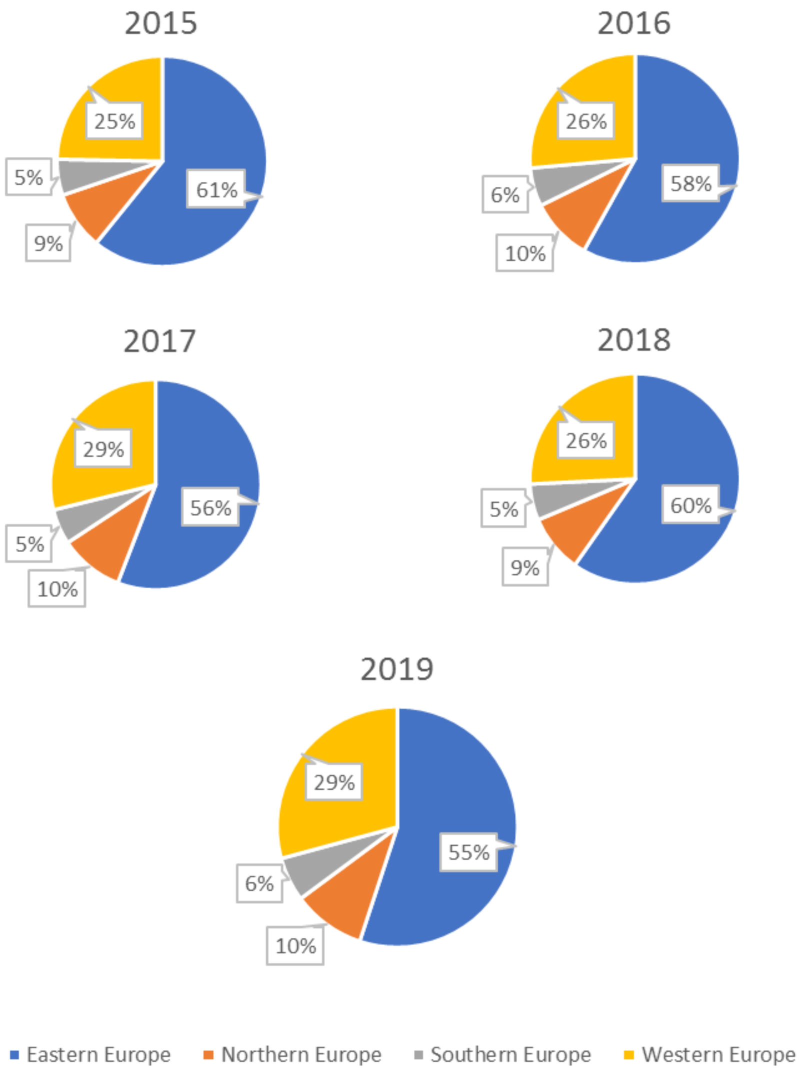


Figure 6 Potato production shares by different European regions during 2015-2019 (Anon. 2021a)

Potato is considered an important crop in developed and developing countries because of its versatile utilization (Lutaladio and Castaldi 2009). Approximately 85% of the biomass of a potato plant is edible: much higher than the 50% of edible biomass from cereals (Lutaladio and Castaldi 2009). In Europe, potato is the fourth most important crop by production (107.26 million tons) after wheat, sugar beet, and maize, while the ninth most important crop by land used for harvesting (4.69 million hectares). Potato yields the second highest per unit area production (22,840 kg ha^{-1}) among the top five crops produced by European countries (Table 1).

Table 1 Area harvested and yield per unit land of the five most produced crops in Europe in 2019 (Anon. 2021a)

Crop	**Production (Million Tons)**	**Area (Million ha)**	**Yield (kg ha^{-1})**
Wheat	266.123	62.39	4266
Sugar beet	194.46	3.17	61,412
Maize	132.773	18.35	7234
Potatoes	107.265	4.69	22,840
Barley	95.634	24.22	3948

Modern cultivars are successful in improving tuber yield (Anon. 2021a), yet they are sensitive to drought. Drought is a multidimensional stress as it affects physiology, morphology, ecology, biochemical and molecular traits of plants (Salehi-Lisar and Bakhshayeshan-Agdam 2016). 92% fresh water usage is associated to agriculture and decrease in fresh water reservoirs would cause water shortage stress (Nouri et al. 2019). Arid and semiarid regions are expected to face serious drought stress in coming decades. We have already witnessed some of the worst droughts in previous few decades (Schubert et al. 2004). The water crisis is expected to increase due to climate change that negatively affects crop production (Thiele et al. 2010; Monneveux et al. 2013). Several climate models forecast reduced annual rainfall and increased temperature with frequent droughts that negatively affect worldwide crop productivity (Pachauri et al. 2014). With decrease in annual rainfall, rainfed agricultural area will also need irrigation to sustain their yields.

Potato is a cool climate loving crop and is cultivated in different regions of the world. We have developed high yielding potato cultivars but abiotic stresses can cause up to 50% reduction in tuber yield (Wang et al. 2003). Drought stress is studied as one of the major tuber yields limiting abiotic stresses. Potato is a water efficient crop but its shallow roots make it prone to drought (Watkinson et al. 2008). Several *in vitro* and field studies have been conducted to understand the effect of drought stress on potatoes (Schittenhelm et al. 2006; Hassanpanah 2010; Albiski et al. 2012; Monneveux et al. 2013). Reduction in the number of shoots (Albiski et al. 2012), plant height (Schittenhelm et al. 2006; Albiski et al. 2012), leave numbers and area (Jefferies and MacKerron 1989), stolons (Haverkort et al. 1990), root length, and expansion (Albiski et al. 2012) have been reported in previous studies.

Plants have adopted various strategies to withstand drought stress through avoidance or tolerance (Yue et al. 2006). However, it is very complicated to characterize drought tolerance in potato cultivars as the different yields of different cultivars are not related to specific physiological or morphological traits (Stark et al. 2013). Different potato cultivars adapt to drought stress in different ways e.g., by higher assimilation portioning to tuber or by producing more tubers or by producing few but larger tubers (Deblonde and Ledent 2001). Understanding the mechanism of potato response to drought stress is a challenge to enhance crop drought tolerance. Water scarcity enforces the need for potato genotypes identification that exhibits high tolerance to drought stress (Monneveux et al. 2013).

Widely used drought tolerance indicators in potatoes are leaf water content (Omae et al. 2005) and yield (Farshadfar and Elyasi 2012). Leaves are involved in photosynthesis and account for most of the water loss via transpiration; therefore, better canopy development, such as leaf shape, leaf areas, number of leaves, and stem length indicates a drought tolerance in potatoes (Schittenhelm et al. 2006). Under drought conditions leaf wilting is the most proper visual response to drought accompanied by a reduction in the number of leaves and stem length. Several agro-physiological parameters such as leaf area index, leaf area duration, chlorophyll content, and decrease in water loss have been established to be related to drought tolerance (Deblonde et al. 1999; Lahlou et al. 2003; Khan et al. 2015). Moreover, root system development has important implications for plant development and survival under drought conditions, as they absorb water and dissolved nutrients. Potatoes having a shallow root system; therefore, drought tolerance partially depends on root development as well (Iwama 2008; Joshi et al. 2016). Potato cultivars with larger and more expanded root systems are more likely to be able to retrieve water from the soil; therefore, being less susceptible to periodic drought (Wishart et al. 2013; Villordon et al. 2014). Measurement of the size and extent of the root system of different cultivars gives key information for breeding cultivars adapted to regions with frequent shortages of rainfall. That is why drought stress response of the genotypes can be observed by variation in several above ground and/or below ground plant development parameters.

1.1. Objectives to achieve

This study aimed to attempt to describe the differences between two Hungarian bred potato genotypes’ responses to drought in terms of the agro-physiological parameters and to establish which characters were the most related to the yield and/or drought tolerance.

The objectives are as follows:

a) Determine the effect of drought stress and identify any drought tolerance in Hungarian potato genotypes.
b) Determine the drought tolerance strategy of Hungarian potato genotypes.
c) Determine the variation and role of morphological characteristics of potato genotypes in drought tolerance.
d) Establish the relation between growth parameters and drought tolerance (if any) in potatoes.
e) Determining the plant developmental stage most susceptible to drought stress.
f) Determining the variation in chlorophyll content during different plant developmental stages and within plants.

2. LITERATURE OVERVIEW

2.1. Potato production technology and yield constraints

Potato - a member of the Solanaceae family - is an annual herbaceous plant. Since its expansion from the Andean highlands, around 4500 potato cultivars have been adapted to different environments (Pieters and El Souki 2005). Based on harvesting time, these cultivars are grouped in early varieties (75-90 days), mid varieties (90-100), and late varieties (100-110 days). As a short-duration crop, potato fits well in multiple intercropping systems worldwide. Potatoes can be grown in different soils (alluvial, laterite, hill, red, and black) ranging in pH from 5-7.5, but loamy soils with high organic matter are favorable for potato cultivation (Reddy et al. 2018). Traditionally, seed tubers containing 2-3 healthy eyes are used for potato propagation. Larger seed tubers are cut into pieces of 3.5-5 cm in diameter, with each piece having a couple of eyes to be used for propagation (Reddy et al. 2018). Seedbed preparation includes ploughing to a 20-35 cm depth followed by tilling (Salavati et al. 2018). In hot weather conditions, soil turning and keeping it fellow is also adopted to reduce soil-borne pathogen and weed problems (Reddy et al. 2018). Seed tubers are sown into ridges, and the furrow irrigation method is most popular for irrigation (Singh et al. 2021). Depending on the cultivar, potatoes can grow up to 107 cm tall; therefore, earthing up is also recommended 30 days after planting.

Potato is a cool climate-loving crop and does not perform well at high temperatures (Haverkort and Verhagen 2008; Pulatov et al. 2015). Sunny days and cool nights provide a better crop growth environment; however, vegetative growth of potato and tuber development require different temperatures. For vegetative growth, 16-25 °C is considered the optimum temperature, while for the tuber initiation and bulking stage, 4-18 °C is considered optimum (Reddy et al. 2018). Tuber formation initiates after 20-25 days of sowing (Watanabe 2015), and plants produce blossoms in a white to purple color that may or may not drop off depending upon weather conditions. Based on the climate, soil types, and variety, plants require 350-550 mm rainfall during their life cycle (Reddy et al. 2018). Irrigation is stopped 10-15 days before harvesting, and harvesting is performed before the temperature reaches more than 30 °C.

Potato can be cultivated in diverse climatic conditions, and its production can be elevated significantly. Potato can yield 35 t ha^{-1} depending on environmental conditions and the variety of potatoes (Reddy et al. 2018). Nevertheless, several biotic and abiotic factors limit potato productivity causing a reduction in the potential yield of potatoes. Biotic factors affecting potato production include diseases caused by fungi, bacteria, nematodes, and viruses. The most common fungal and bacterial diseases reported in potatoes are late blight (Mekonen and Tadesse 2018), early blight (Horsfield et al. 2010), black scurf and stem canker (Rahman et al. 2014), and powdery scab (Gilchrist et al. 2011). Yield loss of up to 71%, 30%, 18%, and 58% was observed because of late blight (*Phytophthora infestans*), powdery scab (*Spongospora subterranea*), black scurf and stem canker (*Rhizoctonia solani*) and early blight (*Alternaria solani*), respectively (Table 2). Some of the most common bacterial diseases are common scab (Wang et al. 2019), bacterial wilt (Ding et al. 2013), and blackleg and soft rot (Ngadze 2018). Recent researchers have reported 24.58% yield loss by common scab (*Streptomyces scabies*), 34.9% yield loss by bacterial wilt (*Ralstonia solanacearum*), and 39.57% blackleg and soft rot (*Erwinia carotovora*) (Table 2).

Table 2 Potato yield loss (%) due to biotic stresses

Diseases	**Varieties**	**Yield Loss (%)**	**Reference**
Late blight	Bellete	53.74%	(Mekonen and Tadesse 2018)
	Gudenie	71.50%	
Powdery scab	Diacol Capiro	30%	(Gilchrist et al. 2011)
Black scurf and stem canker	Diamant	18.13%	(Rahman et al. 2014)
Early blight	Nadinc	Up to 58%	(Horsfield et al. 2010)
Common scab	Kexin No. 1	24.58%	(Wang et al. 2019)
Bacterial wilt	Helan 7	34.9%	(Ding et al. 2013)
Blackleg and soft rot	BP1	39.57%	(Ngadze 2018)
Potato leafroll virus (PLRV)	Victoria	91.8%	(Byarugaba et al. 2020)
	Kingi	84.8%	
	Sifra	22.1%	
Potato virus Y (PVY)	Victoria	87.2%	
	Kingi	85.1%	
	Sifra	14.1%	

Like other biotic factors, viral diseases are also considered potential yield-limiting factors in potatoes. Different publishers have estimated yield losses of 40% to 83% because of viral diseases (Nadeem et al. 2011; Hameed et al. 2014). Most common potato viral diseases include potato leafroll virus (PLRV), potato virus Y (PVY), potato virus S (PVS), potato virus M (PVM) and potato virus X (PVX). In extensive research, Byarugaba et al. (2020) reported the yield loss of as high as 91.8% and 87.2% because of PLRV and PVY, respectively, in susceptible varieties; while, yield loss of 22.1% and 14.1% because of PLRV and PVY, respectively, in virus resistant varieties (Table 2). Along with pathogenic diseases, various parasitic nematodes and weeds also affect potato yield. Root-knot nematode (Meloidogyne sp.) and potato cyst nematodes (Globodera sp.) are parasitic nematodes that can cause yield loss in tubers. Moreover, if not managed, weeds can compete with the main crop for resources and can reduce tuber yield considerably (Shedayi et al. 2011).

Besides biotic stresses, abiotic stresses also pose a serious threat to potato productivity. According to estimates, abiotic stress causes up to 50% average yield losses of different crops around the globe (Wang et al. 2003). Researchers discuss abiotic factors that influence potato productivity include temperature, solar radiation, photoperiod, soil salinity, and drought (Battisti and Naylor 2009; Camargo et al. 2015). Temperature plays a vital role in the yield determination of potatoes. Potato requires 16-25 °C ideally during vegetative growth, while 4-18 °C during the tuber initiation and bulking stage (Reddy et al. 2018). Drastic increases or decreases can have devastating effects on tuber yield. Increasing temperature at the vegetative phase may cause a high respiration rate, physiological wilting, reduced photosynthetic activity, and shortened life cycle. In contrast, the temperature increase at the reproductive phase can result in a smaller tuber, a slow tuberization rate, and a shorter reproductive phase leading to lower tuber yield (Hijmans 2003; Levy and Veilleux 2007; Hatfield and Prueger 2015).

On the other hand, a decrease in temperature (≤ 0 °C) at the early developmental stage may injure the seedling, alter the water movement in the plant, and affect the water and nutrient uptake of the plant (Hijmans 2003; Liao et al. 2016). A further decrease in temperature (≥ -3 °C) can demolish the whole field of potatoes (Pino et al. 2007). Salinity is another major abiotic factor affecting potato productivity. Potato is a salinity-sensitive crop, and significant yield losses can be observed by soil salinity (Obidiegwu et al. 2015). Poor water management, irrigation practices, reduced rainfall, and high evaporation rate in hot climates enhance the chances of soil salinity (Athar and Ashraf 2009). Potato is a water-efficient crop, but its shallow root system makes it susceptible to drought stress (Sun et al. 2015). Drought is one of the major abiotic constraints in potato productivity, affecting potatoe’s physiology, biochemical process, and yield (Fahad et al. 2017; Hirut et al. 2017). Therefore, the potato crop needs the optimum water to maintain its yield.

2.2. Potato water requirement and climate change

Potato is a comparatively water-efficient crop that produces more calories per unit of water utilized (Sun et al. 2015). According to Renault and Wallender (2000), 105 L water is required to produce one kilogram of potatoes, which is significantly less than other globally most produced crops (rice, wheat, and maize); these require 1408 L, 1159 L, and 710 L of water to produce one kilogram of rice, wheat, and maize, respectively. Despite of the high water use efficiency, potato is very susceptible to drought stress. One primary reason is the need for a large amount of irrigated water (Schafleitner et al. 2009). Depending upon agroclimatic conditions and soil available water, potato, on average, may require irrigation water between 143 mm to 313 mm (Knox et al. 1997). Li et al. (2022) and Vishnoi et al. (2012) reported that potatoes need 126-381 mm and 212-226 mm irrigation water to achieve potential potato yield in China and India, respectively. In dryer years - such as 2018 in the United Kingdom - the minimum irrigation water requirement increased up to 154 mm (Knox and Hess 2019). Byrd et al. (2014) also reported that during dry years in the United States, potatoes use 10 mm water every 24-36 h after flowering to harvesting, making the total irrigation water requirement up to 610 mm. Compared to potatoes, most other crops in Europe require less irrigation water. The irrigation requirement of sugar beet (0-253 mm), cereals (0-82 mm), carrots (0-258 mm), and strawberries (0-132 mm) are significantly less than potato (Knox et al. 1997).

Most potato cultivars have a shallow root system (Lahlou and Ledent 2005), making it challenging to absorb water from deeper soil layers in case of water shortage. Root length varies among the cultivars; however, the root length of potato cultivars has been reported to positively correlate with tuber yield in drought conditions (Lahlou and Ledent 2005). Moreover, transpiration losses due to canopy characteristics also vary in potato cultivars from stem-type canopy to leaf-type canopy (Aliche et al. 2018). The stem-type canopy performs better under drought stress conditions (Schittenhelm et al. 2006). Under severe stress, these characteristics can cause yield reduction as high as 87% reported by Luitel et al. (2015), in which case the cultivar Désirée could not maintain plant height and number of leaves. Therefore, potatoes are provided with additional water in the UK, USA (Daccache et al. 2011; Byrd et al. 2014), and some Mediterranean regions to obtain marketable yield (Cantore et al. 2014).

Due to the high drought susceptibility of potatoes (Schafleitner et al. 2009), climate change is thought to affect potato production globally. Varying levels of climate change are being observed in different regions, and its effect is also being studied globally, regionally, and locally (Arnell and Reynard 1996). Climate change has been reported to increase global average temperature; however, its effect on local weather is unpredictable, but it is likely to follow the increasing trend that can affect crop production significantly (Harkness et al. 2020). Besides temperature increases, precipitation is also being affected by climate change. Rain frequency throughout the year is like to be changed with more rainfalls in winter and fewer rainfalls in the summer (Rial-Lovera et al. 2017). Although potato production is predicted to increase in some regions with increased temperature due to stretch in the growing season (Daccache et al. 2011), water unavailability will significantly affect tuber yield. According to an estimate, 74-95% of the rainfed area of the United Kingdom suitable for potato production might be lost due to lack of rain (Daccache et al. 2012). Therefore, in the future, most rainfed areas will also need irrigation to sustain yield, which will increase irrigation water demand and increase potato production costs (Daccache et al. 2012).

2.3. Drought and its global impact

Abiotic stresses are significant obstacles in human attempts to increase crop productivity. Among these abiotic stresses, drought is one of the major and multidimensional stresses (Anjum et al. 2011) as it affects the morphology, physiology, ecological, biochemical, and molecular traits of plants (Salehi-Lisar and Bakhshayeshan-Agdam 2016). Drought is a broad term and is defined differently in different fields **(**Fig. 7**)**. In meteorology, a prolonged period of no rain or very little rain is called drought (meteorological drought) (Solh and van Ginkel 2014). The biological perspective also takes into account the effect of the absence of rain (or little rain) on plant life, i.e., reduced water potential in plant tissues due to moisture deficit in the soil (hydrological drought) caused by a period of little or no rain (Mitra 2001). Agriculture - focusing on the yield - defines drought as a water shortage period leading to soil moisture deficit that ultimately negatively affects the yield of plants (Mitra 2001). Hydrological drought may further be divided into intermittent and terminal drought. Intermittent drought is the series of water shortage periods during the growing season of plants, but soil moisture is restored after intermittent drought, allowing the plants to resume their growth. However, the soil moisture level is not restored after terminal drought, severely affecting plant growth and in extreme cases may cause early plant death (Neumann 2008). Although lack of precipitation is the main causal agent of drought, it is also affected by other climatic factors, such as temperature. Moreover, non-climatic factors such as human activities, land cover and soil type may also affect water availability (Cook et al. 2018).

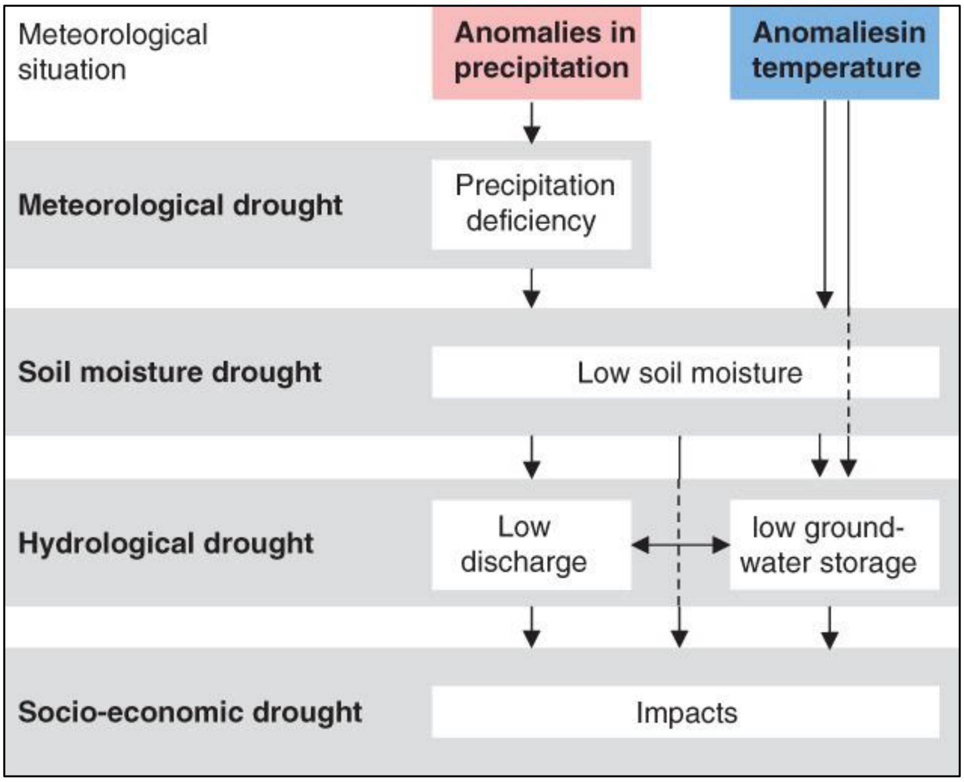


Figure 7 Schematic representation of different drought categories and their development (Van Loon 2015)

Drought is not new to humanity. The previous century witnessed some of the worst drought events. Drought in 1976 in Europe, the Dust Bowl in the United States during the 1930s (Schubert et al. 2004), and the food crisis in Russia and China in the 1920s (causing 4 million deaths) (EM-DAT, 2021) (Anon. 2021b) are a few examples of the most devastating drought events in the 20th century. The 21st century has also witnessed several drought events around the globe during the first two decades. In the first decade of the 21st century, the Australian continent was hit by a multi-year drought (McGrath et al. 2012). Europe faced a severe drought in 2003 and 2006 that affected crop production and affected cooling water problems, navigation issues, and caused almost 70,000 deaths (Robine et al. 2008; Rebetez et al. 2009) **(**Fig. 8**)**. Later on, the Amazon rain forest faced a lack of rain in 2005 and 2010, causing massive loss of vegetation (Lewis et al. 2011). The Iberian Peninsula faced a multi-year drought from 2008, affecting its groundwater level and reservoir storage (Andreu et al. 2009). At the beginning of the second decade, Russia also faced severe heat and drought stress during 2010 and 2011 (Grumm 2011), which resulted in huge forest fires. In the same years, parts of China and Scandinavia were also hit by drought, causing food and drinking water shortages (Cattiaux et al. 2010; Lu et al. 2011). In 2011, an enduring drought resulted in mass migration and deaths in Africa (Viste et al. 2013). Droughts in 2012 in the central USA, southern USA, and Russia; in 2013 in Brazil, New Zealand, Central Europe, and Namibia; and winter drought in 2014 in Scandinavia caused huge agricultural, economic, and environmental problems. In recent years, a multi-year drought in California severely affected agricultural and domestic water usage (Aghakouchak et al. 2014; Dettinger and Cayan 2014). The prolonged drought period is considered among the most destructive natural threats affecting economic costs and causing social problems (Wilhite 2016). From 1900 to 2010, drought-affected more than 2 billion people around the globe (Georgi et al. 2012). Therefore, it is imperative to tackle drought stress.

Figure 8 Examples of impacts of the 2003 summer drought in Europe, including effects on agriculture, health, transport, energy, and ecology (Van Loon 2015)

Crops are irrigated throughout the growing season to sustain yield. In total, 92% of freshwater usage is linked to agriculture; however, most regions face freshwater shortages at present (Nouri et al. 2019). Arid and semiarid regions that represent 40% of the world's agricultural land (Ehsanpour and Razavizadeh 2005) face serious water shortage challenges (Salvin et al. 2000; Ibrahim et al. 2012). The water crisis is expected to increase due to climate change that negatively affects crop production (Thiele et al. 2010; Monneveux et al. 2013). Several climate models forecast reduced annual rainfall and increased temperature with frequent droughts that negatively affect worldwide crop productivity (Pachauri et al. 2014). According to the Palmer Drought Severity Index, periods of drought stress are expected to increase in the next 30-90 years due to reduced precipitation and increased evaporation in many regions, including Europe (Dai 2013). Besides the frequency of extreme abiotic stresses, the magnitude of such stresses as drought is also predicted to increase with time (Rosenzweig et al. 2001), affecting food production around the globe (Rosenzweig et al. 2001). Moreover, redistribution of rainfall is also expected due to climate change that will affect irrigated agricultural lands and rainfed areas (Hijmans 2003; Monneveux et al. 2013). With the ever-increasing drought threat, it is important to study the response of main crops to drought stress.

2.4. Effect of drought stress on potato

Drought affects plant growth in multiple ways depending upon the duration and intensity of drought and plant developmental stage (Pinheiro and Chaves 2011). Drought causes stomatal closure, increased leaf sugar concentration, and reactive oxygen species. Stomatal closure under drought stress helps the plant to conserve water and maintain leaf water potential, but it also reduces CO_2 uptake by the plant, thus affecting the photosynthesis process (Chaves et al. 2002; Serraj et al. 2004; Mafakheri et al. 2010; Muthoni and Kabira 2016). An increase in leaf tissue sugar concentration also leads to feedback inhibition of photosynthesis that affects plant growth and yield (Basu et al. 1999). Moreover, reactive oxygen species such as superoxide radicals and hydrogen peroxide accumulation also increase under drought stress. Reactive oxygen species bind with oxygen molecules leaving cells deprived of oxygen, which may cause cell death due to extreme oxidative damage (Finkel and Holbrook 2000). However, all these phenomena are at cellular levels and not visible with naked eyes. Reduction in vegetative growth such as plant height, number, and size of leaves are the first visible signs of drought stress (Deblonde and Ledent 2001). The complex effect of drought depends upon the severity of drought, stage of plant development, and susceptibility of the genotype to drought stress is presented in Figure 9.

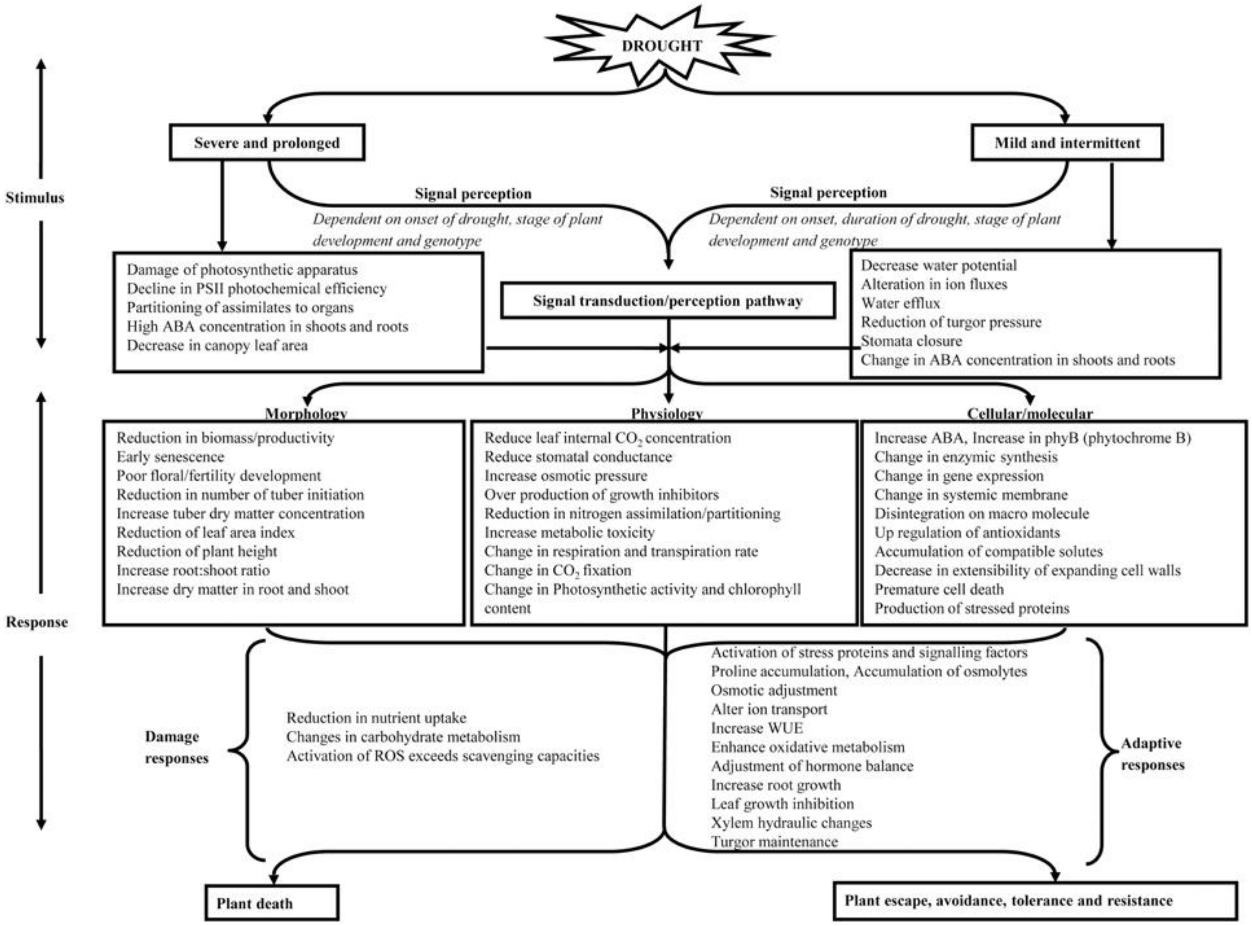
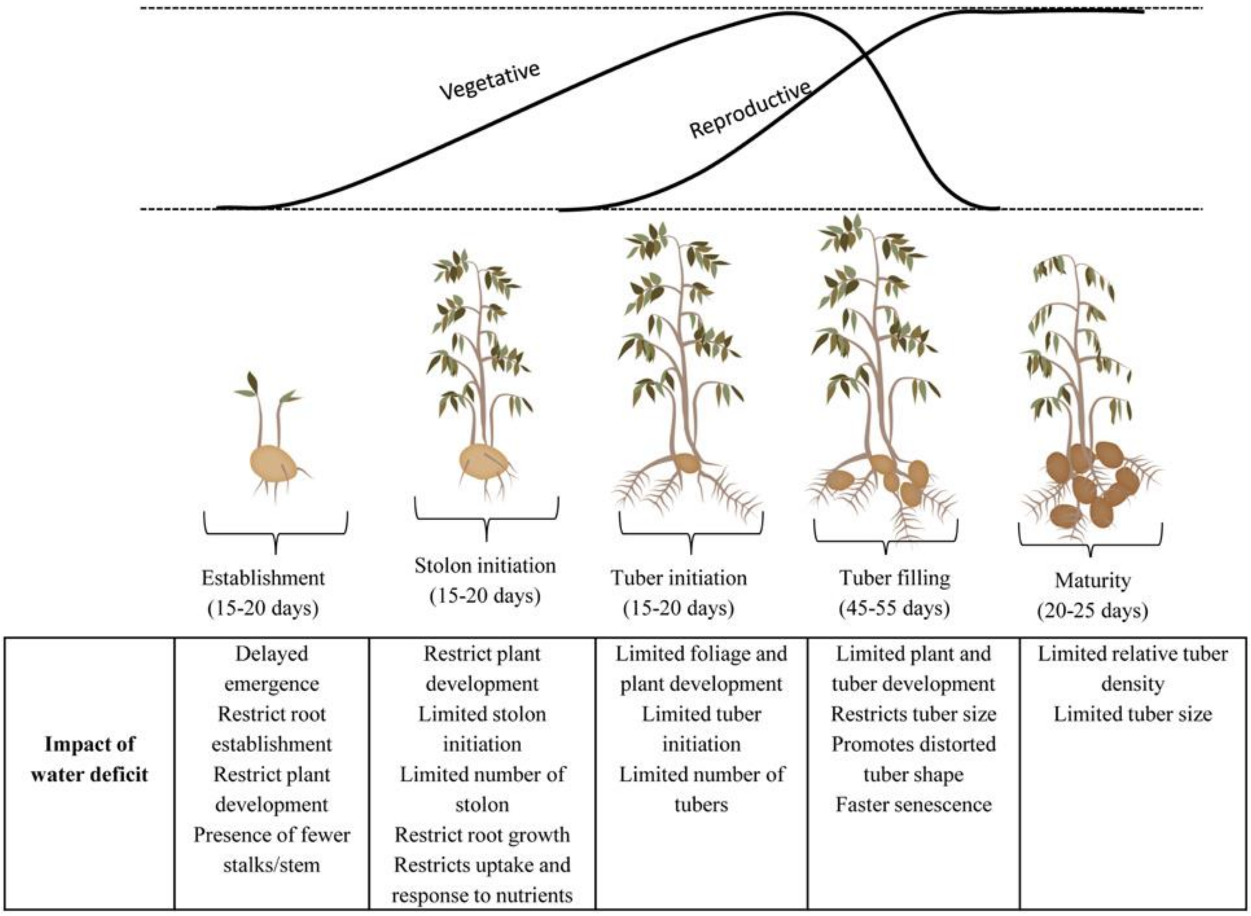


Figure 9 Different types of drought and there effect on plants at morphological, physiological and molecular level (Obidiegwu et al. 2015)

Potato is considered a drought-sensitive crop. Potato developmental stages can be divided into five stages: plant establishment, stolon initiation, tuber initiation, tuber bulking, and maturity stage (Obidiegwu et al. 2015) **(**Fig. 10**)**. Drought may affect potato yield by affecting vegetative growth such as plant height, number, and size of leaves (Deblonde and Ledent 2001), or by affecting leaf photosynthesis by chlorophyll reduction, leaf area index, or leaf area duration reduction. Besides vegetative growth, drought may affect the reproductive stage of potatoes by shortening the growth cycle (Kumar et al. 2007) or by reducing the size (Schafleitner et al. 2009) and numbers of tubers (Eiasu et al. 2007) produced by plants. Moreover, drought may also affect the quality of tubers produced (Ekanayake and Midmore 1989; Jefferies 1995). Therefore, drought stress on potatoes can be grouped in the effect of drought stress on above-ground parts, below-ground parts, and yield.



	Establishment	Stolon initiation	Tuber initiation	Tuber filling	Maturity
Impact of water deficit	Delayed emergence Restrict root establishment Restrict plant development Presence of fewer stalks/stem	Restrict plant development Limited stolon initiation Limited number of stolon Restrict root growth Restricts uptake and response to nutrients	Limited foliage and plant development Limited tuber initiation Limited number of tubers	Limited plant and tuber development Restricts tuber size Promotes distorted tuber shape Faster senescence	Limited relative tuber density Limited tuber size

Figure 10 Effect of drought stress on different growth stages of potato development (Obidiegwu et al. 2015)

2.4.1. Effects of drought on above ground growth in potato

Canopy development is among the most drought-sensitive stages in plants (Shao et al. 2009). Canopy development means the production of leaves, stems (stolons), and an increase in individual leaf area and plant height. Drought has been reported to have an inhibitory effect on stem height (Chang et al. 2018), production of new leaves (Aliche et al. 2018), stem number (Chang et al. 2018), and individual leaf area (Kesiime et al. 2016) of potatoes. Canopy growth depends upon high turgor pressure that helps in cell expansion and thus growth (Kesiime et al. 2016). Plants need a constant supply of transpirable water to maintain high turgor pressure. However, under drought stress conditions, water availability to plants is reduced, affecting canopy growth. In most plants, leaf growth stops if available soil water is less than 40-50% (Szabolcs 1999). However, leaf growth in potatoes stops when available soil water is less than 60% (Weisz et al. 1994), showing the water shortage sensitivity of potato plants. Therefore, reduced leaf and stem growth are the first observable effect of water shortage in potato plants (Jefferies and MacKerron 1989). Although the effects of drought stress depend upon timing, duration, and intensity of drought stress, both early and late drought exhibit an inhibitory effect on canopy growth (Aliche et al. 2018). Early drought slows the canopy growth, thus increasing the time required to reach optimum canopy cover, while late drought causes shedding of mature leaf and inhibition of new leaf formation (Aliche et al. 2018). Chang et al. (2018) reported a 75% to 78% reduction in stem length of potato plants affected by early drought.

Besides drought timing, the effect of drought also varies among different maturing cultivars (Chang et al. 2018). A comprehensive investigation of 103 potato cultivars reported that late-maturing cultivars might be less affected by late drought than early maturing cultivars (Aliche et al. 2018). Late maturing cultivars have a more extended vegetative growth period. They can further delay achieving full canopy cover under late drought stress, thus minimizing the effects of late drought (Romero et al. 2017). On the other hand, potato stem numbers may be less affected as plants already produce optimum stem numbers before the start of late drought (Lahlou et al. 2003). Similarly, Deblonde and Ledent (2001) also reported more negligible effect of late drought on the on early cultivars' plant height.

Leaf area index (LAI) and leaf area duration(LAD) are considered more important in determining tuber yield (Najm et al. 2010). Drought stress significantly reduces LAI and LAD in potato crops. A recent study involving three potato cultivars (Russet Burbank, Moonlight, and Karaka) reported that drought significantly reduced LAI of all understudy cultivars (Michel et al. 2019). These results were also confirmed in another study where drought stress significantly reduced the LAI in Banba cultivar (Pourasadollahi et al. 2019). Under drought stress, cell expansion is reduced, affecting leaf size in potatoes that directly affects LAI. However, LAI of potatoes is more affected by drought stress in late cultivars than in early maturing cultivars (Gaur et al. 2017; Salavati et al. 2018; Pourasadollahi et al. 2019). The variation in LAI of potato cultivars under drought stress can be because of different canopy architecture (Michel et al. 2019). Under normal conditions, plants increase their LAI during vegetative growth up to a specific time, and then LAI starts reducing, followed by senescence. However, LAI starts reducing earlier under drought conditions, thus affecting leaf area duration (LAD) (Fig. 11). Michel and others (2019) reported that potato plants reduced LAI as early as 30 days after planting in water shortage conditions. This reduces the total radiation interception area and the duration of radiation interception that determines biomass production (Chang et al. 2018). Jefferies and MacKerron (1989) argued that biomass production is more affected by LAD than LAI at a specific time. These results were reconfirmed in a recent study where drought stress significantly reduced tuber yield by affecting the LAD of two potato cultivars, Karú INIA and Desirée (Ávila-Valdés et al. 2020).

Multiple effects of drought stress on canopy growth of potatoes lead to a reduction in photosynthesis (Pieters and El Souki 2005). Plants require water, carbon dioxide, and light to complete the normal photosynthesis process. Drought stress affects the amount and rate of photosynthesis in plants. Reduction in the number of leaves and individual leaf areas affects the amount of photosynthesis (Gaur et al. 2017). On the other hand, a shortage of water and CO_2 reduces the rate of photosynthesis. Drought stress reduces relative water content in potato leaves , increasing the intercellular ionic concentration (Lawlor 2002). High intercellular ionic concentration inhibits ATP synthesis that affects ribulose bisphosphate production. Ribulose bisphosphate (RuBP) is the primary acceptor of carbon dioxide during photosynthesis. Therefore, reduction in RuBP production directly affects photosynthesis (Tezara et al. 1999; Flexas et al. 2006). In some crops, such as soybean and sunflower, reduction in RuBP production has been mentioned as the main inhibitory effect of drought (Vu et al. 1987; Tezara et al. 1999). Besides RuBP production and water, photosynthetic carbon dioxide concentration also decreases under drought stress. During water shortage, plants close their stomata to reduce water losses, which also reduces carbon dioxide uptake by plants (Cornic 2000). A lower concentration of carbon dioxide in the mesophyll leads to substrate unavailability necessary for plant growth and respiration (Flexas et al. 2006). Bota et al. (2004) reported that stomatal conductance could limit the growth of common bean and common wine grapes under drought conditions. However, the effect of drought on the growth of plants is cultivar-dependent and may vary within cultivars depending upon the timing and duration of drought (Bota et al. 2004).

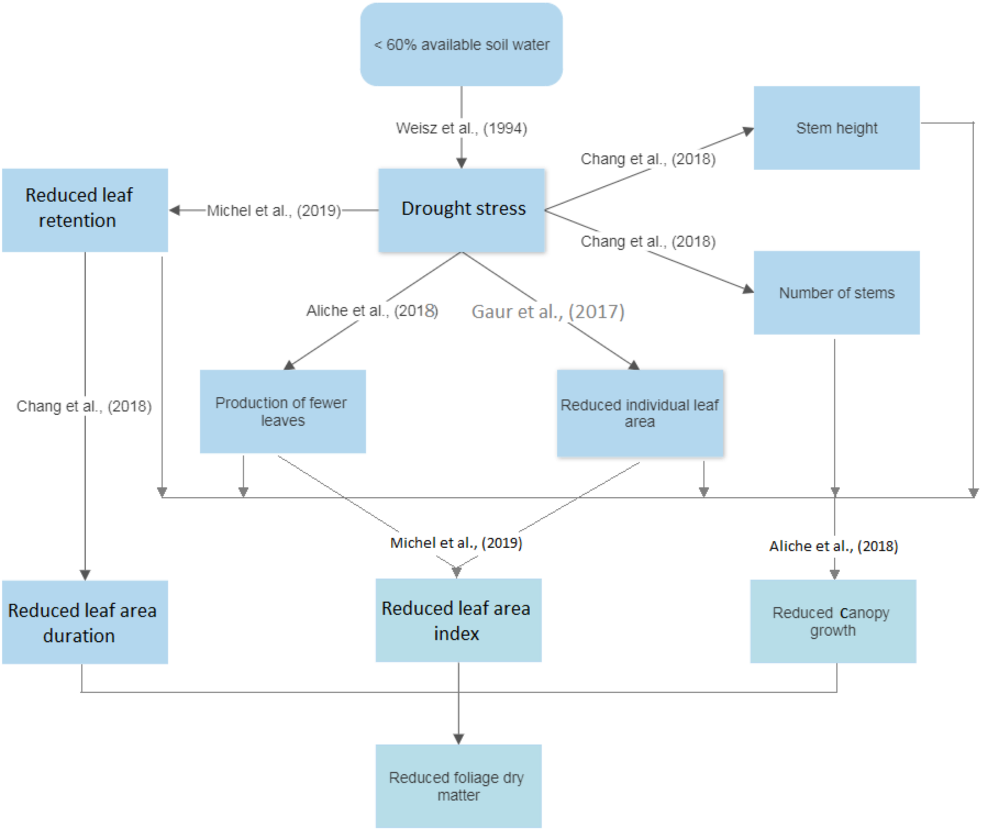


Figure 11 Schematic diagram of the effect of drought stress on above-ground growth of the potato (Weisz et al. 1994; Gaur et al. 2017; Aliche et al. 2018; Chang et al. 2018; Michel et al. 2019)

2.4.2. Effects of drought on below ground growth in potato

Underground parts of potatoes include roots, stolons, and tubers. Since tubers are the economic part, therefore, the effect of drought stress on tubers will be discussed in a separate section. Potato possesses a shallow and weak soil penetrating root system, making potato plants susceptible to drought stress (Stalham et al. 2007; Joshi et al. 2016). In potato root system architecture, root length and root mass are well studied, yet no definite effect of drought stress on underground plant development could be reported (Table 3). Potato roots may reach as deep as 100 cm; however, most of it is concentrated in the upper 30 cm soil. Contradictory results were observed where some researchers reported a decrease in root length under drought stress (Albiski et al. 2012). In contrast, some researchers reported an increase or no change in root length under drought stress (Steckel and Gray 1979; Lahlou and Ledent 2005; Boguszewska-Mańkowska et al. 2020).

Table 3 Effect of drought stress on various morphological traits of potato as reported by different researchers

Morphological Trait	Observation	References
Foliage cover	Reduction	(Aliche et al. 2018; Demirel et al. 2020)
Stem thickness	Reduction	(Chang et al. 2018)
Stem number	Reduction	(Lahlou and Ledent 2005; Chang et al. 2018; Pourasadollahi et al. 2019)
Plant dry matter	Reduction	(Boguszewska-Mańkowska et al. 2018, 2020; Chang et al. 2018; Alhoshan et al. 2019; Pourasadollahi et al. 2019)
Shoot fresh weight	Reduction	(Chang et al. 2018)
Leaf area index	Reduction	(Lahlou and Ledent 2005; Li et al. 2016; Michel et al. 2019; Pourasadollahi et al. 2019; Handayani and Watanabe 2020)
Leaf size	Reduction	(Handayani and Watanabe 2020)
Leaf area duration	Reduction	(Lahlou and Ledent 2005; Michel et al. 2019; Pourasadollahi et al. 2019; Handayani and Watanabe 2020)
Leaf water potential	Reduction	(Handayani and Watanabe 2020)
Number of leaves	Reduction	(Deblonde and Ledent 2001; Aliche et al. 2018; Chang et al. 2018)
Relative water content	Reduction	(Lawlor 2002; Pourasadollahi et al. 2019; Boguszewska-Mańkowska et al. 2020; Demirel et al. 2020; Handayani and Watanabe 2020)
Plant height	Reduction	(Rykaczewska 2017; Chang et al. 2018; Pourasadollahi et al. 2019; Demirel et al. 2020; Handayani and Watanabe 2020)
Tuber fresh weight	Reduction	(Lahlou et al. 2003; Carli et al. 2014; Obidiegwu et al. 2015; Aliche et al. 2018; Boguszewska-Mańkowska et al. 2018; Chang et al. 2018)
Tuber yield	Reduction	(Rykaczewska 2017; Chang et al. 2018; Boguszewska-Mańkowska et al. 2020)
Tuber dry mass	Reduction	(Lahlou et al. 2003; Ierna and Mauromicale 2006; Crusciol et al. 2009; Stark et al. 2013; Soltys-Kalina et al. 2016; Rykaczewska 2017; Boguszewska-Mańkowska et al. 2018; Chang et al. 2018; Pourasadollahi et al. 2019)
Number of tubers	Increase	(Lahlou et al. 2003; Rykaczewska 2017)
	Reduction	(Lahlou et al. 2003; Eiasu et al. 2007; Luitel et al. 2015; Aliche et al. 2018; Pourasadollahi et al. 2019)

Table 3 Continued

Morphological Trait	Observation	References
Stolon number	Increase	(Lahlou and Ledent 2005)
	Reduction	(Haverkort et al. 1990)
Root length	Increase	(Steckel and Gray 1979; Lahlou and Ledent 2005; Boguszewska-Mańkowska et al. 2020)
	Reduction	(Albiski et al. 2012)
Root number and thickness	Reduction	(Boguszewska-Mańkowska et al. 2020)
Root biomass	Reduction	(Mane et al. 2008)
Root water potential	Reduction	(Liu et al. 2005)
Root dry matter	Increase	(Tourneux et al. 2003; Lahlou and Ledent 2005; Anithakumari et al. 2011)
	Reduction	(Lahlou and Ledent 2005; Mane et al. 2008; Boguszewska-Mańkowska et al. 2020)
Chlorophyll	Reduction	(Sadeghipour and Aghaei 2012; Alhoshan et al. 2019)
	Increase	(Handayani and Watanabe 2020)
Carotenoids	Reduction	(Alhoshan et al. 2019)
Antioxidants	Increase	(Alhoshan et al. 2019)

Similarly, the root dry mass of potatoes has also been reported to decrease (Lahlou and Ledent 2005; Mane et al. 2008), increase (Tourneux et al. 2003; Lahlou and Ledent 2005; Anithakumari et al. 2011), and remain constant (Mane et al. 2008) under water shortage. Moreover, opposing results were also reported for the stolon number due to drought stress (Haverkort et al. 1990; Lahlou and Ledent 2005). Many arguments have been made to justify these variations in observations. Most studies discuss the variation in genotype and environment interaction (Gluska 2004; Iwama 2008; Joshi et al. 2016; Rudack et al. 2017; Rykaczewska 2017; Zarzyńska et al. 2017; Boguszewska-Mańkowska et al. 2020). Different cultivars respond differently to the specific intensity and duration of the drought (Epstein and Grant 1973). Moreover, cultivars maturing at different times also vary in their response to water stress. Later cultivars have been reported to produce deeper and greater root mass than early maturing cultivars under the same drought stress (Kashiwagi et al. 2000). Experimental variation and experimental error are also significant reasons for these conflicting results. Studying underground parts is also affected by soil type, experimental location, tuber physiological age, and root handling (Steckel and Gray 1979; Stalham et al. 2007; Obidiegwu et al. 2015). The unpredictability of all these factors makes it more challenging to study the effect of drought stress on underground parts of potatoes.

2.5. Effects of drought on potato tuber yield

Tuber yield is the primary concern in potato cultivation; therefore, it is the most extensively studied characteristic in potato production. In the last five decades, the effect of drought stress on tuber yield has been studied in several different ways. The effect of drought on fresh tuber mass (Lahlou et al. 2003; Carli et al. 2014), tuber number (Deblonde and Ledent 2001), tuber dry matter (Deblonde et al. 1999), and marketable tuber yield (Cantore et al. 2014) have been studied in detail.

2.5.1. Effects of drought on fresh tuber mass

Fresh tuber yield depends upon dry matter allocation to tubers and water content of tubers (Jefferies and Mackerron 1993), where water content contributes up to 80% in fresh tuber mass depending upon the cultivars (Navarre et al. 2009). Therefore, fresh tuber mass is highly affected by water shortage (Carli et al. 2014; Obidiegwu et al. 2015). Jefferies and MacKerron (1989) reported that long-term water stress - starting from the emergence and lasting till harvesting - reduced the relative water content of tubers of Maris Piper by 69% in comparison to well-irrigated potatoes. However, the response of potatoes to water shortage is highly cultivar dependent. Remarka and Desiree cultivars were exposed to similar drought stress conditions in a field study. Results showed a 44% and 11% reduction in fresh tuber yield of Remarka and Desiree, respectively (Lahlou et al. 2003). A recent study (Aliche et al. 2018) reported a decrease in fresh tuber weight of 103 commercial potato cultivars under drought stress. The same study also discussed the variation in fresh tuber weight of cultivars under drought stress, with a maximum reduction of 54% observed for the Connantre cultivar (Aliche et al. 2018). In another study, Boguszewska-Mańkowska and others (Boguszewska-Mańkowska et al. 2020) studied the effect of drought stress on the fresh tuber weight of four potato cultivars. They reported that the fresh tuber weight of all cultivars reduced under drought stress and varied from 1248 g (in Gwiazada) to 788 g (in Cekin). In these studies, a decrease in tuber water content has been mentioned to cause a reduction in fresh tuber yield. On the other hand, few Andean cultivars have increased tuber water content under water shortage stress (Lefèvre et al. 2012). This deviation can be an adaptive response of potato cultivars to drought stress involving osmotic regulation (Khosravifar et al. 2008). However, these exceptionally behaving Andean cultivars are genetically distinct from commercial cultivars and represent a subspecies of potatoes (*Solanum tuberosum subsp. Andigenum*). Since increased tuber water content can improve fresh tuber mass (Jefferies and MacKerron 1989), these tubers can be considered for studying and producing drought tolerant cultivars.

Besides cultivars, fresh tuber weight is also affected by the length and severity of drought stress. Both late and early drought significantly affect the yield of potatoes. Early stress (from emergence to tuber initiation stage) significantly reduced fresh tuber weight of early maturing and late-maturing cultivars. However, late drought (lasting from emergence to tuber bulking stage) affects early maturing cultivars more severely than late-maturing cultivars (Chang et al. 2018). Early maturing cultivars such as Chubaek have shorter growth periods, and under drought stress, they delay tuber growth leading to reduced fresh tuber weight. On the contrary, late-maturing cultivars such as Jayoung showed enhanced haulm growth, delayed tuberization, and tuber bulking, and got time to recover from drought stress which helped produce higher fresh tuber weight (Chang et al. 2018). Similar results were also reported in several other studies (Curwen 1993; Al Mahmud et al. 2015; Salehi-Lisar and Bakhshayeshan-Agdam 2016).

2.5.2. Effects of drought on number of tubers

Besides fresh tuber weight, drought also affects the number of tubers produced by potato plants (Eiasu et al. 2007). However, the number of tubers produced by plants depends on the timing and duration of drought stress. If exposed to water shortage stress throughout the life of the potato plant (from emergence to harvest), tuber numbers decrease in all cultivars (Aliche et al. 2018). Similarly, exposure to a single short-term early stress also exhibits an inhibitory effect on the tuber number produced by the plant (Haverkort et al. 1990); however, late short-term drought stress showed a higher effect on tuber dry matter than on the number of tubers (Muthoni and Shimelis 2020). In another study, Chang et al. (2018) also reported that drought stress at tuber initiation and stolonization limits tuber yield by reducing the number of tubers produced by plants. These observations are in line with the results of previous studies that argue that the number of tubers produced is most sensitive to drought stress at the tuber initiation stage (Minhas and Bansal 1991; King and Stark 1997). On the other hand, some studies have reported an increase in tuber number under drought stress (Lahlou et al. 2003; Rykaczewska 2017). This can be due to the adaptive response of cultivars to sustain the yield under drought stress (Aliche et al. 2018) or the effect of an already existing abiotic stress, e.g., heat stress that delays tuberization and results in the production of more tubers but of smaller size (Haverkort 1987). Rykaczewska (2017) also reported an increase in small-sized tubers (< 3 cm) under drought stress; however, the number of large marketable tubers (> 3 cm) decreased under drought stress.

2.5.3. Effects of drought on dry tuber mass

Potato yield and quality are also determined by the dry mass of tubers (Dull et al. 1989). Total tuber dry mass depends upon substrate production by leaves (Allen and Scott 1980) and its allocation by plants to tubers. Therefore, drought stress indirectly affects total tuber dry mass by reducing canopy growth or reducing photosynthetic activities in leaves (Jefferies and MacKerron 1989). Total tuber dry mass is considered more important than fresh tuber mass because it gives an idea of the efficiency of cultivars to translocate assimilates into tubers (Jovanovic et al. 2010). Assimilate translocation depends on tuber water content (Jefferies and MacKerron 1989) and is used to describe tuber quality, particularly the quality of processing cultivars (Pritchard and Scanlon 1997). Due to the economic significance of total tuber dry mass and dry matter translocation into tubers, researchers have studied them extensively.

Steckel and Gray (1979) studied the effect of prolonged drought stress on total dry tuber mass in drought-tolerant and drought-sensitive cultivars. They reported a consistent decrease in total tuber dry matter due to drought stress in all cultivars. The reduction in tuber dry matter was remarkably similar between drought-sensitive and drought-tolerant cultivars. However, drought-tolerant cultivars produced fewer but larger tubers (> 40 mm in length), making the yield more marketable than drought-sensitive cultivars (Steckel and Gray 1979). These results directed the researchers to focus on many variables in different cultivars to understand the effect of water shortage on dry tuber mass. Jefferies and Mackerron (1993) studied the response of 19 cultivars to long-term drought stress starting from emergence. They reported an average reduction of 44% in total tuber dry mass and a 52% increase in average dry matter concentration in tubers under drought stress. They suggested that increased dry matter concentration is not because of high dry matter production; instead, it is associated with high assimilate translocation into tubers under drought stress. They also reported that drought stress increased dry matter concentration in all cultivars; however, varying responses were observed in total dry matter of different cultivars where drought stress significantly reduced total dry matter of most cultivars. Interestingly, some cultivars, such as Baillie, Ulster Scepter, and Duke of York, did not show any significant changes in total tuber dry matter. The authors suggested that poor performance in terms of tuber dry matter under irrigated conditions was the reason for nonsignificant changes in those cultivars (Jefferies and Mackerron 1993). Steyn et al. (1998) proposed an alternative hypothesis suggesting that some cultivars produce relatively higher tuber dry matter under water shortage stress regardless of their performance under well-irrigated conditions. Lahlou and others (Lahlou et al. 2003) also reported a decrease of 38%, 15%, 13%, and 11% in Remarna, Monalisa, Nicola, and Desiree’s dry tuber weight under drought stress. They also reported that drought stress reduced the dry tuber mass regardless of the maturity type of cultivar. In the past two decades, several researchers have reported a reduction in dry tuber weight under the influence of drought stress (Haverkort et al. 1990; Ierna and Mauromicale 2006; Crusciol et al. 2009; Stark et al. 2013; Soltys-Kalina et al. 2016; Rykaczewska 2017).

In several studies, reduction in net photosynthesis under water shortage stress has been argued as the main reason for total tuber dry mass reduction (Ohashi et al. 2006; Ahmadi et al. 2010; Sadeghipour and Aghaei 2012; Li et al. 2016). Drought stress affects the relative water content of leaves (Lawlor 2002), which affects plants' metabolic activities. Stomatal conductance is reduced when leaf water potential reaches below -0.6 MPa (Ahmadi et al. 2010), causing a reduction in carbon dioxide absorption (Ohashi et al. 2006) and reduced net photosynthesis rate (Pourasadollahi et al. 2019). Moreover, water stress also causes a reduction in chlorophyll content (Sadeghipour and Aghaei 2012) and leaf area index and leaf area duration (Li et al. 2016). All these factors directly affect photosynthesis, that in turn affects tuber dry matter. However, reduction in tuber dry matter depends on the severity of stress and cultivars. Ruttanaprasert et al. (2016) exposed five potato cultivars to three water regimes. He reported that the reduction in the total dry weight of tubers of all understudy cultivars increased with the severity of drought stress. Average tuber dry weight under well irrigated, mild drought stress (50% available soil water), and severe drought stress conditions (25% available soil water) were 30.6 g plant^{-1}, 10.8 g plant^{-1}, and 1.6 g plant^{-1}, respectively. Similarly, all cultivars varied in tuber dry matter production at all water regimes. Under mild drought stress, reduction in dry tuber mass of varieties varied from 49.3% to 85.2%, and under extreme conditions, it varied from 93.2% to 98.2% (Ruttanaprasert et al. 2016). Variation among cultivars in tuber dry mass production can be due to differences in their growth habit as early maturing cultivars produce higher mean tuber weight than late maturing cultivars (Chang et al. 2018).

2.6. Drought mitigation strategies

We have not been successful in developing drought-tolerant potato genotypes. Earlier potato breeding focused on yield improvement under optimal conditions. Numerous genes related to drought stress have been identified in recent years; however, we are still a long way from developing drought-tolerant potato genotypes. At present, the effects of drought stress can be alleviated by selecting the most appropriate potato genotype according to climate and improving agronomic practices.

Effective soil management (tillage, mulching, residue management, organic matter, and nutrition management) can be used to mitigate the adverse effects of drought stress. It increases water infiltration and reduces evapotranspiration (Ferrero et al. 2005; Sekhon et al. 2010). Soil tillage impacts water availability to crops by manipulating soil surface roughness, but the use of hills to produce potatoes limits the tillage practice in potato production. Organic mulches can mitigate the effects of drought stress by controlling the evaporation, absorbing water vapors on mulch tissue, and increasing the infiltration (Lipiec et al. 2006). Animal manure and other carbon-rich wastes can also improve the nutrient status of soils and the water-holding capacity of soils (Fazal and Bano 2016). Biochar and compost have been reported to alleviate drought stress (Thomas et al. 2013), improve the soil structure (Tejada et al. 2009), and increase the water-holding capacity of soils (Sodhi et al. 2009). However, the effectiveness of compost depends upon the type of compost, the frequency of treatment with compost, and the type of soil (Sodhi et al. 2009).

Nutrient management also affects soil health; thus, the water holding capacity of soil. Several inorganic nutrients such as Zn, N, P, K, and Se have been reported to alleviate drought stress in wheat (Aown et al. 2012; Gevrek and Atasoy 2012; Nawaz et al. 2013). Pilon et al. (2014) also reported that foliar and soil application of silicon improves drought tolerance in potatoes. Foliar application of Zn, B, and Mn and soil application of NPK increase the yield and micronutrient concentration of grains. Besides soil management, foliar application of natural and synthetic plant growth regulators can also mitigate the adverse effects of drought. Application of glycine betaine (Farooq et al. 2009), 1-aminocyclopropane-1-carboxylic acid, ABA (Beaudette et al. 2007; Parent et al. 2009), and gibberellic acid can all reduce the effects of drought stress. However, very little work has been reported on the effectiveness of the foliar application of plant growth regulators in mitigating drought stress in potatoes. It is an emerging technique in agronomy that needs further understanding before becoming part of an effective drought management practice in potatoes.

Drought stress can also be mitigated by effective water management. Using modern targeted techniques can save up to 50% water compared to flood irrigation (Lipiec et al. 2006). Managing the time of irrigation can also alleviate the adverse effects of drought. Irrigation at the tuber initiation and bulking stage can improve tuber yield. The soil needs to capture more rainwater in drylands to minimize drought stress. It can be achieved by increasing rainwater harvesting, particularly by increasing soil organic matter.

Moreover, the usage of treated wastewater is also getting popular to increase available water for agriculture. Treated wastewater is also a rich source of nutrients (Ricart and Rico 2019). Wastewater can be cleaned by activated sludge, membrane filtration, and bioreactors; however, it is expensive and unsuitable for a larger scale (Suhani et al. 2020). The Israeli government has set an example by reusing 85% of treated wastewater under the integrated water resource management (IWRM) policy (Golan 2016).

Although good agronomic practices can help alleviate drought stress, site-specific production technology, and drought-resistant genotypes are required. Agronomic practices should be adjusted according to the local climate, and strategies to increase water use efficiencies should be adopted. Targeting breeding approaches can be implemented to develop drought-resistant potato genotypes, for which we need the fundamental knowledge of molecular responses of potatoes to drought stress. Much work at the molecular level is being conducted to understand the response of potato genotypes to varying degrees of drought stress.

3. MATERIALS AND METHODS

3.1. Experimental location and growth conditions

To evaluate the effect of drought stress on potatoes a pot experiment was established in the greenhouse of Hungarian University of Agriculture and Life Sciences, Georgikon Campus, Potato Research Centre, Keszthely, Hungary (Fig. 13). For this purpose, soil and peat mixture (1:1 by weight) was used in 50 kg soil bearing pots (diameter at top = 41 cm; the height of pot = 40 cm) (Fig. 12) and a controlled environment (day/night temperature 25/21℃, relative humidity 50%, and 18 h photoperiod) was maintained in the greenhouse.

Figure 12 Pots used for the experiment (d= 41 cm, h=40 cm)

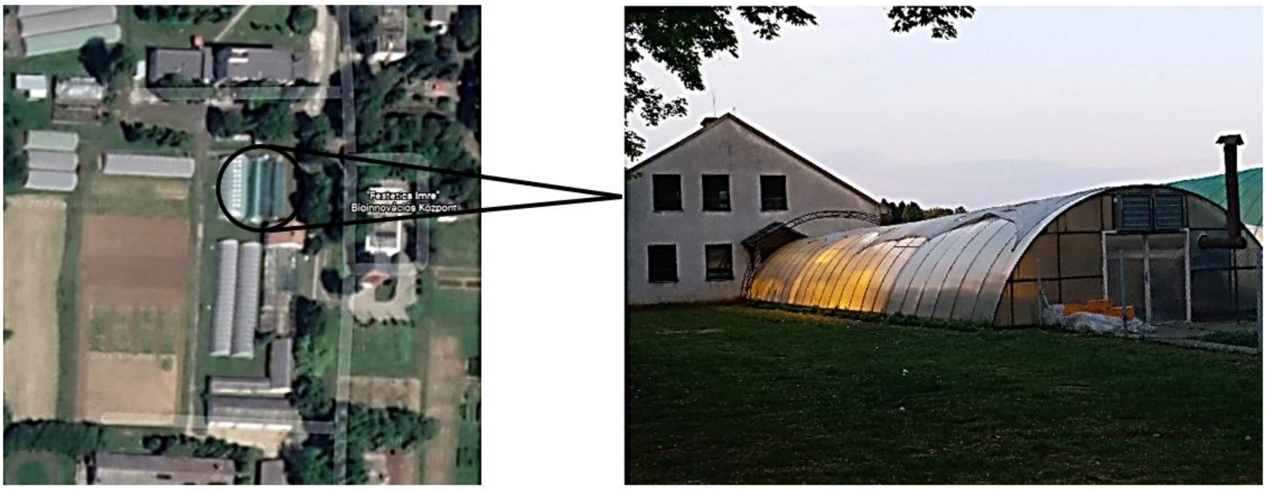


Figure 13 Experimental location at greenhouse of Hungarian University of Agriculture and Life Sciences, Georgikon Campus, Keszthely, Hungary

3.2. Plant material

Two mid-late high yielding potato genotypes 'Demon' and 'Hopehely' (Fig. 14) were collected from Potato Research Centre, Keszthely, Hungary. Both genotypes are high-yielding and immune to potato virus Y (PVY) and potato virus A (PVA), highly resistant to leaf drift virus. Both are moderately resistant to foliar phytophthora (*Phytophthora infestans*). Moreover, both are resistant to tuberculosis (*Mycobacterium tuberculosis*) and Ro1 and Ro4 potato nematode races. Physiological characteristics of both genotypes are given in Table 4.

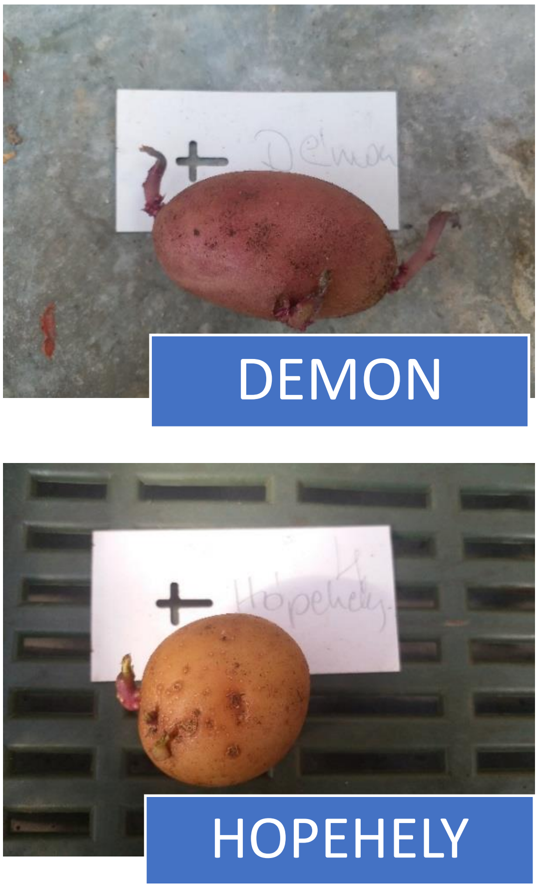


Figure 14 Potato genotypes used in the experiment

Table 4 Characteristics of genotypes used in the experiment

Characteristics	**'Hopehely'**	**'Demon'**
Breeding time	100-110 days	100-110 days
Tuber skin	Pale pinkish to yellowish brown	Dark rose
Tuber shape	Round	Oval
Tuber flesh	White	Yellow
Tuber dry matter content	Medium (19-20%)	Medium (19-20%)
Leaves size	Large	Small
Stems	Few thick stems	Strong tall stems
Yield potential	High yielding (60-80 t ha^{-1})	High yielding (50-60 t ha^{-1})
Storage characteristics	Resistant to deterioration Long shelf life Easy storing Free from tuber physiological defects	Resistant to deterioration Long shelf life Easy storing Free from tuber physiological defects

3.3. Drought stress induction

Both genotypes were exposed to two water levels, i.e., control (80% water holding capacity) and drought stressed (50% water holding capacity). Randomized complete block design (RCBD) was used with sixteen (16) replications. 5 kg pre-washed and dried gravel was used to line the pot base and was covered by a plastic net. A pipe was also embedded in the gravel for watering and aeration purposes. Remaining empty pot was filled with soil peat mixture (1:1 by weight). Soil from "A" horizon of an Eutric cambisol soil having a sandy clay loam texture was collected from the research farm area of the Hungarian University of Agriculture and Life Sciences, Georgikon Campus, and Baltic peat of low pH was brought from Latvia. Both soil and peat were sieved through a 10 mm sieve to obtain a finer and favorable growth medium. 10 kg of soil and 10 kg of peat were mixed using a cement mixer to obtain a homogenized mixture that was used as growth medium in pots. The water holding capacity of the soil peat mixture was determined by the gravimetric method (Cseri et al. 2013) to quantify the amount of irrigation to be supplied to control and stressed pots. Pot weight was controlled weekly to ensure desired water level. Sowing was completed on 28 March 2018. 3 tubers were sown in each pot to ensure germination. All treatments were given same amount of water till germination completion. Drought stress was induced at germination completion (18 DAS) and thinning was performed to maintain two plants per pot.

3.4. Sequential harvesting and observations

For growth analysis, 4 replications per treatment were harvested and sampled in 4 consecutive sampling times during the experimental period: 1. on tuber initiation stage (36 DAS), 2. on flowering stage (54 DAS), 3. on tuber bulking stage (72 DAS), and 4. in scenescence (90 DAS). Biomass was divided into leaves, stems, roots, and tubers. During 90 days experiment the following observations were recorded:

3.4.1. Plant height

Plant height was measured in centimeters (cm) at each sampling. Harvested plants were cut from the collar (point on the stem where roots start to grow) and height of tallest stem was measured using a measuring tape (Fig. 15).

Figure 15 Measuring plant height with a measuring tape

3.4.2. Number of leaflets per plant

Since potato plants produce compound leaves containing 3-7 leaflets, therefore, number of leaflets were counted instead of number of leaves at each harvesting. Leaflets of harvested plants were counted manually followed by taking the average to get average number of leaflets per plant.

3.4.3. Specific leaflet weight

Specific leaflet weight (SLW) gives idea about leaf thickness. SLW (g cm^{-2}) was measured using following formulas:

$$SLW = \frac{Leaf\ weight}{Leaf\ area}$$

Leaf area was measured by grid counting method.

3.4.4. Foliage fresh weight

Leaves and stem of each replication were immediately weighed and averaged to get average foliage fresh weight per plant in grams.

3.4.5. Foliage dry matter

Foliage dry matter was also measured in grams at each harvesting. Leaves and stems were sun dried followed by oven drying at 105°C. Dry weight was measured at 24 hours intervals until constant weight was obtained that was used as foliage dry matter (Figure 16).

Figure 16 Oven drying of foliage samples

3.4.6. Leaf area index

Leaf area index (LAI) is an important indicator of radiation and precipitation interception, water balance and energy conversion. Leaf area of a representative sample was measured by grid counting method. LAI was measured at each harvesting by using the formula described by Watson (1947):

$$LAI = \frac{Total\ leaf\ area\ of\ the\ plant}{Ground\ area\ occupied\ by\ plant}$$

3.4.7. Leaf area duration

Leaf area duration (LAD) that describes the ability of the plant to maintain the green leaves over unit area of land thorughout its life, was measured in days unit between each harvesting by using the formula described by Power et al. (1967):

$$LAD = \frac{LAI_1 + LAI_2}{2} \times (t_2 - t_1)$$

Where t_1 and t_2 are the time of first and second sampling and LAI_1 and LAI_2 are leaf area index at t_1 and t_2 respectively.

3.4.8. Chlorophyll content in leaves

Chlorophyll content per unit area was determined using Soil Plant Analysis Development (SPAD) 502Plus, Konica Minolta (Fig. 17). The readings were recorded in SPAD units. SPAD values on the top leaflet, 1st side leaflets, and 2nd side leaflets of the 3rd, 4th, and 5th compound leaf from the apex, and at 3 points (top, middle and basal) within a leaflet were taken weekly (Fig. 18) starting near flowering stage (51 DAS). 81 readings (3 × 27) were taken on each plant and average of the reading was used as chlorophyll content.

Figure 17 SPAD 502

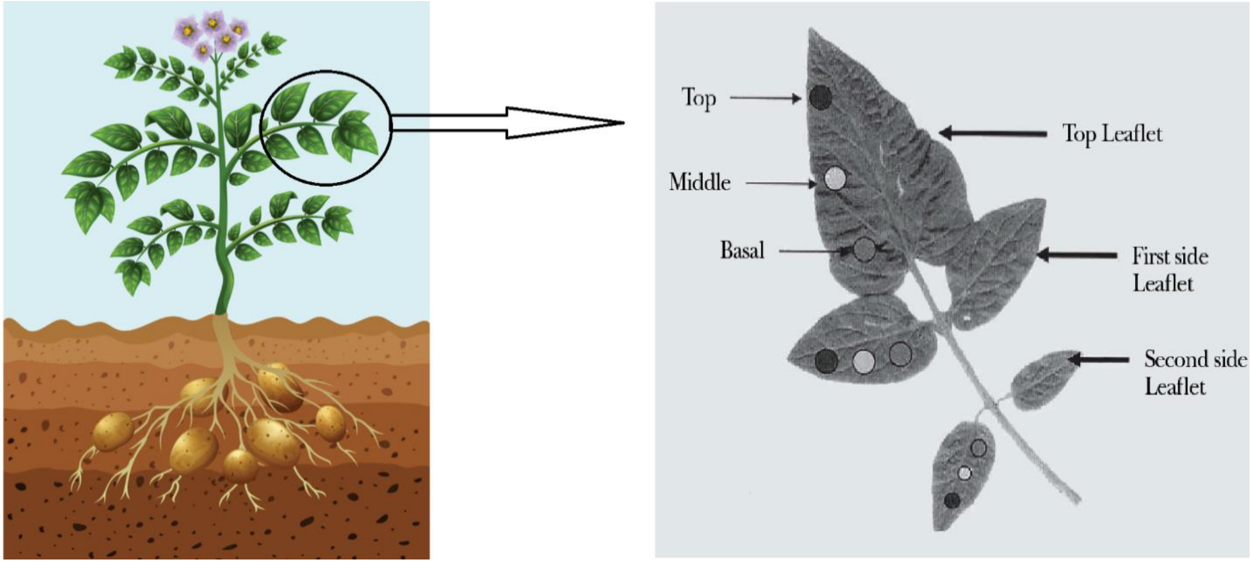


Figure 18 Diagram of a compound leaf, leaflet on the compound leaf, and measuring point on the leaflet of potato used for chlorophyll measurement Source: (Li et al. 2012)

3.4.9. Nitrogen content in the foliage

Nitrogen content in the foliage (%) was also determined at each harvesting stage. To determine nitrogen content; foliage samples were sun-dried followed by oven drying. The dried samples were first ground using a Restch SN200 cutting mill and then further ground to dust-sized particles (10-50 µm) using Fritsch Analysette 3 Spartan Pulverisette 0. 100 mg ground samples were then placed in tin containers (8x55 mm) to deliver samples to Elementar Vario Macro Cube CHNS analyser (Germany) (Fig. 19) using 96 wells plates where total nitrogen content was determined.

Figure 19 Elementar Vario Macro Cube CHNS analyzer (Germany)

3.4.10. Relative water content

Relative water content (RWC) was measured at each harvesting by using the formula described by Barrs, (1968):

$$RWC = \frac{Fresh\ leaf\ weight - Dry\ leaf\ weight}{Turgid\ leaf\ weight - Dry\ leaf\ weight} \times 100$$

Five fully expanded leaves were plucked from each treatment and weighed immediately to obtain fresh weight. Leaves were then soaked in double distilled water and kept in dark to saturate them. After 24 hours leaves were weighed again after drying any adhering droplets to obtain turgid leaf weight. Dry leaf weight was obtained by dehydrating the leaves at 70℃ for 48 hours. RWC was then calculated in percent by following the formula given above.

3.4.11. Leaf area ratio

Leaf area ratio ($cm^2\ g^{-1}$) was calculated at each harvesting by using the formula described by Rajput and Rajput (2017)

$$LAR = \frac{Leaf\ area\ per\ plant}{Total\ plant\ dry\ weight}$$

3.4.12. Antioxidant activity

For enzymatic antioxidant activity, leaf samples were collected at 72 DAS and stored at -52 °C. Enzymes were extracted by adapting the published method by Yasmeen et al. (2013). To extract the enzymes, 0.5 g leaf samples were homogenized in 5 mL of 50 mM phosphate buffer with pH 7.8. The homogenate was then centrifuged at 15,000× g at 4 °C for 20 min. The supernatant was used to measure the superoxide dismutase (SOD) activity and catalase (CAT) activity.

SOD activity was determined by following the protocol described by Giannopolitis and Ries (1977). The SOD activity inhibits the photochemical reduction of nitroblue tetrazolium (NBT) at 560 nm. The monitoring of this inhibition is used to assay SOD activity. The reaction mixture comprises of enzyme extract (50 µL), 50 µM nitroblue tetrazolium (1 mL), 75 mM ethylenediaminetetraacetic acid (500 µL), 50 mM phosphate buffer, 1.3 µM riboflavin (1 mL) and 13 mM methionine (500 µL). The reaction mixture was kept under 30 W fluorescent lamp for 5 mins to initiate the reaction. After replacing the reaction mixture from light, the NBT photo reduction produced blue formazane which was used to measure the increase in absorbance at 560 nm. The absorption was measure with Thermo Scientific^{TM} Gallery^{TM} Discrete Analyzer. The same reaction mixture without enzyme extract was used as blank. The SOD activity was determined and expressed as SOD IU min^{-1} mg^{-1} protein.

The CAT activity assayed by the decomposition of H_2O_2 and change in absorbance due to H_2O_2 was observed every 30 s for 5 min at 240 nm using a Thermo Scientific^{TM} Gallery^{TM} Discrete Analyzer. Reaction mixture for CAT contained 900 µL H_2O_2 (5.9 mM) and 2 mL phosphate buffer (50 mM). Reaction was started by adding 100 µL enzyme extract to the reaction mixture. The Catalase activity was expressed as IU min^{-1} mg^{-1} protein (Chance and Maehly 1955).

3.4.13. Fresh plant weight

Biomass produced by plants other than tubers was used as fresh plant weight. Foliage and roots of potato plants were weighed at each harvesting stage to obtain fresh plant weight.

3.4.14. Root length

Harvested plants were cut from the collar (point on the stem where roots start to grow) to separate roots from foliage. Root length was measured at each harvesting in cm using a measuring tape.

3.4.15. Root fresh weight

Roots play a fundamental role in water and nutrient absorption. Roots were carefully harvested, cleaned of soil particles, and weighed to record root fresh weight at each harvesting.

3.4.16. Root dry weight

Harvested roots were washed carefully and sun dried, followed by oven drying to obtain root dry weight. Oven temperature was controlled at 105℃. Dry weight was measured at 24 hours intervals until constant weight was obtained that was used as root dry weight.

3.4.17. Numbers of tuber per plant and tuber yield

At each harvesting, new tubers were separated from plants and counted manually to obtain number of tubers per plant. All tubers were cleaned and weighed separately to record tuber yield per plant.

3.5. Statistical analysis

SPSS/PASW Statistics for Windows, version 18 (SPSS Inc., Chicago, USA) was used for statistical analysis. Experimental data were assessed for normality of distribution and homogeneity of variances. Analysis of variance (ANOVA) was performed to determine significant differences amongst treatments followed by Tukey’s Honest Significant Difference test to recognize specific differences amongst treatments. Pearson correlation was performed to determine the relationship between variables. A $p<0.05$ was considered significant. Corrgrams were constructed using Statgraphics 19 centurion (STATGRAPHICS TECHNOLOGIES, Inc., Virginia, USA).

4. RESULTS

4.1. Effect of drought stress on plant height of potato genotypes

A factorial ANOVA was performed to analyze the effect of genotypes, drought stress, plant developmental stage and their interaction on shoot height of potato. We observed that genotype, drought stress and plant developmental stage showed a statistically significant effect on shoot height ($p<0.01$). We also observed a significant difference in shoot height by the interaction between genotype and drought stress ($f(1,45)=63.03$, $p<0.001$) (Table 5).

Table 5 Variance analysis for the effect of drought stress on shoot height of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	3660.3	3660.25	30.75	0.00^{**}
Water levels (B)	1	5130.1	5130.14	43.09	0.00^{**}
Plant developmental stage (C)	3	4892.8	1630.94	13.70	0.00^{**}
A×B	1	7503.9	7503.89	63.03	0.00^{**}
A×C	3	33.9	11.29	0.09	0.96^{ns}
B×C	3	948.2	316.06	2.65	0.06^{ns}
A×B×C	3	1066.4	355.47	2.99	0.04^{*}
Error	45	5357.0	119.05		
Total	63	28782.4			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level.

Drought stress significantly reduced shoot height of ‘Demon’. Maximum shoot height (118.5 cm) was observed for ‘Demon’ genotype under control conditions. ‘Demon’ reached maximum shoot height at tuber bulking stage under control condition, while stem elongation of ‘Demon’ plants stopped at flowering stage under drought stress producing significantly shorter plants. Tukey post-hoc test revealed that drought stress did not show any significant effect on shoot height of ‘Hopehely’ (Fig. 20).

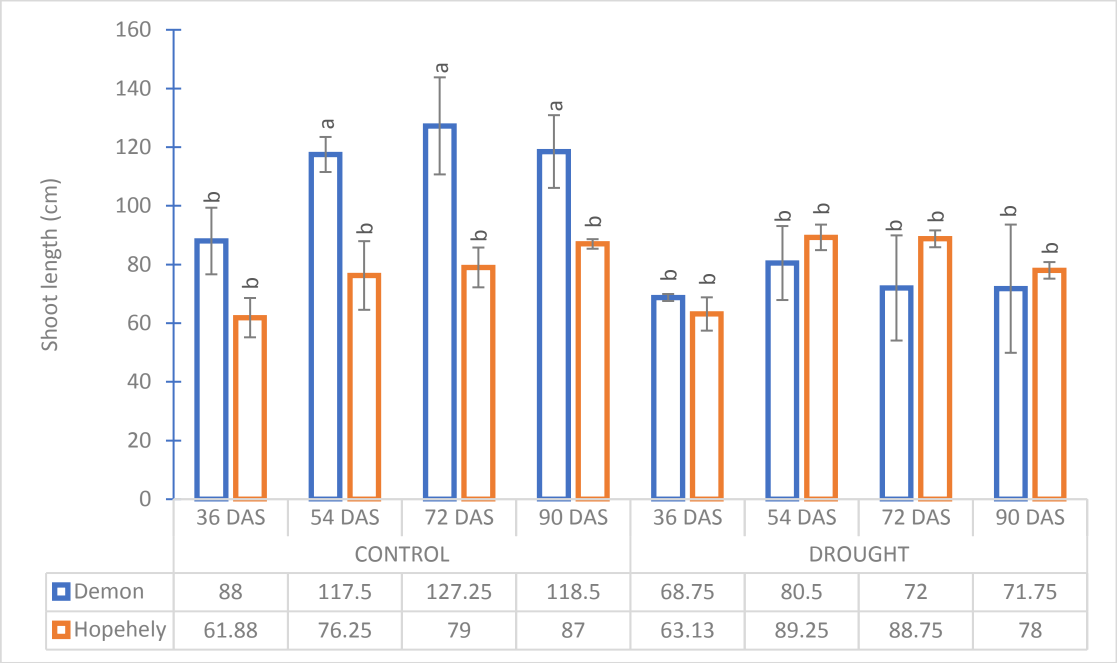


Figure 20 Effect of drought stress on shoot height of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test.

4.2. Effect of drought stress on number of leaflets produced by potato genotypes

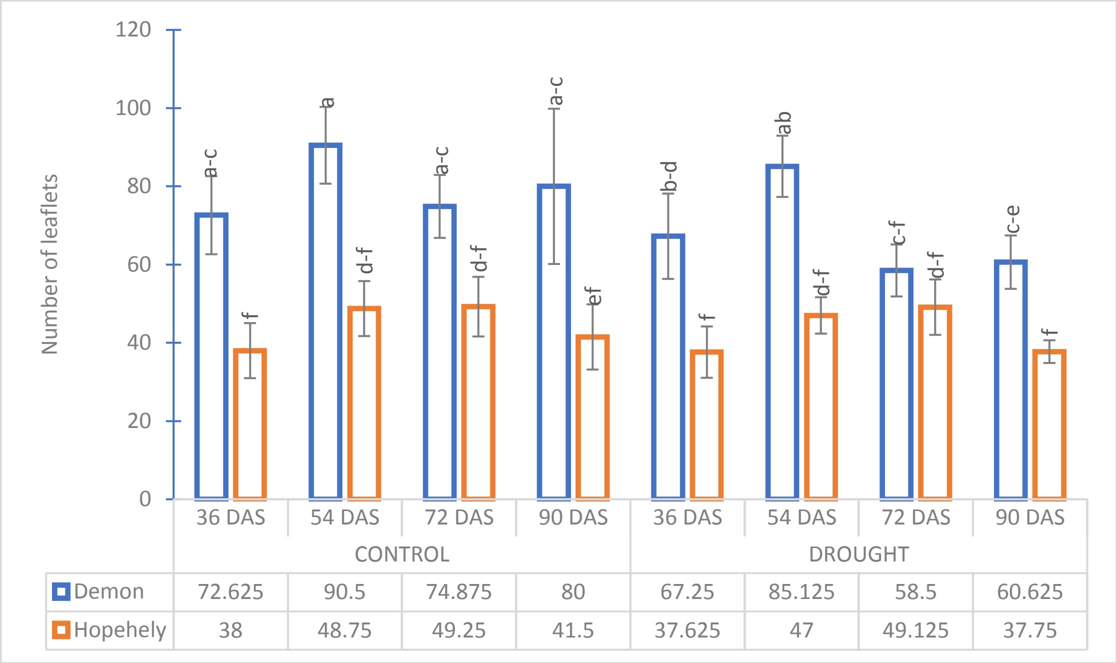
Simple main effect analysis showed that all independent variables showed significant effect (p<0.01) on number of leaflets produced by plants. Significant effect on number of leaflets was also observed by genotype×drought stress (f(1,43)=5.32, p=0.03), and genotype×plant developmental stage (f(3,45)=4.5, p=0.01) (Table 6).

Table 6 Analysis of variance for the effect of drought stress on number of leaflets produced by potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	14460.1	14460.1	187.52	0.00^{**}
Water levels (B)	1	689.1	689.1	8.94	0.00^{**}
Plant developmental stage (C)	3	1942.2	647.4	8.40	0.00^{**}
A×B	1	410.1	410.1	5.32	0.03^{*}
A×C	3	1039.9	346.6	4.50	0.01^{**}
B×C	3	201.8	67.3	0.87	0.46^{ns}
A×B×C	3	136.3	45.4	0.59	0.62^{ns}
Error	45	3470.0	77.1		
Total	63	22704.9			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

Means comparison showed that ‘Demon’ produced significantly higher number of leaflets per plant than ‘Hopehely’. Both genotypes produced new leaflets until flowering. Highest number of leaflets were produced by ‘Demon’ at flowering stage under control and drought stress. Post-hoc test revealed a significant decrease in number of leaflets in ‘Demon’ under drought stress between flowering and tuber bulking stage while no significant differences were observed in the leaflets number of ‘Hopehely’ in response drought stress (Fig. 21).



	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
	CONTROL				DROUGHT			
■ Demon	72.625	90.5	74.875	80	67.25	85.125	58.5	60.625
■ Hopehely	38	48.75	49.25	41.5	37.625	47	49.125	37.75

Figure 21 Effect of drought stress on number of leaflets produced by potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

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4.3. Effect of drought stress on shoot weight of potato genotypes

Analysis of variance showed a significant effect of genotype (p=0.03), drought stress (p<0.01), plant developmental stage (p<0.01) and interaction of genotype and drought stress (p<0.01) on shoot weight of potato plants. The interaction between the effects of drought stress and plant developmental stage on shoot weight was also statistically significant (f(3,45)=4.88, p=0.01) (Table 7).

Maximum shoot weight (186.16 g) was recorded for ‘Demon’ plants at tuber bulking stage under control conditions that was statistically equal to the shoot weight of ‘Demon’ plants (184.93 g) recorded at flowering stage. Under drought stress, ‘Hopehely’ plants produced heaviest stems (168.34 g) at flowering stage that was at par with shoot weight of ‘Demon’ plants (153.9 g) at similar developmental stage. Tukey post-hoc test revealed that ‘Demon’ produced significantly higher shoot weight than ‘Hopehely’ under control conditions. We also observed that drought stress significantly reduced shoot weight of ‘Demon’ while ‘Hopehely’ maintained its shoot weight under drought stress when compared to well-watered plants. Shoot weight of ‘Demon’ significantly reduced during flowering and tuber bulking stage under drought stress (Fig. 22).

Table 7 Analysis of variance for the effect of drought stress on shoot weight of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	2379.0	2379.0	5.35	0.03*
Water levels (B)	1	13351.8	13351.8	30.03	0.00**
Plant developmental stage (C)	3	13833.5	4611.2	10.37	0.00**
A×B	1	14259.3	14259.3	32.08	0.00**
A×C	3	1688.0	562.7	1.27	0.29^{ns}
B×C	3	6506.2	2168.7	4.88	0.01**
A×B×C	3	1807.3	602.4	1.36	0.27^{ns}
Error	45	20004.4	444.5		
Total	63	76537.8			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

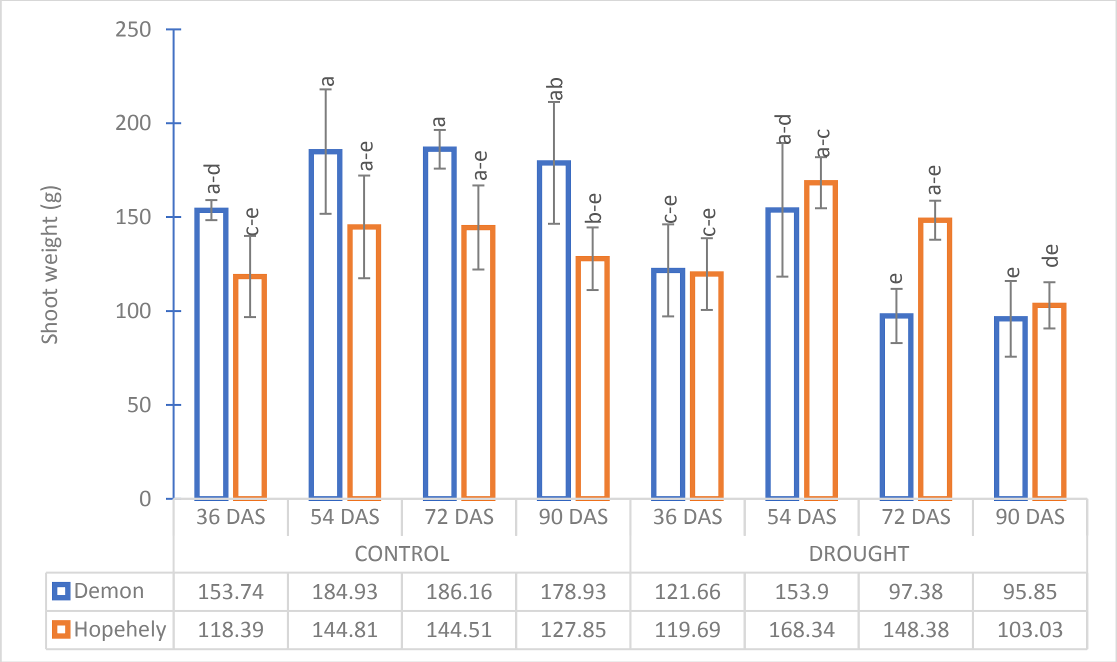


Figure 22 Effect of drought stress on shoot weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.4. Effect of drought stress on specific leaf weight (SLW) of potato genotypes

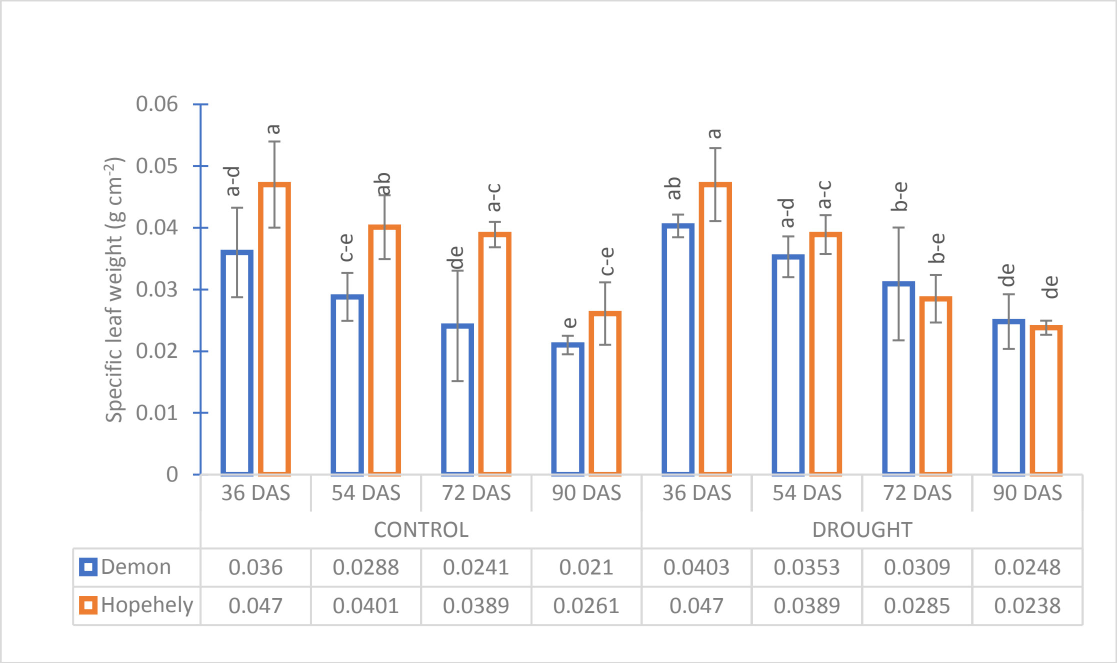
Leaf thickness can be measured as specific leaf weight. Analysis of variance showed that SLW significantly varied between genotypes ($p<0.01$) and plant developmental stage ($p<0.01$). It also showed that there was a statistically significant interaction between genotype and drought stress ($f(1,45)=11.49$, $p<0.01$), though drought stress did not show any significant effect ($p=0.47$) on SLW (Table 08).

Table 8 Analysis of variance for the effect of drought stress on specific leaf weight of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	0.00060	0.00060	22.23	0.00^{**}
Water levels (B)	1	0.00001	0.00001	0.52	0.47^{ns}
Plant developmental stage (C)	3	0.00300	0.00100	36.96	0.00^{**}
A×B	1	0.00031	0.00031	11.49	0.00^{**}
A×C	3	0.00010	0.00003	1.26	0.29^{ns}
B×C	3	0.00005	0.00002	0.59	0.62^{ns}
A×B×C	3	0.00010	0.00003	1.20	0.32^{ns}
Error	45	0.00122	0.00003		

**significant at 1% probability level, ^{ns} non-significant at 5% probability level

‘Hopehely’ produced significantly thicker leaves than ‘Demon’ under control and drought conditions. Drought stress did not show any significant effect on SLW of either genotype. Both genotypes at different developmental stage showed significant variation in SLW. Maximum SLW for both genotypes was observed at tuber initiation stage and followed downward trend after that under control and drought (Fig. 23).



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
Demon	0.036	0.0288	0.0241	0.021	0.0403	0.0353	0.0309	0.0248
Hopehely	0.047	0.0401	0.0389	0.0261	0.047	0.0389	0.0285	0.0238

Figure 23 Effect of drought stress on specific leaf weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test.

4.5. Effect of drought stress on foliage fresh weight of potato genotypes

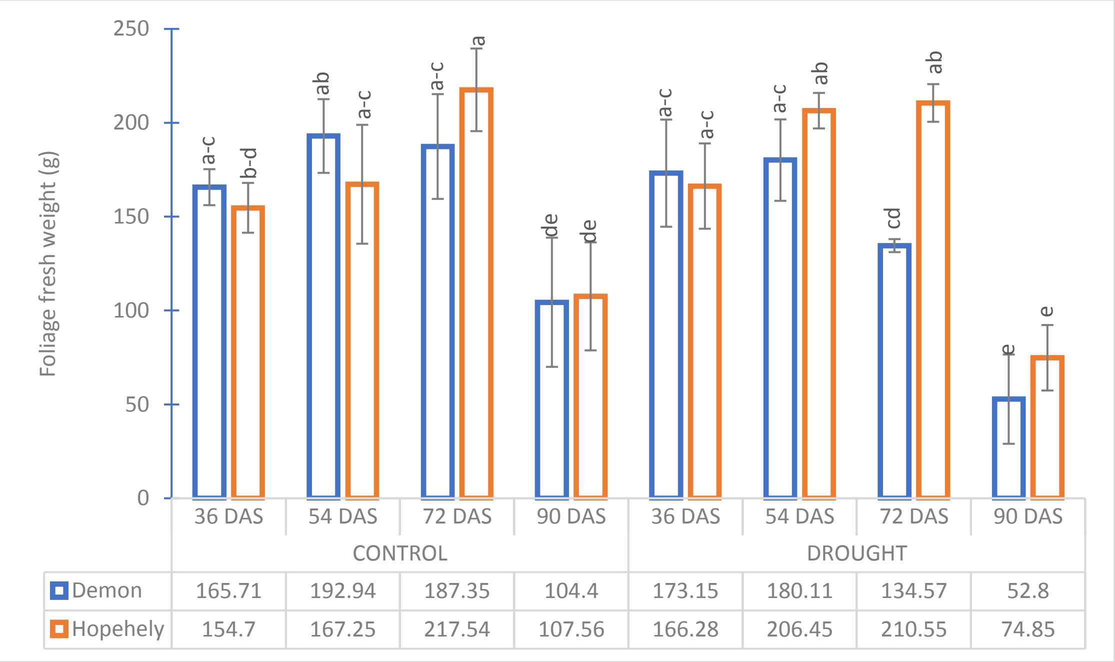
Statistical analysis showed that foliage fresh weight was significantly affected by all independent variables (p<0.05) and all their possible interaction with each other (p<0.01) except the interaction between the effects of genotype, drought stress and plant developmental stage (f(3,45)=1.03, p=0.39) (Table 9).

Table 9 Analysis of variance for the effect of drought stress on foliage (leaves) fresh weight of potato genotypes

Source of variation	Df	SS	MS	F	p-value
Genotype (A)	1	3257	3256.8	6.60	0.01^{**}
Water levels (B)	1	2435	2434.7	4.93	0.03^{*}
Plant developmental stage (C)	3	113108	37702.5	76.40	0.00^{**}
A×B	1	3650	3650.3	7.40	0.01^{**}
A×C	3	8970	2989.9	6.06	0.00^{**}
B×C	3	9303	3100.9	6.28	0.00^{**}
A×B×C	3	1526	508.8	1.03	0.39^{ns}
Error	45	22208	493.5		
Total	63	165653			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

‘Hopehely’ produced significantly heavier leaves than ‘Demon’ under control and drought conditions. Mean comparison showed that drought stress significantly reduced foliage fresh weight in ‘Demon’ while no significant effect was observed in ‘Hopehely’. Significant reduction in ‘Demon’ foliage weight was recorded between flowering and tuber bulking stage in response to drought stress. While foliage fresh weight was significantly reduced between tuber bulking and senescence in both genotypes under control and drought stress (Fig. 24).



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
☐ Demon	165.71	192.94	187.35	104.4	173.15	180.11	134.57	52.8
☐ Hopehely	154.7	167.25	217.54	107.56	166.28	206.45	210.55	74.85

Figure 24 Effect of drought stress on foliage fresh weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test.

4.6. Effect of drought stress on foliage dry matter of potato genotypes

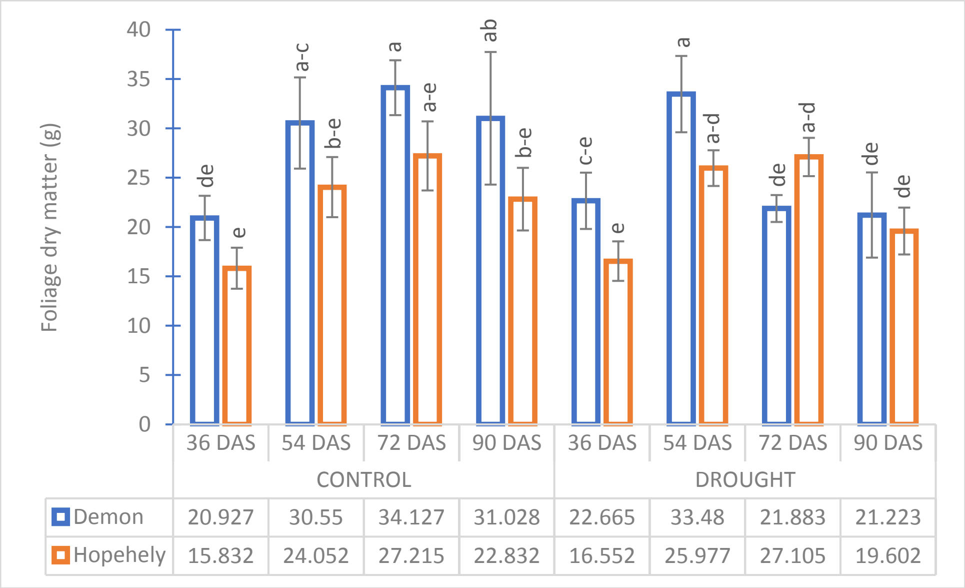
Analysis of variance showed that genotype, drought stress and plant developmental stages had a statistically significant effect on foliage dry matter ($p \leq 0.01$). The interaction between the effects of genotype, drought stress and plant developmental stage also showed statistically significant effect on foliage dry matter ($p \leq 0.02$), while only genotype×plant developmental stage had a non-significant effect on foliage dry matter ($p=0.06$) (Table 10).

‘Demon’ produced significantly higher dry matter than ‘Hopehely’. However, drought stress significantly reduced foliage dry matter in ‘Demon’ plants. Under control conditions, foliage dry matter of both genotypes increased gradually and reached maximum at tuber bulking stage. Similar trend was also observed for ‘Hopehely’ under drought conditions. However, ‘Demon’ plants under drought produced maximum foliage dry matter earlier (flowering stage) that decreased significantly afterwards. Under drought stress, a significant reduction was observed in ‘Demon’ foliage dry mass between flowering and tuber bulking stage (Fig. 25).

Table 10 Analysis of variance for the effect of drought stress on foliage dry matter of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	336.95	336.952	31.82	0.00**
Water levels (B)	1	81.70	81.699	7.72	0.01**
Plant developmental stage (C)	3	903.60	301.201	28.45	0.00**
A×B	1	69.62	69.618	6.58	0.01**
A×C	3	83.85	27.949	2.64	0.06ns
B×C	3	270.47	90.156	8.52	0.00**
A×B×C	3	122.92	40.972	3.87	0.02*
Error	45	476.45	10.588		
Total	63	2395.87			

*significant at 5% probability level, **significant at 1% probability level, ns non-significant at 5% probability level



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
◻ Demon	20.927	30.55	34.127	31.028	22.665	33.48	21.883	21.223
◻ Hopehely	15.832	24.052	27.215	22.832	16.552	25.977	27.105	19.602

Figure 25 Effect of drought stress on foliage dry matter of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.7. Effect of drought stress on leaf area index (LAI) of potato genotypes

Factorial ANOVA showed that LAI was significantly affected by genotype and drought stress interaction (f(1,45)=18.37, p<0.01). Simple main effects showed that genotype did not have statistically significant effect (p=0.1) on LAI but drought stress (p=0.01) and plant developmental stages (p<0.01) had a significant effect on LAI (Table 11).

Table 11 Analysis of variance for the effect of drought stress on leaf area index of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	11.691	11.6911	2.81	0.10^{ns}
Water levels (B)	1	27.595	27.5949	6.62	0.01**
Plant developmental stage (C)	3	228.155	76.0516	18.26	0.00**
A×B	1	76.507	76.5067	18.37	0.00**
A×C	3	14.078	4.6927	1.13	0.35^{ns}
B×C	3	20.355	6.7850	1.63	0.19^{ns}
A×B×C	3	33.439	11.1463	2.68	0.06^{ns}
Error	45	187.447	4.1655		
Total	63	606.096			

**significant at 1% probability level, ^{ns} non-significant at 5% probability level

Highest LAI under control conditions was calculated for ‘Demon’ plants (13.47) while under drought stress for ‘Hopehely’ plants (11.94). Tukey post-hoc test revealed that drought stress significantly reduced LAI of ‘Demon’. However, non-significant increase in LAI was observed for ‘Hopehely’ plants under drought stress conditions. LAI of both genotypes increased till tuber bulking stage and then significant reduction was observed between tuber bulking and senescence (Fig. 26).

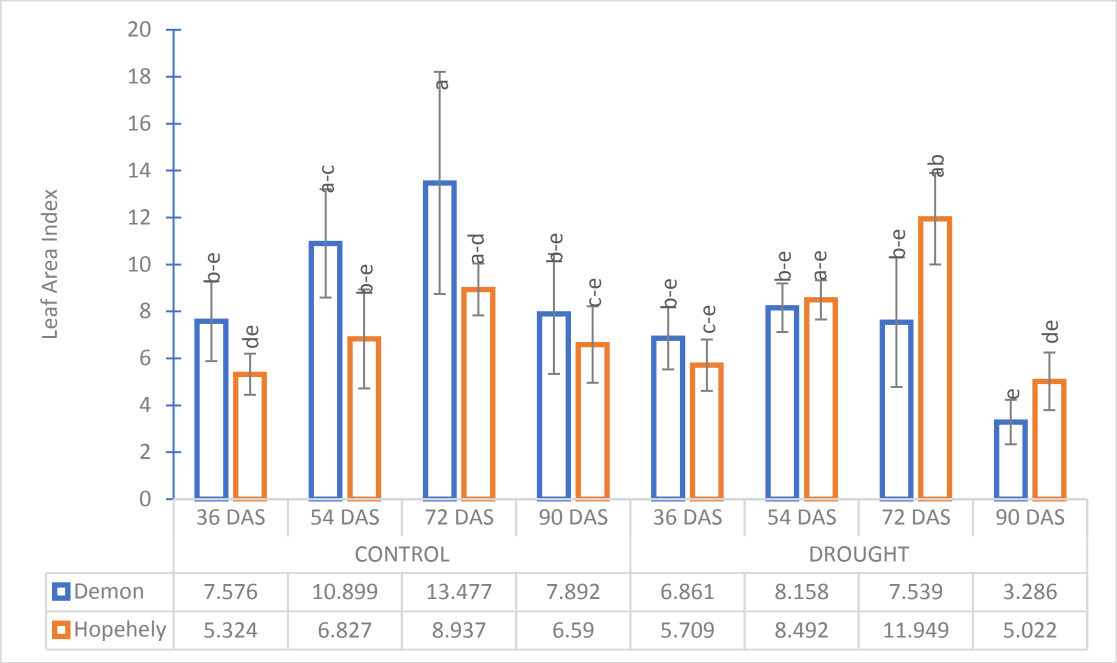


Figure 26 Effect of drought stress on leaf area index of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.8. Effect of drought stress on leaf area duration of potato genotypes

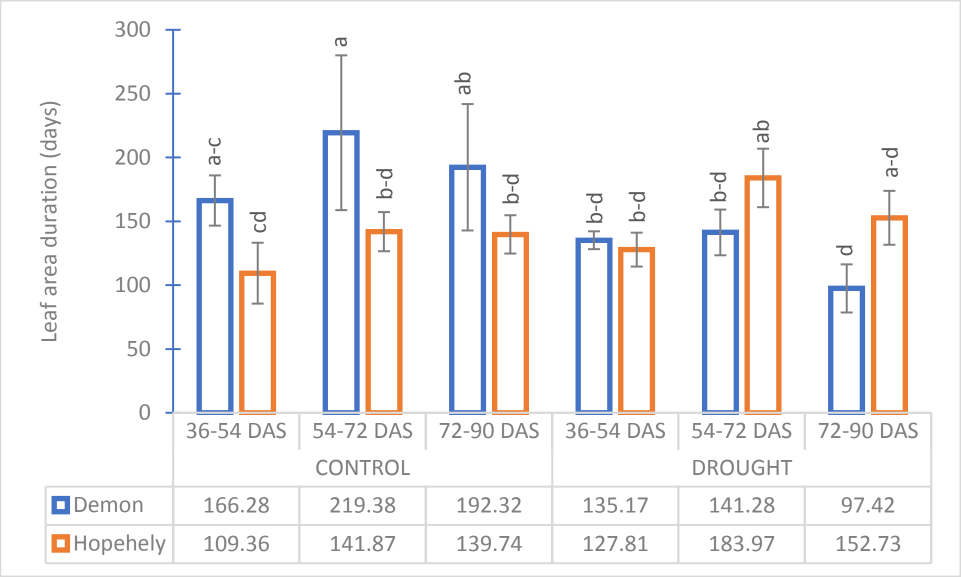
Genotypes and drought stress interaction significantly affected (f(1,33)=33.95, p<0.01) leaf area duration (LAD) of plants. Simple main effect analysis showed that genotype (p=0.05), drought stress (p=0.01) and plant developmental stage (p<0.01) have a statistically significant effect on LAD values (Table 12).

Table 12 Analysis of variance for the effect of drought stress on leaf area duration of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	3095.2	3095.2	4.09	0.05^{*}
Water levels (B)	1	5682.9	5682.9	7.51	0.01^{**}
Plant developmental stage (C)	2	11547.8	5773.9	7.63	0.00^{**}
A×B	1	25694.8	25694.8	33.95	0.00^{**}
A×C	2	2256.7	1128.3	1.49	0.24^{ns}
B×C	2	2482.5	1241.2	1.64	0.20^{ns}
A×B×C	2	2847.9	1424.0	1.88	0.17^{ns}
Error	33	24977.8	756.9		
Total	47	81852.4			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

Under control conditions, LAD of ‘Demon’ was significantly higher than ‘Demon’ but drought stress significantly reduced LAD of ‘Demon’. On the other hand, LAD of ‘Hopehely’ was higher under drought stress but statistically at par with control conditions. LAD of both genotypes was highest during flowering and tuber bulking stage (54-72 DAS). ‘Demon’ plants under drought stress reached the senescence earliest while other plants still had green leaves on them (Fig. 27).



	CONTROL 36-54 DAS	CONTROL 54-72 DAS	CONTROL 72-90 DAS	DROUGHT 36-54 DAS	DROUGHT 54-72 DAS	DROUGHT 72-90 DAS
Demon	166.28	219.38	192.32	135.17	141.28	97.42
Hopehely	109.36	141.87	139.74	127.81	183.97	152.73

Figure 27 Effect of drought stress on leaf area duration of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.9. Effect of drought stress on leaf area ratio of potato genotypes

Leaf area ratio is the measure of the efficiency of plants with which the use its photosynthetic resources. Genotypes and drought stress interaction significantly affected (f(1,45)=9.31, p<0.01) leaf area ratio (LAR). The main effect analysis showed that only pant developmental stage showed statistically significant effect (p<0.01) on LAR while both genotype and drought stress had a statistically non-significant effect (p>0.05) on LAR (Table 13).

Table 13 Analysis of variance for the effect of drought stress on leaf area ratio of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	3293	3292.6	1.47	0.23^{ns}
Water levels (B)	1	3776	3775.8	1.69	0.20^{ns}
Plant developmental stage (C)	3	70717	23572.5	10.52	0.00^{**}
A×B	1	20842	20842.3	9.31	0.00^{**}
A×C	3	4549	1516.5	0.68	0.57^{ns}
B×C	3	7877	2625.7	1.17	0.33^{ns}
A×B×C	3	3526	1175.4	0.52	0.67^{ns}
Error	45	100794	2239.9		
Total	63	218404			

**significant at 1% probability level, ^{ns} non-significant at 5% probability level

Under control conditions, no significant changes were observed in LAR of either genotype during various plant developmental stages, but significant reduction was observed in LAR of both genotypes under drought stress during tuber bulking and senescence stage. Highest LAR was calculated for 'Hopehely' plants at tuber bulking stage under drought stress condition (Fig. 28).

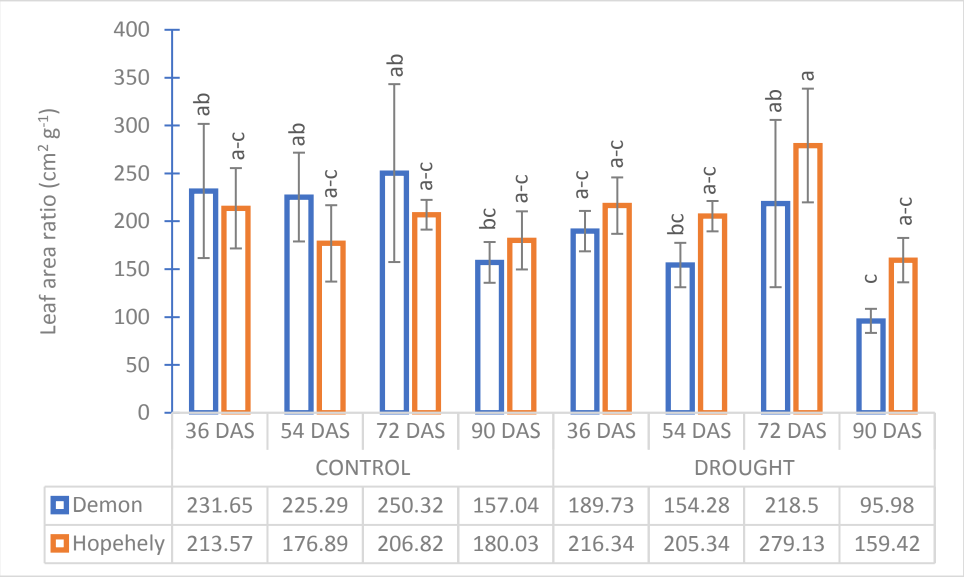


Figure 28 Effect of drought stress on leaf area ratio of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.10. Effect of drought stress on chlorophyll concentration of potato genotypes

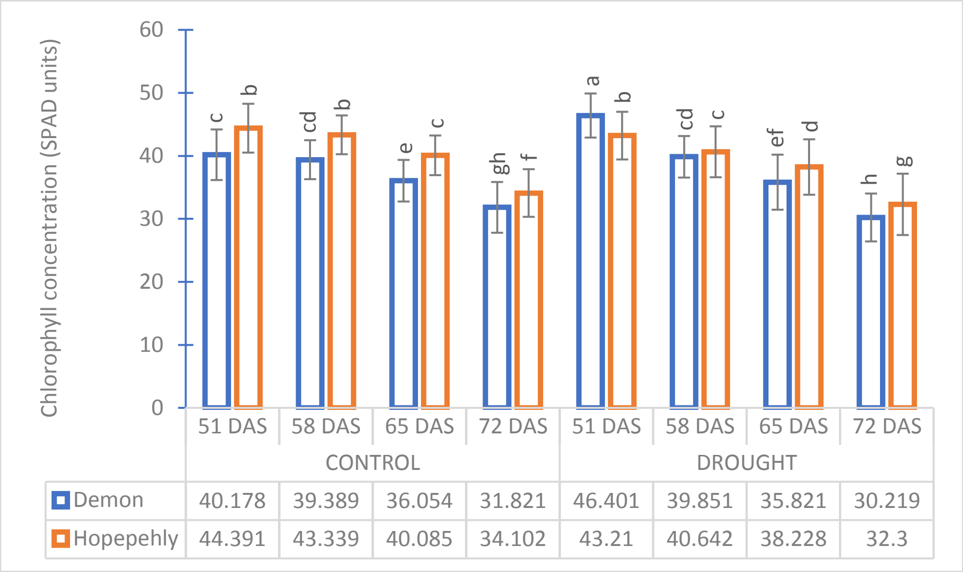
Statistical analysis showed that genotype and plant developmental stages had a significant effect ($p<0.01$) on plant chlorophyll content. We observed that the effect of drought stress was statistically non-significant ($p=0.07$) on chlorophyll content. Factorial analysis also revealed that all possible interactions between the effects of independent variables on chlorophyll content were statistically significant ($p<0.01$) (Table 14).

Table 14 Analysis of variance for the effect of drought stress on chlorophyll concentration in the leaves of potato genotypes

Source of variation	Df	SS	MS	F	p-value
Genotype (A)	1	1851.8	1851.8	127.73	0.00^{**}
Water levels (B)	1	48.7	48.7	3.36	0.07^{ns}
Plant developmental stage (C)	3	31319.4	10439.8	720.11	0.00^{**}
A×B	1	1035.6	1035.6	71.44	0.00^{**}
A×C	3	416.0	138.7	9.57	0.00^{**}
B×C	3	1203.5	401.2	27.67	0.00^{**}
A×B×C	3	786.1	262.0	18.07	0.00^{**}
Error	1712	24819.8	14.5		
Total	1727	61481.0			

**significant at 1% probability level, ^{ns} non-significant at 5% probability level

'Hopehely' produced significantly higher chlorophyll content that 'Demon' under control as well as drought condition. Chlorophyll content of 'Hopehely' decreased significantly in response to drought stress while 'Demon' did not show any significant difference in chlorophyll content due to drought stress. Moreover, we also observed that chlorophyll content in both genotypes decreased significantly every week after flowering under control as well as drought conditions (Fig. 29)



	CONTROL				DROUGHT			
	51 DAS	58 DAS	65 DAS	72 DAS	51 DAS	58 DAS	65 DAS	72 DAS
◻ Demon	40.178	39.389	36.054	31.821	46.401	39.851	35.821	30.219
◻ Hopepehly	44.391	43.339	40.085	34.102	43.21	40.642	38.228	32.3

Figure 29 Effect of drought stress on chlorophyll concentration in potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test.

Table 15 shows that chlorophyll content in ‘Demon’ plants varied significantly with in the plants at different plant developmental stages under control and drought stress. Compound leaves, leaflets on those compound leaves and measuring points on those leaflets showed statistically significant effect on chlorophyll content (p<0.05). Coefficient of variation (CV) for chlorophyll content in ‘Demon’ plants ranged between 6.09 - 8.70 under control while 4.82 - 12.82 under drought stress. While in ‘Hopehely’, CV ranged between 5.49 - 9.39 under control and 6.52 - 11.39 under drought stress. Compound leaves, leaflets and measuring points showed statistically significant variation (p<0.05) in ‘Hopehely’ as well under control and drought stress at different plant developmental stages (Table 16).

Table 15 Analysis of variance for the effect of SPAD measuring point on chlorophyll content in 'Demon' plants

Source of variation		*51 DAS*		*58 DAS*		*65 DAS*		*72 DAS*	
				Under control conditions					
	df	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Compound leaf (A)	2	5.46	0.01	6.57	0.00	4.15	0.02	2.89	0.06
Leaflet (B)	2	0.03	0.97	8.55	0.00	6.79	0.00	11.76	0.00
Measuring point (C)	2	4.97	0.01	9.82	0.00	10.32	0.00	10.00	0.00
A×B	4	9.03	0.00	0.66	0.62	1.55	0.19	0.51	0.73
A×C	4	0.09	0.98	10.13	0.00	0.12	0.97	0.06	0.99
B×C	4	0.33	0.86	0.23	0.92	0.13	0.97	0.17	0.95
A×B×C	8	0.22	0.99	0.35	0.94	0.29	0.97	0.10	0.99
CV (%)		8.70		6.09		7.88		8.31	
				Under drought stress					
	df	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Compound leaf (A)	2	1.57	0.21	3.33	0.04	14.85	0.00	4.15	0.02
Leaflet (B)	2	3.70	0.02	1.38	0.25	6.78	0.00	0.47	0.62
Measuring point (C)	2	10.24	0.00	7.25	0.00	17.16	0.00	4.88	0.01
A×B	4	5.80	0.00	2.24	0.07	7.19	0.00	0.18	0.94
A×C	4	0.82	0.51	0.46	0.76	0.43	0.79	0.06	0.99
B×C	4	0.15	0.96	0.43	0.78	0.32	0.86	0.08	0.99
A×B×C	8	0.60	0.77	0.14	0.99	0.18	0.99	0.10	1.00
CV (%)		*4.82*		*7.68*		*7.07*		*12.82*	

p-value<0.05 is statistically significant, p-value>0.05 is statistically not significant

Mean comparisons showed that SPAD values for chlorophyll content in 'Demon' significantly reduced from top compound leaves to lower compound leaves at each observation time during control as well as drought stress. Top leaflets of compound leaves in 'Demon' also produced significantly higher chlorophyll content than lower leaflets. On leaflets, top measuring points showed significantly higher SPAD reading for chlorophyll content than middle and basal measuring point under both control and drought stress (Table 17).

Table 16 Analysis of variance for the effect of SPAD measuring point on chlorophyll content in 'Hopehely' plants

Source of variation		*51 DAS*		*58 DAS*		*65 DAS*		*72 DAS*	
Under control conditions									
	df	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Compound leaf (A)	2	5.80	0.00	6.02	0.00	6.48	0.00	4.00	0.02
Leaflet (B)	2	2.44	0.09	3.20	0.04	5.81	0.00	0.05	0.95
Measuring point (C)	2	24.03	0.00	16.23	0.00	0.10	0.90	16.02	0.00
A×B	4	4.41	0.00	5.01	0.00	2.06	0.09	3.32	0.01
A×C	4	1.02	0.40	0.98	0.42	1.03	0.39	0.40	0.81
B×C	4	0.09	0.99	0.59	0.67	1.32	0.26	0.37	0.83
A×B×C	8	0.34	0.95	0.16	0.99	0.93	0.49	0.20	0.99
CV (%)		6.37		5.49		6.88		9.39	
Under drought stress									
	df	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**	**F-value**	**p-value**
Compound leaf (A)	2	13.55	0.00	4.29	0.01	2.59	0.08	7.78	0.00
Leaflet (B)	2	2.00	0.14	5.37	0.00	9.11	0.00	6.06	0.00
Measuring point (C)	2	19.42	0.00	0.10	0.90	0.35	0.70	7.18	0.00
A×B	4	0.84	0.51	2.98	0.02	3.15	0.02	2.16	0.08
A×C	4	0.13	0.97	1.15	0.33	0.42	0.79	0.08	0.99
B×C	4	0.57	0.68	1.32	0.26	0.84	0.50	0.15	0.96
A×B×C	8	0.56	0.81	0.51	0.84	1.04	0.41	0.09	0.99
CV (%)		*6.25*		*6.62*		*6.97*		*11.39*	

p-value<0.05 is statistically significant, p-value>0.05 is statistically not significant

Table 17 Mean comparison of SPAD values in different foliage parts of 'Demon' at different water levels

Source of variation		51 DAS	58 DAS	65 DAS	72 DAS
Variation among compound leaves					
Control	Compound leaf$_3$	41.74b	40.41a	37.17ab	32.49a
	Compound leaf$_4$	39.55c	39.39ab	35.52c	31.95a
	Compound leaf$_5$	39.25c	38.36b	35.47c	31.02ab
Drought stress	Compound leaf$_3$	46.91a	40.49a	37.56a	31.71a
	Compound leaf$_4$	46.29a	40.28a	35.57bc	29.70bc
	Compound leaf$_5$	45.99a	38.78b	34.33c	29.23c
Variation among leaflets on compound leaves					
Control	Top leaflet	40.24b	40.63a	37.42a	32.93a
	1st side leaflet	40.22b	39.23bc	35.72bc	32.43a
	2nd side leaflet	40.07b	38.31c	35.02bc	30.10b
Drought stress	Top leaflet	46.99a	40.54a	36.53ab	30.65b
	1st side leaflet	46.61a	39.54ab	36.38ab	30.24b
	2nd side leaflet	45.60a	39.46a-c	34.55c	29.76b
Variation among measuring points on leaflets					
Control	Top measuring point	41.57c	40.83ab	37.63a	33.23a
	Middle measuring point	39.97d	38.78cd	35.92b	31.79ab
	Basal measuring point	38.99d	38.55cd	34.60bc	30.44bc
Drought stress	Top measuring point	47.63a	41.44a	37.59a	31.65ab
	Middle measuring point	46.31ab	39.68bc	35.76b	30.19bc
	Basal measuring point	45.25b	38.42d	34.10c	28.80c

Means followed by different letters in the same column are significantly different at the 5% probability level. Control- 80% water holding capacity; Drought stress- 50% water holding capacity

Mean comparisons of SPAD values for chlorophyll content in 'Hopehely' also showed a significant reduction in lower compound leaves compared to top compound leaves at each observation time during control as well as drought stress conditions. Top leaflets of compound leaves in 'Hopehely' also produced significantly higher chlorophyll content than first or second side leaflets under drought stress but under control conditions no significant differences were observed among leaflets of 'Hopehely' plants. Like 'Demon', top measuring points on leaflets showed significantly higher SPAD reading for chlorophyll content than middle and basal measuring point under both control and drought stress (Table 18).

Table 18 Mean comparison of SPAD values in different foliage parts of 'Hopehely' at different water levels

Source of variation		51 DAS	58 DAS	65 DAS	72 DAS
Variation among compound leaves					
Control	Compound leaf$_3$	45.60a	44.32a	41.33a	35.27a
	Compound leaf$_4$	44.22ab	43.31ab	39.92ab	33.87ab
	Compound leaf$_5$	43.35b	42.38bc	39.01bc	33.17b
Drought stress	Compound leaf$_3$	44.79a	41.70cd	38.98bc	33.61ab
	Compound leaf$_4$	43.34b	40.26de	38.14c	32.93b
	Compound leaf$_5$	41.49c	39.96e	37.56c	30.36c
Variation among leaflets on compound leaves					
Control	Top leaflet	45.01a	44.14a	41.33a	34.24a
	1st side leaflet	44.58a	43.09a	39.71ab	34.04a
	2nd side leaflet	43.58ab	42.78ab	39.21bc	34.02a
Drought stress	Top leaflet	43.93ab	41.30bc	39.73ab	33.63a
	1st side leaflet	42.94b	41.17c	37.80cd	32.61a
	2nd side leaflet	42.74b	39.44d	37.15d	30.66b
Variation among measuring points on leaflets					
Control	Top measuring point	46.78a	45.04a	40.20a	36.14a
	Middle measuring point	44.21bc	43.11b	40.13a	34.27b
	Basal measuring point	42.17d	41.87bc	39.92ab	31.88d
Drought stress	Top measuring point	45.34ab	40.78c	38.50a-c	33.97bc
	Middle measuring point	42.86cd	40.62c	38.19bc	32.23cd
	Basal measuring point	41.41d	40.50c	37.98c	30.69d

Means followed by different letters in the same column are significantly different at the 5% probability level. Control- 80% water holding capacity; Drought stress- 50% water holding capacity

4.11. Effect of drought stress on nitrogen content in foliage of potato genotypes

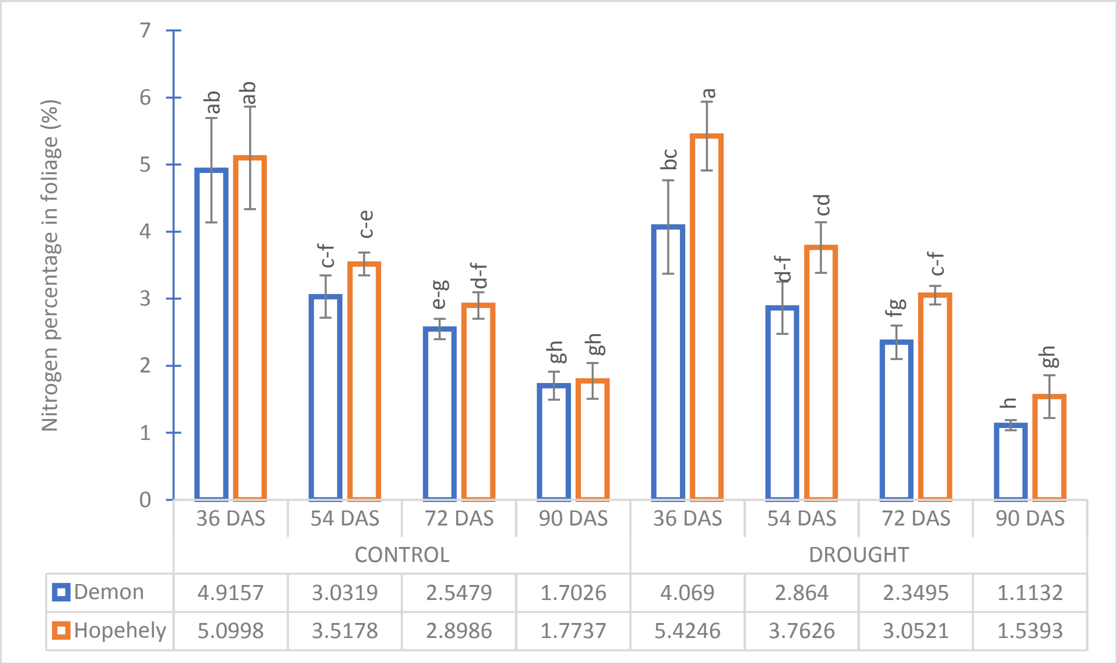
Genotypes and plant developmental stages showed statistically significant effect ($p<0.01$) on nitrogen content in the foliage while drought stress did not show any significant effect ($p=0.12$). Factorial ANOVA showed that there was a statistically significant interaction between the effect of genotype and drought stress (f(1,45)-7.39, $p=0.01$), while there was no statistically significant interaction between any other independent variables (Table 19).

Under well-watered conditions, genotypes did not show a significant difference in nitrogen content. However, under drought stress significantly higher nitrogen content was observed in 'Hopehely' than 'Demon'. Non-significant decrease in nitrogen content was observed in 'Demon' due to drought stress while in ‘Hopehely’ non-significant increase was observed in response to drought stress. Under control and stress conditions, both genotypes produced the highest nitrogen content at tuber initiation stage. Nitrogen content in foliage of both genotypes significantly decreased at each plant development stage. Lowest nitrogen percentage (1.11%) was observed in ‘Demon’ plants at senescence under drought stress conditions (Fig. 30).

Table 19 Analysis of variance for the effect of drought stress on nitrogen percentage in foliage of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	5.006	5.0056	28.21	0.00**
Water levels (B)	1	0.431	0.4314	2.43	0.12^{ns}
Plant developmental stage (C)	3	92.876	30.9586	174.48	0.00**
A×B	1	1.312	1.3121	7.39	0.01**
A×C	3	0.638	0.2128	1.20	0.32^{ns}
B×C	3	0.527	0.1758	0.99	0.40^{ns}
A×B×C	3	0.480	0.1601	0.90	0.44^{ns}
Error	45	7.985	0.1774		
Total	63	109.454			

**significant at 1% probability level, ^{ns} non-significant at 5% probability level



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
▢ Demon	4.9157	3.0319	2.5479	1.7026	4.069	2.864	2.3495	1.1132
▢ Hopehely	5.0998	3.5178	2.8986	1.7737	5.4246	3.7626	3.0521	1.5393

Figure 30 Effect of drought stress on nitrogen percentage in foliage of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.12. Effect of drought stress on relative water content in leaves of potato genotypes

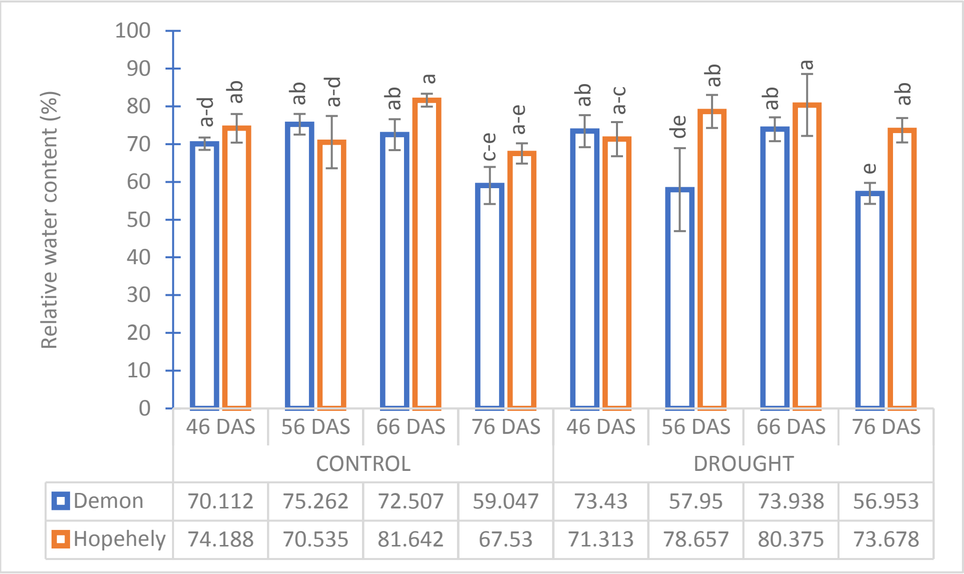
We observed a statistically significant effect of genotype ($p<0.01$), plant developmental stage ($p<0.01$) and their interaction ($f(3,45)=3.75$, $p=0.02$) on relative water content (RWC). Drought stress did not show any significant effect ($p=0.64$) but its interaction with genotype had a statistically significant effect ($f(1,45)=6.28$, $p=0.02$) on RWC (Table 20).

Table 20 Analysis of variance for the effect of drought stress on relative water content in leaves of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	861.94	861.936	35.22	0.00^{**}
Water levels (B)	1	5.14	5.136	0.21	0.64^{ns}
Plant developmental stage (C)	3	1343.91	447.970	18.30	0.00^{**}
A×B	1	153.61	153.605	6.28	0.02^{*}
A×C	3	275.18	91.726	3.75	0.02^{*}
B×C	3	95.97	31.988	1.31	0.28^{ns}
A×B×C	3	606.90	202.299	8.27	0.00^{**}
Error	45	1101.32	24.474		
Total	63	4534.52			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

Water content in the leaves of ‘Hopehely’ was significantly higher than ‘Demon’. Under control conditions, RWC of both genotypes was statistically at par at each developmental stage. Under drought stress, RWC of ‘Hopehely’ was significantly higher than ‘Demon’ at each developmental stage except at the initiation of flowering (46 DAS). Moreover, drought stress significantly reduced RWC of ‘Demon’ at flowering and senescence stage (Fig. 31).



	46 DAS	56 DAS	66 DAS	76 DAS	46 DAS	56 DAS	66 DAS	76 DAS
	CONTROL				DROUGHT			
◻ Demon	70.112	75.262	72.507	59.047	73.43	57.95	73.938	56.953
◻ Hopehely	74.188	70.535	81.642	67.53	71.313	78.657	80.375	73.678

Figure 31 Effect of drought stress on relative water content of potato genotypes leaves. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.13. Effect of drought stress on antioxidant activity in potato genotypes

Catalase (CAT) and superoxide dismutase (SOD) activity was significantly affected by genotypes ($p<0.01$) and drought stress ($p\leq0.02$). Factorial ANOVA revealed that the interaction between genotypes and drought stress had a statistically significant effect on SOD ($f(1,6)=7.21$, $p=0.04$) while a non-significant effect on CAT activity ($f(1,6)=0.29$, $p=0.61$) (Table 21,22).

Means comparison showed that antioxidants (CAT and SOD) activity in ‘Hopehely’ was significantly higher than ‘Demon’ under control as well as drought condition. Drought stress significantly increased SOD activity of both genotypes. Highest antioxidants activity was observed in drought stressed ‘Hopehely’ plants followed by ‘Demon’ plants under drought stress. Lowest antioxidant activity was observed for ‘Demon’ plants grown under control conditions (Fig. 32).

Table 21 Analysis of variance for the effect of drought stress on catalase activity in potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	0.50312	0.50312	91.65	0.00^{**}
Water levels (B)	1	0.05662	0.05662	10.31	0.02^{*}
A×B	1	0.00157	0.00157	0.29	0.61^{ns}
Error	6	0.03294	0.00549		
Total	11	0.61442			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

Table 22 Analysis of variance for the effect of drought stress on superoxide dismutase activity in potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	0.00041	$4.107E^{-04}$	193.67	0.00^{**}
Water levels (B)	1	0.00055	$5.502E^{-04}$	259.47	0.00^{**}
A×B	1	0.00002	$1.528E^{-05}$	7.21	0.04^{*}
Error	6	0.00001	$2.120E^{-06}$		
Total	11	0.00106			

*significant at 5% probability level, **significant at 1% probability level

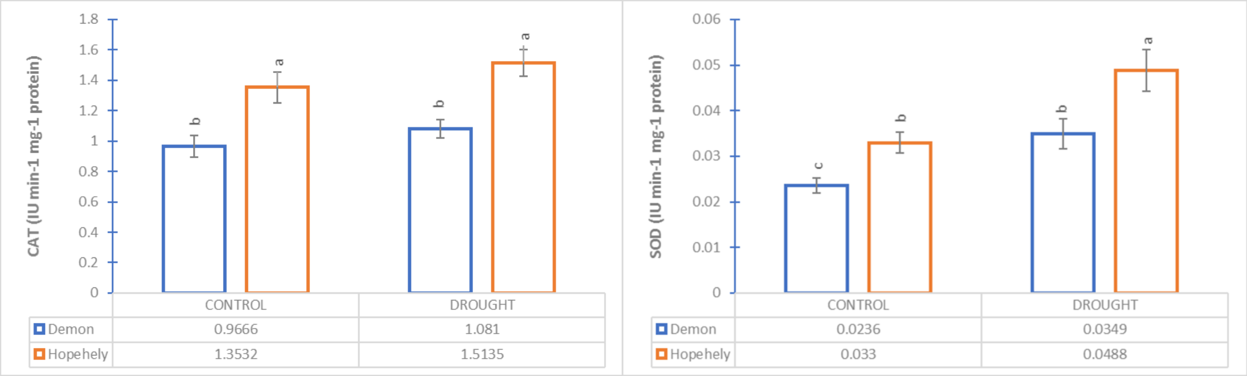


Figure 32 Effect of drought stress on catalase and superoxide dismutase (SOD) activity in potato genotypes leaves. Each value is mean ± STDEV (standard deviation) of three replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.14. Effect of drought stress on fresh plant biomass of potato genotypes

Roots, shoot and leaves of potato genotypes were weighed together to determine fresh plant biomass. Genotypes did not show any significant difference (p=0.84) on fresh plant weight. Drought stress and plant developmental stages showed a statistically significant effect (p<0.01) on fresh plant weight. Factorial ANOVA showed that fresh plant weight was significantly affected by interaction between genotype and drought stress (f(1,45)=20, p<0.01), genotype and plant developmental stage (f(3,45)=3.57, p=0.02), and drought stress and plant developmental stage (f(3,45)=6.43, p<0.01) (Table 23).

Drought stress significantly reduced fresh plant weight of ‘Demon’. Highest fresh plant weight was produced by ‘Demon’ (283.32 g) under control conditions that was significantly reduced to 148.65 g under drought stress. Under drought conditions, ‘Hopehely’ produced highest fresh plant weight at flowering and tuber bulking stage. Plant biomass of both genotypes increased till flowering and then started decreasing afterwards. Under drought stress, significant reduction in fresh plant weight of both genotypes was observed between tuber bulking and senescence stage. Tukey post-hoc test also showed significant reduction in fresh plant weight of ‘Demon’ between flowering and tuber bulking stage (-102.06 g at tuber bulking) in response to drought stress while ‘Hopehely’ showed non-significant reduction (-15.86 g at tuber bulking) in fresh plant weight at same plant developmental stage (Fig. 33).

Table 23 Analysis of variance for the effect of drought stress on fresh plant weight of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	69	68.8	0.04	0.84^{ns}
Water levels (B)	1	27190	27189.5	16.81	0.00^{**}
Plant developmental stage (C)	3	181239	60412.9	37.36	0.00^{**}
A×B	1	32339	32338.8	20.00	0.00^{**}
A×C	3	17298	5766.1	3.57	0.02^{*}
B×C	3	31185	10395.1	6.43	0.00^{**}
A×B×C	3	5541	1847.1	1.14	0.34^{ns}
Error	45	72764	1617.0		
Total	63	374424			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

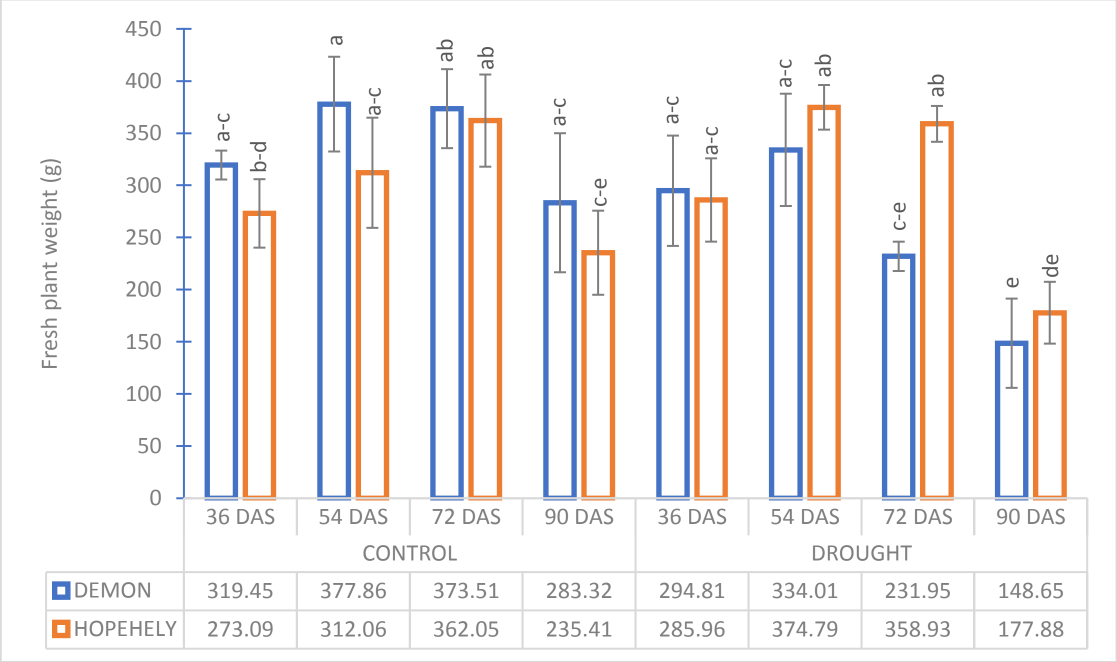


Figure 33 Effect of drought stress on fresh plant weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

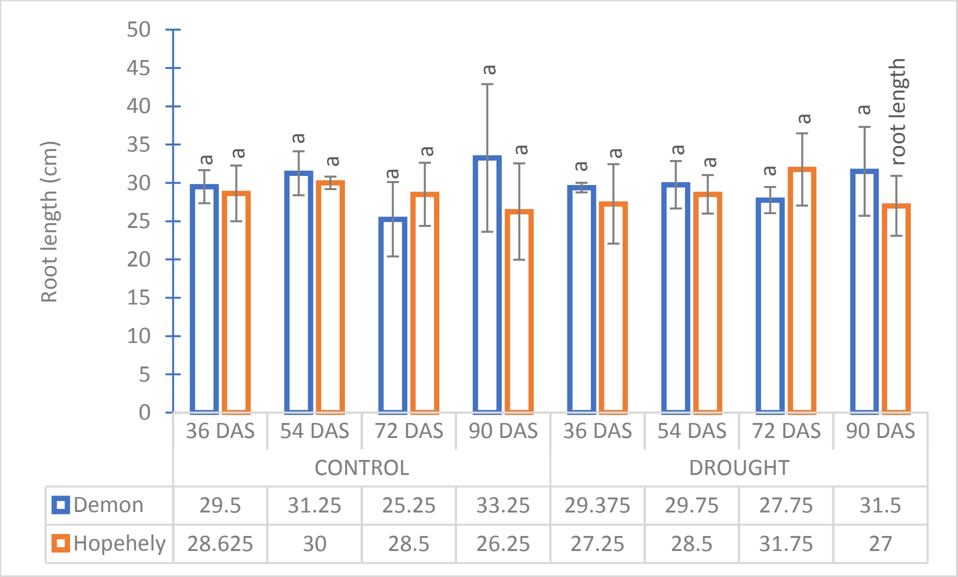
4.15. Effect of drought stress on root length of potato genotypes

A factorial ANOVA was performed to analyze effect of potato genotypes, drought stress and plant developmental stage on root length of potato plants. Results showed that the interaction between above mentioned independent variables did not have any statistically significant effect on root length (p>0.05). Moreover, simple main effects analysis revealed that genotype (p=0.29), drought stress (p=0.98) and plant developmental stage (p=0.75) did not have a statistically significant effect on root length (Table 24). Root length in both genotypes ranged between 25.25 cm to 33.25 cm (Fig. 34).

Table 24 Analysis of variance for the effect of drought stress on root length of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	23.77	23.7656	1.16	0.29^{ns}
Water levels (B)	1	0.02	0.0156	0.00	0.98^{ns}
Plant developmental stage (C)	3	24.81	8.2708	0.41	0.75^{ns}
A×B	1	1.00	1.0000	0.05	0.82^{ns}
A×C	3	176.30	58.7656	2.88	0.05^{ns}
B×C	3	45.30	15.0990	0.74	0.53^{ns}
A×B×C	3	7.37	2.4583	0.12	0.95^{ns}
Error	45	918.66	20.4146		
Total	63	1230.44			

*significant at 5% probability level, ^{ns} non-significant at 5% probability level



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
Demon	29.5	31.25	25.25	33.25	29.375	29.75	27.75	31.5
Hopehely	28.625	30	28.5	26.25	27.25	28.5	31.75	27

Figure 34 Effect of drought stress on root length of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.16. Effect of drought stress on root fresh weight of potato genotypes

Genotypes, drought stress and plant developmental stages showed a statistically significant effect ($p<0.01$) on root fresh weight. Analysis of variance also revealed that interaction between drought stress and plant developmental stage had a statistically significant effect on root fresh weight ($f(3,45)=2.96$, $p=0.04$). All other interactions between the effects of independent variables were statistically non-significant ($p>0.05$) (Table 25).

Table 25 Analysis of variance for the effect of drought stress on root fresh weight of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	2783.9	2783.9	43.96	0.00^{**}
Water levels (B)	1	838.8	838.8	13.24	0.00^{**}
Plant developmental stage (C)	3	39215.6	13071.9	206.40	0.00^{**}
A×B	1	6.8	6.8	0.11	0.74^{ns}
A×C	3	395.8	131.9	2.08	0.12^{ns}
B×C	3	561.9	187.3	2.96	0.04^{*}
A×B×C	3	100.3	33.4	0.53	0.66^{ns}
Error	45	2849.9	63.3		
Total	63	46962.3			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

‘Hopehely’ produced significantly higher root fresh weight than ‘Demon’ under control and drought conditions. Drought stress significantly reduced root fresh weight of both genotypes particularly at early plant developmental stage. Root fresh weight decreased significantly during plant development. Both genotypes produced maximum root fresh weight at tuber initiation stage that significantly reduced at later plant developmental stages under well-watered and drought conditions (Fig. 35).

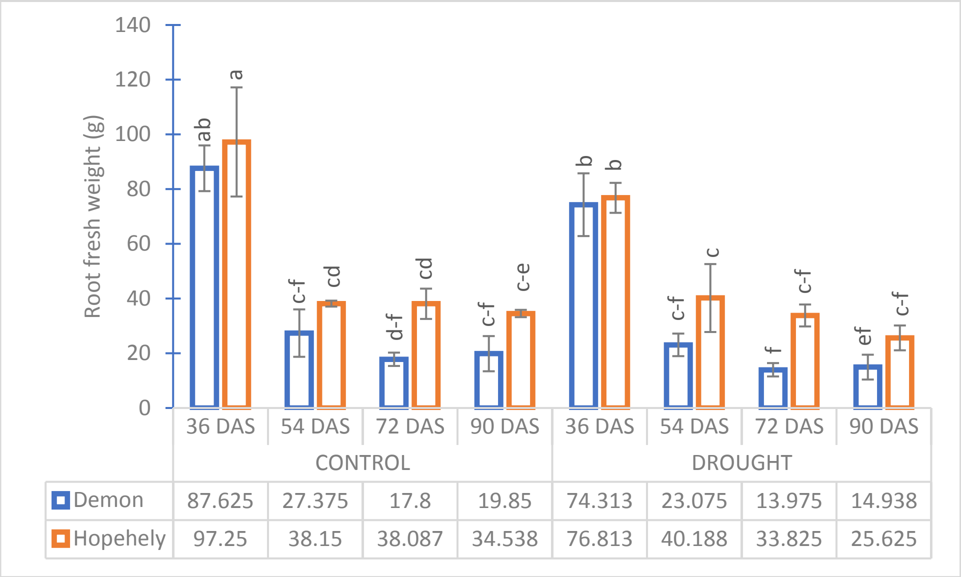


Figure 35 Effect of drought stress on root fresh weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.17. Effect of drought stress on root dry weight of potato genotypes

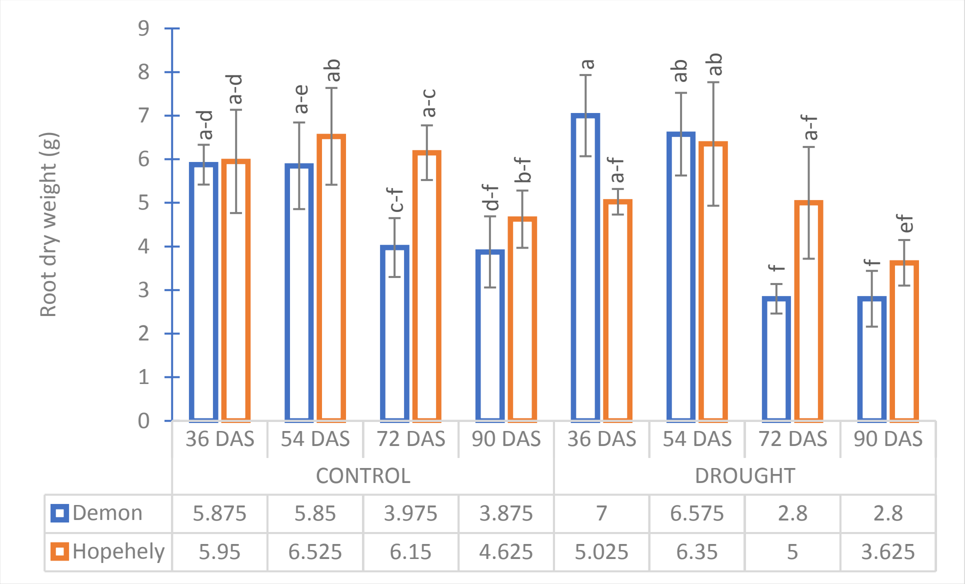
Analysis of variance showed that genotype (p=0.01), drought stress (p=0.04) and plant developmental stages (p<0.01) had a statistically significant effect on root dry weight. Genotype×drought stress also showed statistically significant effect (f(3,45=8.89, p<0.01) on root dry weight. Factorial ANOVA also revealed a statistically significant interaction between the effects of drought stress and plant developmental stage (f(3,45=2.93, p=0.04) (Table 26).

Table 26 Analysis of variance for the effect of drought stress on root dry weight of potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	5.063	5.0625	6.63	0.01^{**}
Water levels (B)	1	3.331	3.3306	4.36	0.04^{*}
Plant developmental stage (C)	3	71.974	23.9912	31.41	0.00^{**}
A×B	1	2.031	2.0306	2.66	0.11^{ns}
A×C	3	20.371	6.7904	8.89	0.00^{**}
B×C	3	6.723	2.2410	2.93	0.04^{*}
A×B×C	3	2.988	0.9960	1.30	0.28^{ns}
Error	45	34.369	0.7638		
Total	63	149.100			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level

‘Demon’ plants reached maximum root dry weight earlier (36 DAS) compared to ‘Hopehely’ that reached maximum root dry weight at flowering (54 DAS) under control and drought stress. Highest root dry weight was recorded for ‘Demon’ plants under drought stress at tuber initiation stage that was statistically at par with root dry weight of ‘Hopehely’ at tuber initiation and bulking stage under control and drought stress conditions. Drought stress significantly reduced root dry weight of ‘Demon’ during flowering and tuber bulking stage (Fig. 36).



	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
	CONTROL				DROUGHT			
Demon	5.875	5.85	3.975	3.875	7	6.575	2.8	2.8
Hopehely	5.95	6.525	6.15	4.625	5.025	6.35	5	3.625

Figure 36 Effect of drought stress on root dry weight of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test

4.18. Effect of drought stress on number of tubers produced by potato genotypes

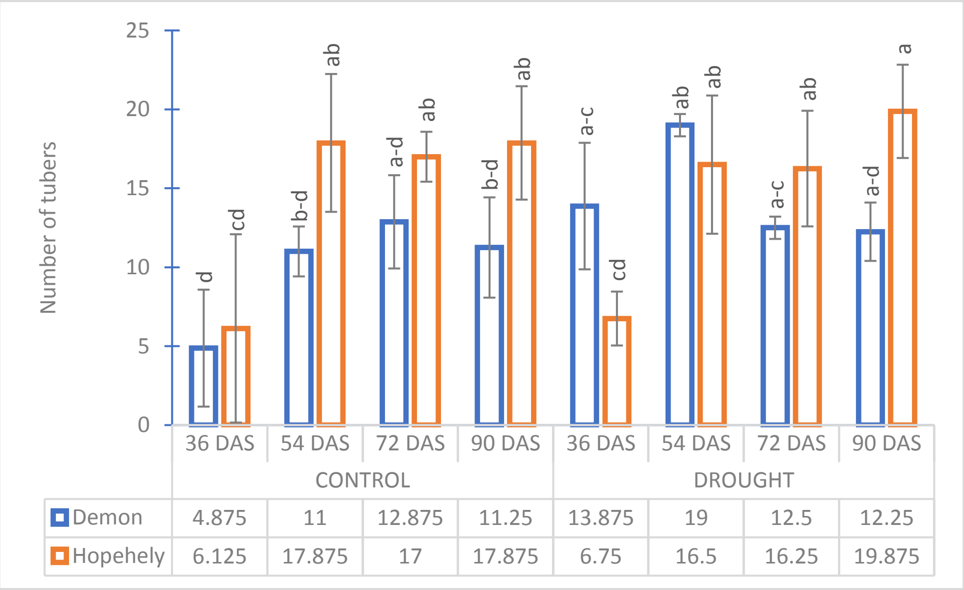
We examined a statistically significant effect of genotypes (p<0.01), drought stress (p<0.01), plant developmental stage (p<0.01), genotype × drought stress (f(1,45)=6.45, p=0.01), and drought stress×plant developmental stage (f(3,45)=6.27, p<0.01) on the number of tubers produced by plants. We also observed that effect of genotype × plant developmental stage (f(3,45)=1.91, p=0.14) and genotype×drought stress×plant developmental stage (f(3,45)-2.54, p=0.07) was non-significant (Table 27).

Table 27 Analysis of variance for the effect of drought stress on number of tubers produced by potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	106.35	106.348	9.42	0.00**
Water levels (B)	1	82.13	82.129	7.28	0.01**
Plant developmental stage (C)	3	682.23	227.410	20.15	0.00**
A×B	1	73.32	73.316	6.50	0.01**
A×C	3	212.39	70.796	6.27	0.00**
B×C	3	64.67	21.556	1.91	0.14^{ns}
A×B×C	3	85.86	28.618	2.54	0.07^{ns}
Error	45	507.86	11.286		
Total	63	1816.25			

**significant at 1% probability level, ^{ns} non-significant at 5% probability level.

'Hopehely' produced significantly more tubers than 'Demon'. Highest number of tubers were produced by 'Hopehely' under drought (19.87) and control (17.87) conditions that were statistically at par. At tuber initiation stage, 'Demon' produced significantly higher average number of tubers (13.87) under drought stress than control plants (4.87) (Fig. 37).



	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
□ Demon	4.875	11	12.875	11.25	13.875	19	12.5	12.25
□ Hopehely	6.125	17.875	17	17.875	6.75	16.5	16.25	19.875

Figure 37 Effect of drought stress on number of tubers produced by potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different (p < 5%) according to Tukey's post-hoc test.

4.19. Effect of drought stress on tuber weight produced by potato genotypes

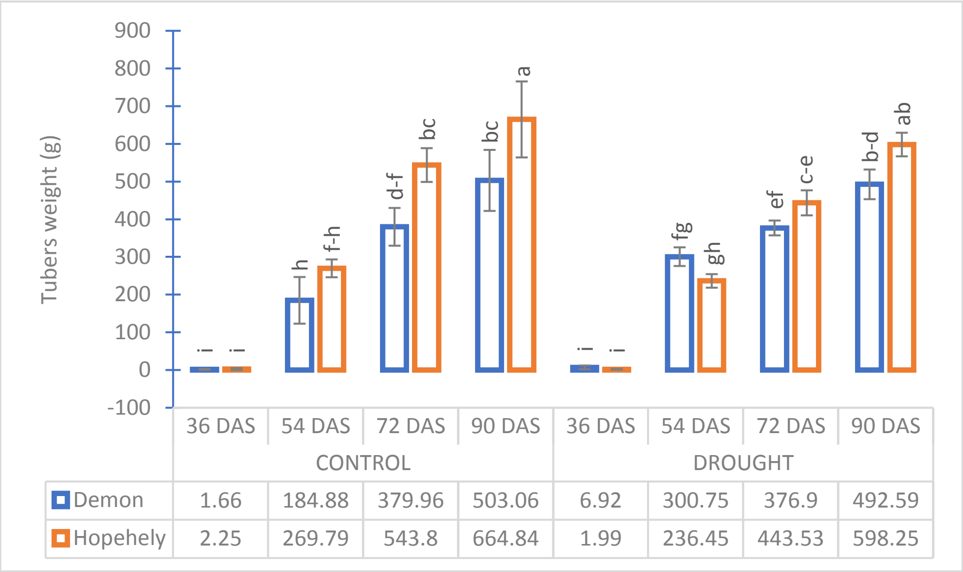
Tuber yield was significantly affected by genotype ($p<0.01$) and plant developmental stages ($p<0.03$) but drought stress did not show any significant effect on tuber yield ($p=0.30$). Factorial analysis revealed that there was a statistically significant interaction between the effects of genotype and drought stress ($f(1,45)=11.84$, $p<0.01$), genotype and plant developmental stages ($f(3,45)=9.82$, $p<0.01$) and drought stress and plant developmental stage ($f(3,45)=3.54$, $p=0.02$) (Table 28).

'Hopehely' produced significantly higher tuber yield than 'Demon' under control and drought. Under both growing conditions, tuber yield of both genotypes increased significantly at each developmental stage reaching maximum at 90 DAS. Highest tuber yield was observed for 'Hopehely' under control conditions (664.8 g) that was statistically at par with its yield under drought stress (598.2 g). A significant increase in 'Demon' tuber yield was observed at flowering stage under drought stress compared to its tuber yield under well-watered conditions (Fig. 38).

Table 28 Analysis of variance for the effect of drought stress on tubers weight produced by potato genotypes

Source of variation	df	SS	MS	F	p-value
Genotype (A)	1	66090	66090	32.99	0.00^{**}
Water levels (B)	1	2156	2156	1.08	0.30^{ns}
Plant developmental stage (C)	3	2859001	953000	475.73	0.00^{**}
A×B	1	23725	23725	11.84	0.00^{**}
A×C	3	58989	19663	9.82	0.00^{**}
B×C	3	21299	7100	3.54	0.02^{*}
A×B×C	3	11169	3723	1.86	0.15^{ns}
Error	45	90145	2003		
Total	63	3134274			

*significant at 5% probability level, **significant at 1% probability level, ^{ns} non-significant at 5% probability level



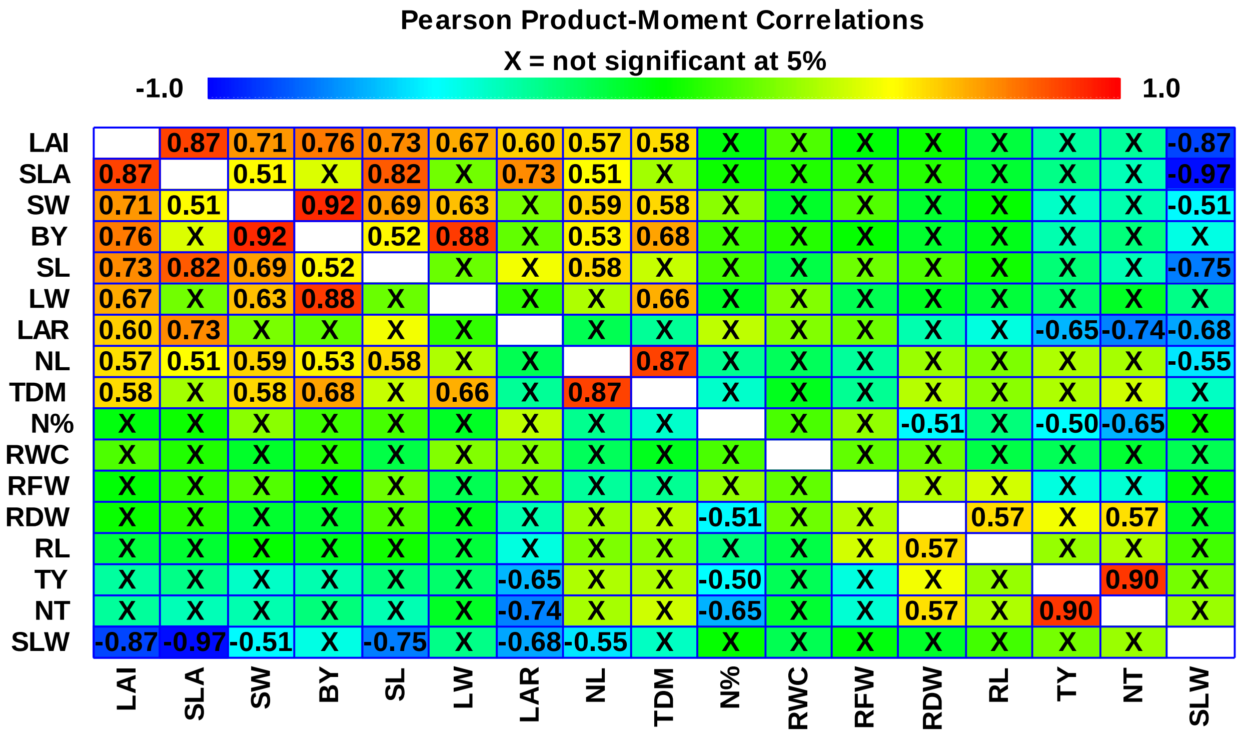
	CONTROL				DROUGHT			
	36 DAS	54 DAS	72 DAS	90 DAS	36 DAS	54 DAS	72 DAS	90 DAS
🟦 Demon	1.66	184.88	379.96	503.06	6.92	300.75	376.9	492.59
🟧 Hopehely	2.25	269.79	543.8	664.84	1.99	236.45	443.53	598.25

Figure 38 Effect of drought stress on tuber yield of potato genotypes. Each value is mean ± STDEV (standard deviation) of four replicates. Different letters indicate groups were significantly different ($p < 5\%$) according to Tukey's post-hoc test

4.20. Correlation analysis

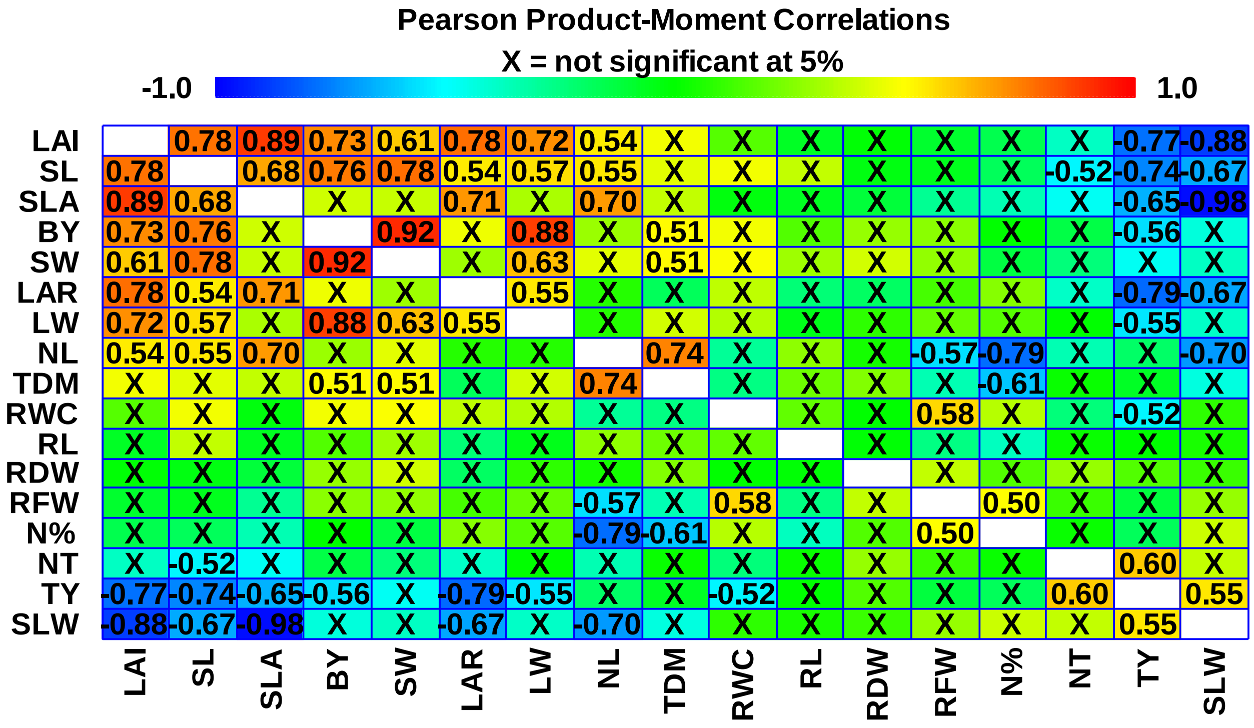
A Pearson correlation was computed to assess the linear relationship between variables. At early plant developmental stage (36 DAS) positive correlation was observed between foliage characteristics. Leaf area index positively correlated with leaf weight, shoot weight, number of leaflets, shoot length, leaf area ratio and total dry matter produced by plant. Fresh plant weight and total dry matter also positively correlated with number of leaflets, leaf weight and shoot weight. A negative correlation was observed between specific leaf weight and leaf area index, specific leaf area, shoot weight, shoot length, number of leaflets and leaf area ratio (Fig. 39).

Correlation analysis at flowering stage (54 DAS) showed similar results. Foliage variables positively correlated with each other. There was a positive correlation between fresh plant weight and total dry matter, leaf weight, shoot weight, shoot length and leaf area index. At this stage, a negative correlation was observed between tuber yield and foliage characteristics (LAI, shoot length, specific leaf area, leaf weight and leaf area ratio). Tuber yield only correlated positively with number of tubers at this developmental stage (Fig. 40).



	LAI	SLA	SW	BY	SL	LW	LAR	NL	TDM	N%	RWC	RFW	RDW	RL	TY	NT	SLW
LAI		0.87	0.71	0.76	0.73	0.67	0.60	0.57	0.58	X	X	X	X	X	X	X	-0.87
SLA	0.87		0.51	X	0.82	X	0.73	0.51	X	X	X	X	X	X	X	X	-0.97
SW	0.71	0.51		0.92	0.69	0.63	X	0.59	0.58	X	X	X	X	X	X	X	-0.51
BY	0.76	X	0.92		0.52	0.88	X	0.53	0.68	X	X	X	X	X	X	X	X
SL	0.73	0.82	0.69	0.52		X	X	0.58	X	X	X	X	X	X	X	X	-0.75
LW	0.67	X	0.63	0.88	X		X	X	0.66	X	X	X	X	X	X	X	X
LAR	0.60	0.73	X	X	X	X		X	X	X	X	X	X	X	-0.65	-0.74	-0.68
NL	0.57	0.51	0.59	0.53	0.58	X	X		0.87	X	X	X	X	X	X	X	-0.55
TDM	0.58	X	0.58	0.68	X	0.66	X	0.87		X	X	X	X	X	X	X	X
N%	X	X	X	X	X	X	X	X	X		X	X	-0.51	X	-0.50	-0.65	X
RWC	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X
RFW	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
RDW	X	X	X	X	X	X	X	X	X	-0.51	X	X		0.57	X	0.57	X
RL	X	X	X	X	X	X	X	X	X	X	X	X	0.57		X	X	X
TY	X	X	X	X	X	X	-0.65	X	X	-0.50	X	X	X	X		0.90	X
NT	X	X	X	X	X	X	-0.74	X	X	-0.65	X	X	0.57	X	0.90		X
SLW	-0.87	-0.97	-0.51	X	-0.75	X	-0.68	-0.55	X	X	X	X	X	X	X	X	

Figure 39 Pearson correlation among variables at tuber initiation stage (36 DAS). where, LAI: leaf area index; SLA: specific leaf area; SW: shoot weight; BY: fresh plant weight; SL: shoot length; LW: leaf weight; LAR: leaf area ratio; NL: number of leaflets per plant; TDM: total dry matter; N%: nitrogen percentage in foliage; RWC: relative water content; RFW: root fresh weight; RDW: root dry weight; RL: root length; TY: tuber yield; NT: number of tubers; SLW: specific leaf weight.

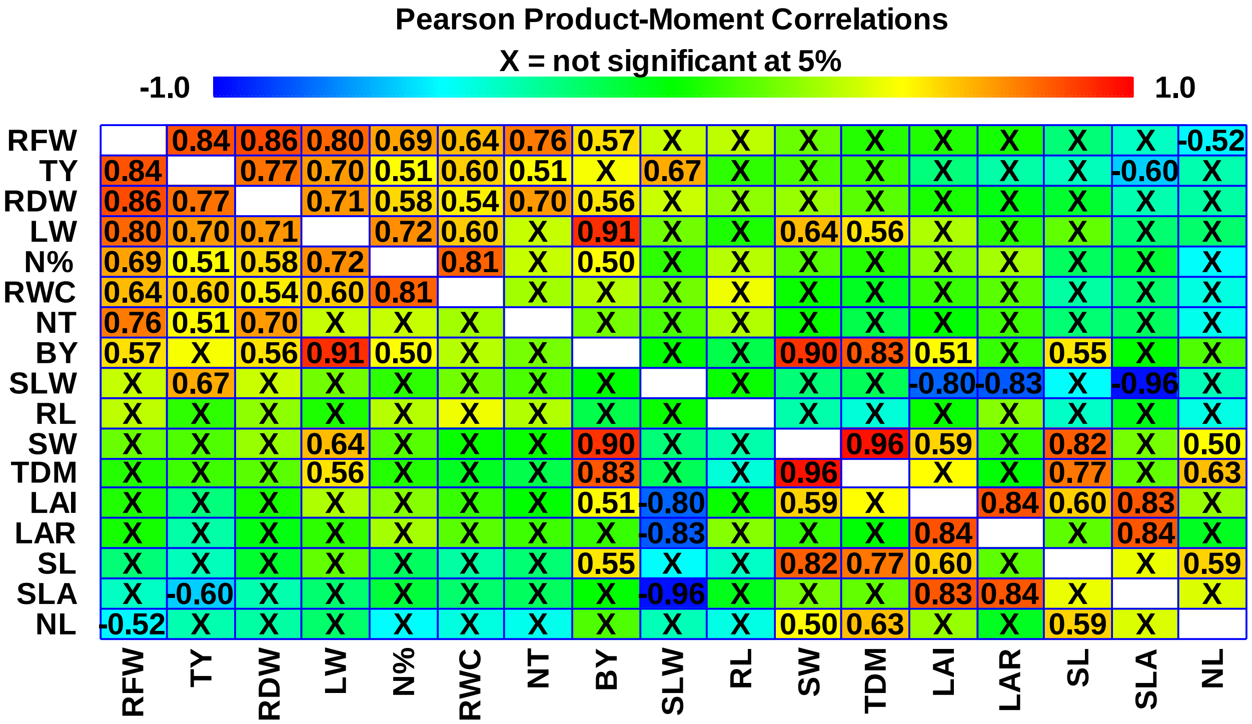


	LAI	SL	SLA	BY	SW	LAR	LW	NL	TDM	RWC	RL	RDW	RFW	N%	NT	TY	SLW
LAI		0.78	0.89	0.73	0.61	0.78	0.72	0.54	X	X	X	X	X	X	X	-0.77	-0.88
SL	0.78		0.68	0.76	0.78	0.54	0.57	0.55	X	X	X	X	X	X	-0.52	-0.74	-0.67
SLA	0.89	0.68		X	X	0.71	X	0.70	X	X	X	X	X	X	X	-0.65	-0.98
BY	0.73	0.76	X		0.92	X	0.88	X	0.51	X	X	X	X	X	X	-0.56	X
SW	0.61	0.78	X	0.92		X	0.63	X	0.51	X	X	X	X	X	X	X	X
LAR	0.78	0.54	0.71	X	X		0.55	X	X	X	X	X	X	X	X	-0.79	-0.67
LW	0.72	0.57	X	0.88	0.63	0.55		X	X	X	X	X	X	X	X	-0.55	X
NL	0.54	0.55	0.70	X	X	X	X		0.74	X	X	X	-0.57	-0.79	X	X	-0.70
TDM	X	X	X	0.51	0.51	X	X	0.74		X	X	X	X	-0.61	X	X	X
RWC	X	X	X	X	X	X	X	X	X		X	X	0.58	X	X	-0.52	X
RL	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X
RDW	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
RFW	X	X	X	X	X	X	X	-0.57	X	0.58	X	X		0.50	X	X	X
N%	X	X	X	X	X	X	X	-0.79	-0.61	X	X	X	0.50		X	X	X
NT	X	-0.52	X	X	X	X	X	X	X	X	X	X	X	X		0.60	X
TY	-0.77	-0.74	-0.65	-0.56	X	-0.79	-0.55	X	X	-0.52	X	X	X	X	0.60		0.55
SLW	-0.88	-0.67	-0.98	X	X	-0.67	X	-0.70	X	X	X	X	X	X	X	0.55	

Figure 40 Pearson correlation among variables at flowering stage (54 DAS). Where, LAI: leaf area index; SL: shoot length; SLA: specific leaf area; BY: fresh plant weight; SW: shoot weight; LAR: leaf area ratio; LW: leaf weight; NL: number of leaflets per plant; TDM: total dry matter; RWC: relative water content; RL: root length; RDW: root dry weight; RFW: root fresh weight; N%: nitrogen percentage in foliage; NT: number of tubers; TY: tuber yield; SLW: specific leaf weight

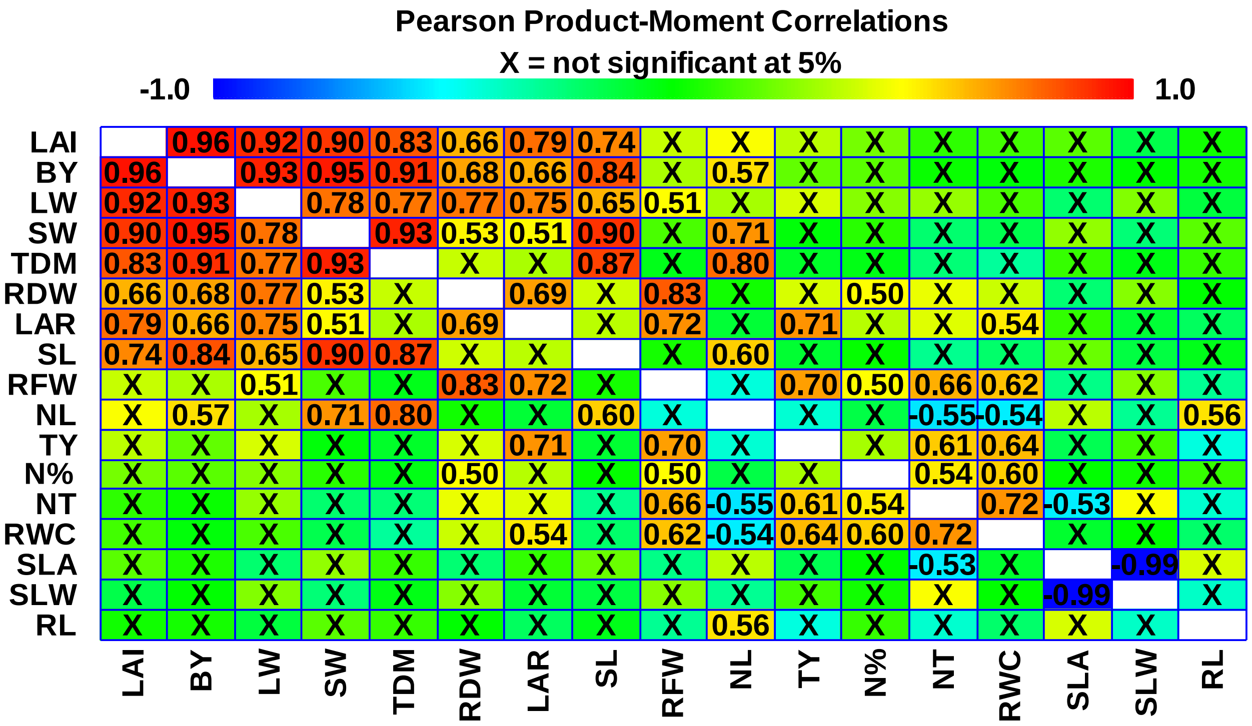
At tuber bulking stage (72 DAS), positive correlation was observed between below ground parts. Tuber yield positively correlated with number of tubers, root fresh weight and dry weight, relative water content of leaves, leaf weight and nitrogen percentage in foliage. Foliage characteristics such as leaf weight also positively correlated with shoot weight, fresh plant weight., total dry matter, relative water content and nitrogen percentage in foliage (Fig. 41).

At senescence tuber yield positively correlated with number of tubers and relative water content of leaves. Root fresh weight also positively correlated with tuber yield and number of tubers. Nitrogen percentage in foliage showed positive correlation with leaves relative water content, number of tubers and root fresh and dry weight. No correlation was observed between tuber yield and fresh plant weight (Fig. 42).



	RFW	TY	RDW	LW	N%	RWC	NT	BY	SLW	RL	SW	TDM	LAI	LAR	SL	SLA	NL
RFW		0.84	0.86	0.80	0.69	0.64	0.76	0.57	X	X	X	X	X	X	X	X	-0.52
TY	0.84		0.77	0.70	0.51	0.60	0.51	X	0.67	X	X	X	X	X	X	-0.60	X
RDW	0.86	0.77		0.71	0.58	0.54	0.70	0.56	X	X	X	X	X	X	X	X	X
LW	0.80	0.70	0.71		0.72	0.60	X	0.91	X	X	0.64	0.56	X	X	X	X	X
N%	0.69	0.51	0.58	0.72		0.81	X	0.50	X	X	X	X	X	X	X	X	X
RWC	0.64	0.60	0.54	0.60	0.81		X	X	X	X	X	X	X	X	X	X	X
NT	0.76	0.51	0.70	X	X	X		X	X	X	X	X	X	X	X	X	X
BY	0.57	X	0.56	0.91	0.50	X	X		X	X	0.90	0.83	0.51	X	0.55	X	X
SLW	X	0.67	X	X	X	X	X	X		X	X	X	-0.80	-0.83	X	-0.96	X
RL	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
SW	X	X	X	0.64	X	X	X	0.90	X	X		0.96	0.59	X	0.82	X	0.50
TDM	X	X	X	0.56	X	X	X	0.83	X	X	0.96		X	X	0.77	X	0.63
LAI	X	X	X	X	X	X	X	0.51	-0.80	X	0.59	X		0.84	0.60	0.83	X
LAR	X	X	X	X	X	X	X	X	-0.83	X	X	X	0.84		X	0.84	X
SL	X	X	X	X	X	X	X	0.55	X	X	0.82	0.77	0.60	X		X	0.59
SLA	X	-0.60	X	X	X	X	X	X	-0.96	X	X	X	0.83	0.84	X		X
NL	-0.52	X	X	X	X	X	X	X	X	X	0.50	0.63	X	X	0.59	X	

Figure 41 Pearson correlation among variables at tuber bulking stage (72 DAS). where, RFW: root fresh weight; TY: tuber yield; RDW: root dry weight; LW: leaf weight; N%: nitrogen percentage in foliage; RWC: relative water content; NT: number of tubers; BY: fresh plant weight; SLW: specific leaf weight; RL: root length; SW: shoot weight; TDM: total dry matter; LAI: leaf area index; LAR: leaf area ratio; SL: shoot length; SLA: specific leaf area; NL: number of leaflets per plant



	LAI	BY	LW	SW	TDM	RDW	LAR	SL	RFW	NL	TY	N%	NT	RWC	SLA	SLW	RL
LAI		0.96	0.92	0.90	0.83	0.66	0.79	0.74	X	X	X	X	X	X	X	X	X
BY	0.96		0.93	0.95	0.91	0.68	0.66	0.84	X	0.57	X	X	X	X	X	X	X
LW	0.92	0.93		0.78	0.77	0.77	0.75	0.65	0.51	X	X	X	X	X	X	X	X
SW	0.90	0.95	0.78		0.93	0.53	0.51	0.90	X	0.71	X	X	X	X	X	X	X
TDM	0.83	0.91	0.77	0.93		X	X	0.87	X	0.80	X	X	X	X	X	X	X
RDW	0.66	0.68	0.77	0.53	X		0.69	X	0.83	X	X	0.50	X	X	X	X	X
LAR	0.79	0.66	0.75	0.51	X	0.69		X	0.72	X	0.71	X	X	0.54	X	X	X
SL	0.74	0.84	0.65	0.90	0.87	X	X		X	0.60	X	X	X	X	X	X	X
RFW	X	X	0.51	X	X	0.83	0.72	X		X	0.70	0.50	0.66	0.62	X	X	X
NL	X	0.57	X	0.71	0.80	X	X	0.60	X		X	X	-0.55	-0.54	X	X	0.56
TY	X	X	X	X	X	X	0.71	X	0.70	X		X	0.61	0.64	X	X	X
N%	X	X	X	X	X	0.50	X	X	0.50	X	X		0.54	0.60	X	X	X
NT	X	X	X	X	X	X	X	X	0.66	-0.55	0.61	0.54		0.72	-0.53	X	X
RWC	X	X	X	X	X	X	0.54	X	0.62	-0.54	0.64	0.60	0.72		X	X	X
SLA	X	X	X	X	X	X	X	X	X	X	X	X	-0.53	X		-0.99	X
SLW	X	X	X	X	X	X	X	X	X	X	X	X	X	X	-0.99		X
RL	X	X	X	X	X	X	X	X	X	0.56	X	X	X	X	X	X	

Figure 42 Pearson correlation among variables at senescence stage (90 DAS). where, LAI: leaf area index; BY: fresh plant weight; LW: leaf weight; SW: shoot weight; TDM: total dry matter; RDW: root dry weight; LAR: leaf area ratio; SL: shoot length; RFW: root fresh weight; NL: number of leaflets per plant; TY: tuber yield; N%: nitrogen percentage in foliage; NT: number of tubers; RWC: relative water content; SLA: specific leaf area: SLW: specific leaf weight; RL: root length

5. DISCUSSION

Drought tolerance in plants is a complex mechanism based on several factors. However, several phenological parameters have been discussed in previous studies (Lahlou et al. 2003; Khan et al. 2015; Sprenger et al. 2016) to determine the drought tolerance of plants. Potato genotypes vary in phenotypic response to drought stress that can help them in tolerating drought stress leading to a better-sustained yield. This study was conducted to describe which phenotypic and physiological characteristics in potato were the most related to yield and drought tolerance.

Potato - a drought-sensitive crop - have five developmental stages i.e. plant establishment, stolon initiation, tuber initiation, tuber bulking, and maturity stage (Obidiegwu et al. 2015). Each developmental stage is sensitive to drought stress. Drought can effect on vegetative growth such as plant height, number of leaves, and size of leaves (Deblonde and Ledent 2001), as well as the reproductive stage of potatoes by shortening the growth cycle (Kumar et al. 2007) or by reducing the size (Schafleitner et al. 2009) and numbers of tubers (Eiasu et al. 2007) produced by plants. Earliest symptoms of drought stress can be observed in vegetative growth of potatoes. Canopy development (production of leaves, stolons, increase in individual leaf area and plant height) is among the most drought-sensitive stages in plants (Shao et al. 2009). Under control conditions both genotypes showed significantly different behavior in canopy development. ‘Demon’ produced significantly taller plants with significantly higher number of leaves than ‘Hopehely’. The increase in leaf number in ‘Demon’ was likely associated with the taller plant that provided with internodes elongation allowing more leaves from the apex of the plant to be exposed (Tadesse et al. 2001). Leaf size was another reason for the high leaf number in ‘Demon’ due to the size/number trade-off as smaller leaves are found on species that produce more of them. Despite significant difference in number of leaves produced by two genotypes, no significant difference was observed in leaf area index of the genotypes. It can also be explained with leaf size as ‘Demon’ produced significantly higher number of leaves but smaller in size as compared to ‘Hopehely’. Westoby and Wright (2003) also reported a negative relationship between the number of leaves per shoot and individual leaf area. Reduction in plant height and leaf area are the first morphological symptoms of drought stress in potatoes (Fleisher et al. 2008). Weisz et al. (1994)

reported that leaf growth in potato declines when transpirable soil water drops below 60%. We observed that drought stress significantly reduced plant height, the number of leaves per plant, and leaf area index of ‘Demon’. Demirel et al. (2017) also reported decrease in plant height and leaf area index of ‘Demon’ in response to abiotic stress. Drought stress reduces the turgor pressure in plants leading to reduced plant height (Szabolcs 1999). Reduction in leaves production by ‘Demon’ can be to minimize evapotranspiration losses but reduction in leaf growth leads to reduced LAI. On the other hand, ‘Hopehely’ under drought conditions maintained its plant height, leaf count and LAI showing drought tolerance during vegetative growth. These results are in line with (Kebede et al. 2019) who showed genotypic differences in the ability to maintain leaf expansion with increasing soil moisture deficit.

Reduction in vegetative growth in plants in response to drought stress can also affect photosynthetic capabilities of plants. Foliage characteristics such as leaf area index (LAI) and leaf area duration (LAD) has been reported as yield determining factor in potatoes (Najm et al. 2010; Chang et al. 2018). LAI represent the total area available for light interception necessary for photosynthesis but under drought stress, total LAI is reduced because of the trade-off between minimizing evapotranspiration and maximizing photosynthesis (Schittenhelm et al. 2006). A recent study reported a significant reduction in the LAI of three potato cultivars (Karaka, Moonlight, and Russet Burbank) due to drought stress (Michel et al. 2019). Similar results were also observed in present study where drought stress significantly reduced LAI of ‘Demon’ genotype. However, ‘Hopehely’ showed an increase in LAI in response to drought stress. The differences seen in LAI between cultivars may be due to differences in canopy architecture (Michel et al. 2019). Under well-watered conditions, LAI of both genotypes increased till tuber bulking stage and then started decreasing. ‘Demon’ produced significantly higher LAD than ‘Hopehely’ under well-watered conditions indicating the ability of ‘Demon’ to maintain green leaves for longer period. Under drought stress, LAI of ‘Demon’ started to decline earlier, reducing LAD and thus total period of radiation interception: the primary determinant of dry biomass production in potato (Allen and Scott 1980). Several researchers have discussed that drought stress at tuber bulking stage inhibited the development of new leaves, reduced leaf expansion and encouraged senescence resulting decreased LAI and LAD (Susnoschi and Shimshi 1985; Kumar and Minhas 1999). Similar results were reported in present study where LAD of ‘Demon’ significantly decreased at tuber bulking stage but that of ‘Hopehely’ increased under drought stress. The increase in LAD of ‘Hopehely’ can be related to its larger leaves that have been demonstrated to persist for much longer under drought stress, increasing LAD and yield (Aliche et al. 2018). Zarzyńska et al. (2017) pointed that root density and LAI are determinant for yield. These finding were corroborated in this study, where correlation analysis showed a strong positive correlation between LAI and total dry matter production in potatoes.

Plant photosynthesis can also be affected by reduced chlorophyll content in response to drought stress. Chlorophyll (present in the leaves) play an important role in photosynthesis. Potato genotype ‘Hopehely’ produced significantly higher chlorophyll content than ‘Demon’ under control and drought condition. It can be due to variation in the foliage development of genotypes. ‘Hopehely’ produced fewer but heavier leaves with significantly higher specific leaflet weight (SLW). Larger and heavier leaves have a great boundary layer thickness that helps in heat exchange, reduces water loss, and maximizes photosynthetic activity by maintaining relative water content (Banik et al. 2016) thus significantly higher chlorophyll content in ‘Hopehely’. Drought stress significantly reduced chlorophyll content in ‘Hopehely’ but no significant differences were observed in chlorophyll content of ‘Demon’. Decline in chlorophyll content in ‘Hopehely’ can be due to shading effect of larger leaves (Björkman 1968). Results also highlighted that chlorophyll content varies significantly within the same plant. In both genotypes, chlorophyll content decreases from top to bottom. It can also be due to the lower light intensity received by lower leaves and base points of the same leave due to the shading effect. These results are in line with (Björkman 1968; Ashworth and Svec 1974) who reported significantly lower chlorophyll content per unit area in leaf base. Plants reached the highest chlorophyll content before flowering as they completed vegetative growth which shows that a high part of absorbed nitrogen was used in chlorophyll production until flowering. Chlorophyll content started decreasing after flowering as plants start transferring assimilates to tubers (Argenta et al. 2004; Reynolds et al. 2005). We also observed that with aging lower leaves loose chlorophyll content earlier than upper leaves.

Li et al. (2016) reported that potato yield under drought stress is reduced because of reduced source capacity rather than sink capacity. They reported that decrease in leaf nitrogen content indicates reduced source capacity (photosynthesis capacity) in potato plants while sink capacity (tubers ability to store assimilates) is not affected. These results were also corroborated in present study where drought stress significantly reduced nitrogen content in ‘Demon’. Nutrient analysis showed that ‘Hopehely’ produced significantly higher nitrogen content than ‘Demon’ under well-watered and drought stress conditions. Interestingly, nitrogen content in ‘Hopehely’ increased under drought stress which can be due to increase in the net photosynthetic rate, LAI and LAD, which is crucial for potato yield improvement under drought stress. Correlation analysis at tuber bulking stage also showed that foliage nitrogen content positively correlated with tuber yield, fresh plant weight, and relative water content. It confirms that tuber yield is more affected by reduction in photosynthate production capacity of potato plants than sink capacity itself.

Relative water content (RWC) can also provide information on drought tolerance in potatoes. In our experiment we observed that RWC positively correlated with tuber yield and foliage nitrogen content. It suggests that drought stress affects potato growth and yield by reducing plant water retention. RWC is one of the most reliable indicators for defining water retention in plants (Rampino et al. 2006; Sánchez-Rodríguez et al. 2010). Studies have shown that RWC in drought susceptible genotypes decreases in response to drought stress (Shaw et al. 2002; Bürling et al. 2013). Both studied genotypes maintained RWC in response to drought stress and no significant reduction was observed. ‘Demon’ would have maintained RWC by reducing evapotranspiration losses by significant reduction in number of leaves and leaf area produced under drought stress. However, ‘Hopehely’ did not decrease its number of leaves or evapotranspiration area and still maintained RWC. It shows the ability of ‘Hopehely’ to retain plant water even under drought stress condition without losing photosynthetic machinery. Moreover, RWC of ‘Hopehely’ was significantly higher than ‘Demon’ under drought stress.

‘Demon’ produced significantly higher foliage dry mass than ‘Hopehely’, but no correlation was observed between foliage dry mass and tuber yield. Although increase in photosynthesis is associated with higher yields under stress conditions (Cattivelli et al. 2008), but the same cannot be said about foliage dry mass, as genotypes might utilize photosynthate in foliage biomass production at the expense of tuber expansion (Iwama 2008; Deguchi et al. 2010). Studies (Schittenhelm et al. 2006) have shown that producing large above ground biomass can be an effective insurance against drought stress but some genotypes may use water faster and suffer from drought stress later (Obidiegwu et al. 2015). We also observed similar results where ‘Demon’ produced higher foliage dry mass at early developmental stage under drought stress but a significant reduction in foliage dry mass was observed at tuber bulking stage unlike ‘Hopehely’. These results are in line with findings of Handayani and Watanabe (2020) who also reported an increase in plant dry matter at early plant developmental stage in response to abiotic stress.

Increased antioxidant activity also hints towards drought tolerance in plants (Ünyayar and ÇEKİÇ 2006; Mao et al. 2012). Reactive oxygen species (ROS) such as superoxide radicals and hydrogen peroxide are accumulated in plants under drought stress (Quandahor et al. 2019). These ROS react with cellular oxygen and deprive cells of oxygen. Overproduction of ROS can disturb normal plant metabolism (Imlay 2003; Ashraf 2009, 2010). To alleviate damages caused by ROS, plants produce antioxidants that scavenge ROS. Activation of antioxidants is correlated with the degree of drought tolerance of the plant (Sunkar et al. 2006). In present study we observed a significant increase in SOD activity in both genotypes under drought stress. SOD activity provides the first line of defense against membrane lipid peroxidation induced by ROS (Mao et al. 2012). SOD and CAT activity was significantly higher in ‘Hopehely’ than ‘Demon’ indicating better drought tolerance in ‘Hopehely’. Quandahor et al. (2019) and Javanovic et al. (2010) also reported similar findings in other potato cultivars.

Root system of potato is considered one of the main reasons of its drought susceptibility. Potato possesses relatively shallow and weak soil penetrating root system, most of which is concentrated in upper 30 cm soil (Stalham et al. 2007; Joshi et al. 2016). These results were corroborated in present study, where root length of potato genotypes ranged between 26-33 cm. Puértolas et al. (2014) reported that dense roots in deeper soil (>40 cm) plays important role in drought tolerance. Increase in root length under drought stress is considered a drought tolerant characteristic (Steckel and Gray 1979; Lahlou and Ledent 2005) but no significant differences were observed in the root length of either genotypes in response to drought stress. Similar results were also reported in previous studies (Steckel and Gray 1979; Lahlou and Ledent 2005; Albiski et al. 2012; Boguszewska-Mańkowska et al. 2020) where decrease or no changes in root length were observed. It can be due to soil compaction and limited space available in the pots (40 cm) which limits root growth (Stalham et al. 2007). Experimental error can also affect analysis of underground parts (Steckel and Gray 1979; Stalham et al. 2007; Obidiegwu et al. 2015) making it more challenging to study the effect of drought stress on root development.

In previous studies, drought tolerant genotypes of potatoes have been reported to produce deeper root systems (Zarzyńska et al. 2017) or higher root dry weights (Lahlou and Ledent 2005; Iwama 2008). Although no significant differences were observed in root length of the two studied genotypes but ‘Hopehely’ produced significantly higher root dry mass than ‘Demon’ under control as well as drought stress. Under drought stress, ‘Demon’ produced non significantly higher root dry mass than control at early developmental stages. However, significant reduction in root dry mass was observed in ‘Demon’ after flowering stage while ‘Hopehely’ maintained root dry mass until tuber bulking stage. Previous studies have reported both increase (Tourneux et al. 2003; Lahlou and Ledent 2005; Anithakumari et al. 2011) and decrease (Lahlou and Ledent 2005; Mane et al. 2008) in root dry mass under the influence of drought stress. It can be due to difference between genotypes used in those studies or difference in experimental conditions and handling. Correlation between root dry mass and tuber yield has also been shown as both positive (Lahlou and Ledent 2005) and negative (Tourneux et al. 2003). In present study, we observed a positive correlation between tuber yield and root dry weight.

Drought tolerance in agronomy focuses on economic yield of the plants (Mitra 2001). Tubers are the economic parts in potatoes and have been studied extensively. Water makes up to 80% of fresh tuber yield (Navarre et al. 2009). Therefore, tuber yield has been reported to decrease significantly in drought susceptible genotypes (Jefferies and MacKerron 1989; Lahlou et al. 2003; Aliche et al. 2018). In present study we also observed non-significant decrease in tuber yield of both genotypes where ‘Hopehely’ produced significantly higher yield than ‘Demon’ under control and drought conditions. Tuber yield depends upon dry matter allocation and water content of tubers (Jefferies and Mackerron 1993). Dry matter allocation to tubers highly depends on vegetative growth of plants. Better foliage development under drought stress can lead to higher yield. ‘Hopehely’ produced significantly heavier leaves. Larger and heavier leaves have thick waxing layer that reduces water loss and maintains relative water content leading to higher photosynthetic activity (Arnell and Reynard 1996; Daccache et al. 2011; Luitel et al. 2015). It can be the reason of significantly higher relative water content in ‘Hopehely’. Higher chlorophyll concentration and N% in the foliage were also observed which shows a higher photosynthetic activity in ‘Hopehely’. Correlation analysis also showed that tuber yield positively correlated with relative water content, foliage nitrogen content, leaf weight and specific leaf weight. It indicates the reason of higher yield in ‘Hopehely’ than ‘Demon’. It is also important to mention that ‘Demon’ plants under drought stress died earlier (at 90 DAS) while ‘Hopehely’ plants still had green leaves as indicated by significantly higher LAD at 90 DAS. It suggests ‘Hopehely’ still had potential to produce more yield while ‘Demon’ plants showed early senescence. These findings corroborate previous work that suggested that LAD was strongly associated with production of biomass and yield (Pourasadollahi et al. 2019; Ávila-Valdés et al. 2020).

Correlation analysis also showed that tuber yield positively correlates with below ground parts such as number of tubers, root fresh weight and dry weight. Drought stress affects the yield of drought sensitive genotypes by decreasing number of tubers produced by them (Haverkort 1987; Chang et al. 2018). Contradictory results were observed in current study where both genotypes produced significantly higher number of tubers under drought stress. This can be due to adaptive response of genotypes to tolerate drought by producing more tubers of smaller size. Similar results have been reported in several other studies (Haverkort 1987; Lahlou et al. 2003; Rykaczewska 2017; Aliche et al. 2018). ‘Hopehely’ produced significantly higher number of tubers than ‘Demon’, thus the higher yield under control and drought conditions. Moreover, production of significantly higher root fresh and dry weight can also be the reason of higher yield in ‘Hopehely’. Better developed root system can help plants to tolerate drought stress. Zarzyńska et al. (2017) also suggested that root density along with LAI are determinant of yield in potatoes. Correlation analysis corroborated these findings in present study.

6. CONCLUSIONS AND RECOMMENDATIONS

The present study provided insights on the phenological response of *Solanum tuberosum* L. to drought stress using two genotypes, ‘Demon’ and ‘Hopehely’, common in Hungary. Morphological development of genotypes varied significantly. ‘Demon’ produced taller plants, smaller leaves, and high number of leaflets while ‘Hopehely’ produced dwarf plants, bigger and heavier leaves with fewer leaflets. Drought significantly affected the vegetative growth of ‘Demon’ but ‘Hopehely’ maintained its vegetative growth under drought stress showing fewer larger leaves are morphologically better drought tolerant than large number of smaller leaves. Reduction in vegetative growth also affected photosynthetic capacity in ‘Demon’ under drought stress. Light interception - necessary for photosynthesis - was reduced in ‘Demon’ under drought stress due to decrease in LAI and LAD. While light interception area (LAI) and duration (LAD) increased in ‘Hopehely’ in response to drought stress. Although, drought stress reduced chlorophyll content - important for photosynthesis - in both genotypes, yet ‘Hopehely’ produced significantly higher chlorophyll content than ‘Demon’. High photosynthetic capability of ‘Hopehely’ was also confirmed by significantly higher nitrogen content production than ‘Demon’. These results indicate that morphology of ‘Demon’ makes its vegetative growth sensitive to drought while that of ‘Hopehely’ makes it drought tolerant. Another indication was relative water content (RWC), that was significantly reduced in ‘Demon’ in response to drought stress while ‘Hopehely’ maintained its relative water content. Moreover, significantly higher enzymatic antioxidant activity in leaves of ‘Hopehely’ also suggests better drought tolerance.

Study of underground parts showed that ‘Hopehely’ had denser root system than ‘Demon’. ‘Hopehely’ produced significantly higher root fresh and dry mass than ‘Demon’ under drought stress. However, no significant difference was observed in the underground parts of genotypes when compared to their control treatments. Differences in root length of both genotypes was also non-significant. The reason of absence of significant differences can be space restrictions. Root length ranged between 25-33 cm while pots used for the experiment were only 40 cm deep (in which 1-2 cm was occupied by gravels at the base and 2-3 cm was left empty at the top). Drought tolerance in agriculture is usually associated with the economic yield (tuber yield in case of potatoes). We observed that ‘Hopehely’ produced significantly higher yield than ‘Demon’ under control and drought stress condition. Under drought stress, ‘Hopehely’ produced non-significantly less tuber yield than control plants. Drought tolerant morphology and denser root system could have helped ‘Hopehely’ to maintain its tuber yield under drought stress. Moreover, ‘Hopehely’ produced more tubers under drought stress that positively correlated with tuber yield. Despite significant reduction in vegetative growth, tuber yield of ‘Demon’ under drought was statistically at par with well-watered plants. The main reason of non-significant difference in ‘Demon’ tuber yield is growing season. ‘Demon’ and ‘Hopehely’ are mid-maturing genotypes (100-110 days) but ‘Demon’ plants under drought stress had completely died at 90 days after sowing. It can be seen by LAD that was significantly low in ‘Demon’ plants under drought stress. It shows that ‘Demon’ followed drought escape route to sustain yield under drought stress.

We can conclude that cultivars with better-developed root system, thicker and fewer leaves are the most beneficial agro-physiological characters related to the yield and drought tolerance in potatoes. LAD is more closely related to tuber yield than LAI. Moreover, we can also conclude that ‘Hopehely’ is morphologically more drought tolerant than ‘Demon’. Based on our findings, we can recommend the usage of ‘Hopehely’ under limited water availability. However, drought tolerance is a complex mechanism that cannot be described by phenological response only, therefore, it will be interesting to study the response of potato genotypes to drought stress at molecular level. Very little work has been done in identifying drought responsive genes in potatoes. ‘Hopehely’ will be a suitable candidate for studying and developing drought tolerant potato genotypes in Hungarian growth conditions.

7. NEW SCIENTIFIC RESULTS

- Two Hungarian potato genotypes, namely ‘Demon’ and ‘Hopehely’ varied significantly in their plant development and their response to drought stress.
- Leaf area duration is more closely related to potato yield than leaf area index in the case of these two genotypes studied.
- Relative water content (RWC) confirmed as an indicator of drought tolerance in the studied potato cultivars.
- Both genotypes produced higher number of tubers to maintain yield under drought stress.
- Based on the results of experiment, Hopehely is recommended to be used under water limited conditions.

8. SUMMARY

Climate change is affecting crop productivity in multiple ways. Biotic stresses may increase or decrease due to climate change, but abiotic stress, particularly heat stress, drought stress, and salinity stress, are more likely to increase. Drought stress is a major yield-limiting factor, particularly for drought susceptible crops such as potatoes. Primarily drought susceptibility of potatoes was associated with the shallow root system. However, studies have shown that canopy development and cultivar type also play a crucial role in drought tolerance of potatoes. Late-maturing cultivars can be used in areas facing late droughts to sustain yield. Under long-term drought conditions, mid-maturing cultivars can be a better option. This research was conducted to determine the response of different potato genotypes to drought stress and to establish the relationship between morpho-physiological characteristics of potatoes and tuber yield.

The experiment was established in the green house of Georgikon campus, Keszthely. Two mid maturing (100-110 days) high yielding potato genotypes (‘Hopehely’ and ‘Demon’) were grown under well-watered (80% water holding capacity) and drought stress (50% water holding capacity) conditions. The experiment was conducted in 50-liter pots and replicated 16 times. 4 replications per treatment were harvested at four different developmental stage i.e., tuber initiation (36 days after sowing), flowering (54 days after sowing), tuber bulking (72 days after sowing) and senescence of anyone treatment (90 days after sowing) to study the effect of drought stress at different plant developmental stages. Mixture of soil and Baltic peat (1:1 by weight) was used as growth medium. Water holding capacity of soil peat mixture was determined by gravimetric method and pot weight was maintained weekly to maintain drought stress.

The results revealed a significant variation in vegetative and under-ground growth of the two genotypes. Under well-watered conditions, ‘Demon’ produced taller plants bearing more leaves, with significantly higher LAI and LAD producing significantly higher dry matter. While ‘Hopehely’ produced dwarf plants that produced fewer leaves and lower LAI and LAD than ‘Demon’. However, underground parts (roots) were more developed in ‘Hopehely’ which produced significantly higher root fresh weight and dry weight than ‘Demon’. Moreover, ‘Hopehely’ produced fewer but significantly heavier (SLW) leaves, that maintained significantly higher relative water content (RWC) and produced significantly higher chlorophyll content. ‘Hopehely’ also produced higher number of tubers than ‘Demon’ and gave significantly higher tuber yield.

We also observed significant variation in the response of understudy genotypes to drought stress. We observed a reduced growing period (early senescence at 90 DAS) in ‘Demon’, producing high dry matter content and number of tubers at early plant developmental stage which are characteristics of drought escape response of plants. Moreover, significant reduction in number of leaves, plant height, LAI and LAD was also observed in ‘Demon’ in response to drought stress affecting the vegetative growth. On the contrary, ‘Hopehely’ plants tolerated the drought stress and did not show any significant decrease in vegetative growth or under-ground plant development. LAI, LAD, and numbers of tubers produced were increased in ‘Hopehely’ in response to drought stress. Therefore, ‘Hopehely’ maintained its yield and produced significantly higher yield than ‘Demon’ under drought stress.

From the results of this study, we can conclude that ‘Hopehely’ has better drought tolerance than ‘Demon’. It also highlights that tuber yield is more affected by leaf area duration than leaf area index under drought stress. Plants that can maintain relative water content show higher LAI and LAD. We observed that production of fewer leaves with high specific leaf weight helps the plants to reduce evapotranspiration losses and maintain RWC. Potatoes produce higher number of tubers under drought stress to sustain tubers yield but it can affect tuber quality. Present study reconfirms previous findings that escaping drought reduces the growth period leading to reduction in yield. In conclusion, we can recommend ‘Hopehely’ over ‘Demon’ for cultivation in Hungary under water limited conditions. However, we need to further study the variation in genotypes at molecular level that will help us in better understanding of drought tolerance in potatoes. Several studies have been conducted in recent time focusing on drought tolerance on potatoes, but we are still far from developing a high yielding drought tolerant potato genotype. We believe studying the genome of ‘Hopehely’ will help in further understanding the drought tolerance in potatoes.

9. APPENDICES

A1: Bibliography

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