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Review

Effect of Drought Stress on Potato Production: A Review

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Abstract: Potato is the third most consumed crop globally after rice and wheat. It is a short-duration crop, versatile in use, suitable for growing in a wide range of environments, and its production is increasing rapidly. The modern potato is considered a drought-sensitive crop, and it is susceptible to yield loss because of drought stress. Unfortunately, drought severity, frequency, and extent have been increasing around the globe because of climate change. Potato drought susceptibility has primarily been attributed to its shallow root system. However, several studies in past decades have suggested that drought susceptibility of potato also depends upon the type, developmental stage, and the morphology of the genotype, and the duration and severity of drought stress. They have been overlooked, and root depth is considered the only significant cause of potato drought susceptibility. This review combines these studies to understand the varying response of potato genotypes. This review also explores the current potato production scenario and the effect of varying degrees of drought stress on potatoes' growth, development, and yield. In the absence of drought-tolerant genotypes, agronomic practices should be improved to mitigate drought stress. Late maturing cultivars, nutrient management, mulching, and foliar application of plant growth regulators can be used during prolonged droughts. Irrigation at tuber initiation and the tuber bulking stage during early droughts can reduce the adverse effects of drought.

Keywords: climate change; abiotic stress; *Solanum tuberosum*; yield; stress tolerance

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1. History of Potato Cultivation and Current Scenario

Potato cultivation originated in New World, where its wild relatives can still be found [1]. In South America, potato cultivation began around 8000 years ago [2], and Spanish conquistadors during the Columbian exchange introduced potatoes to Europe [2]. By the end of the 16th century, potatoes had been introduced into Ireland and the United Kingdom [3]. In Europe, its cultivation started almost 100 years later [3], but monocultural practices led to the destruction of Irish potatoes on a large scale by late blight [2]. Therefore, breeders directed their efforts towards producing resistant and high-yielding cultivars [2].

Potato production in the world has increased from 270 million tonnes in 1961 to 370 million tonnes 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 (Figure 1). China, India, Russia, the USA, and Ukraine are the largest potato-producing countries, followed by Poland, Germany, Belarus, Netherlands, and France (Figure 2). Europe is the second-largest potato-producing region (125.43 million tonnes) after Asia (140.6 million tonnes) (Figure 3) [4].

In Europe, potato production has reduced from 137.1 million tonnes in 1994 to 107.26 million tonnes 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 (Figure 4). Recent FAO stats show [4] 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 (Figure 5).

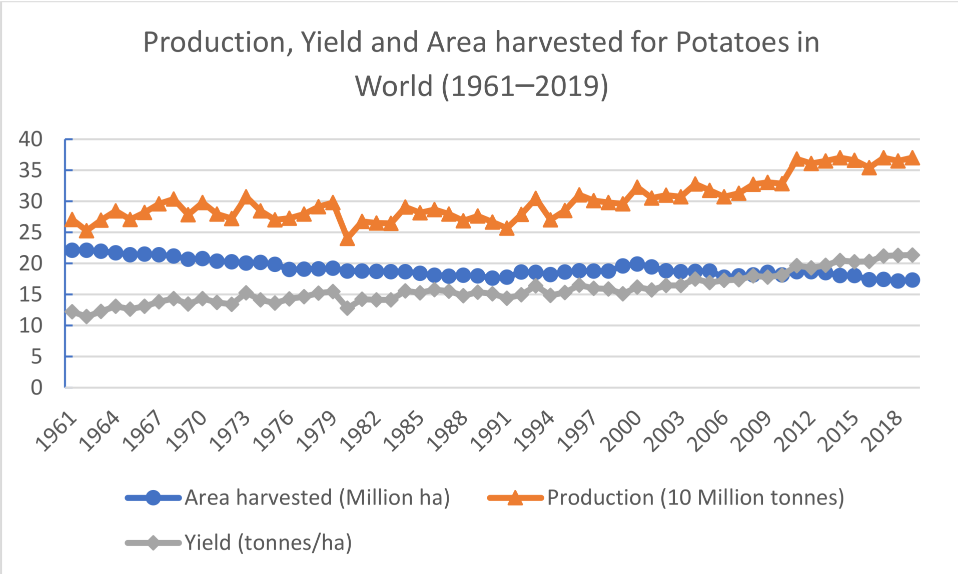

Figure 1. World potato production, yield, and area harvested during 1961–2019 [4].

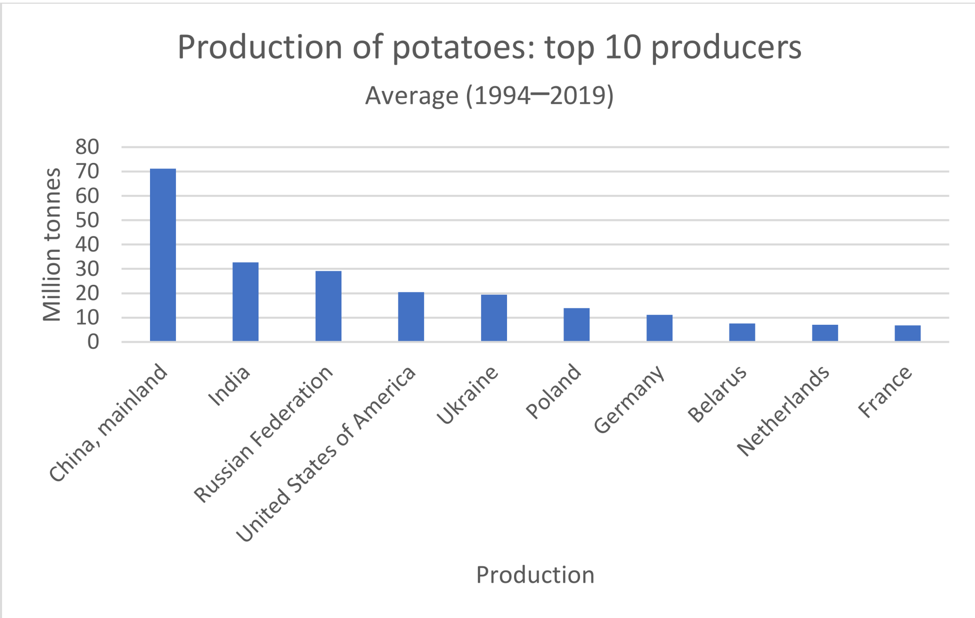

Figure 2. Top 10 potato producers in the world during 1994–2019 [4].

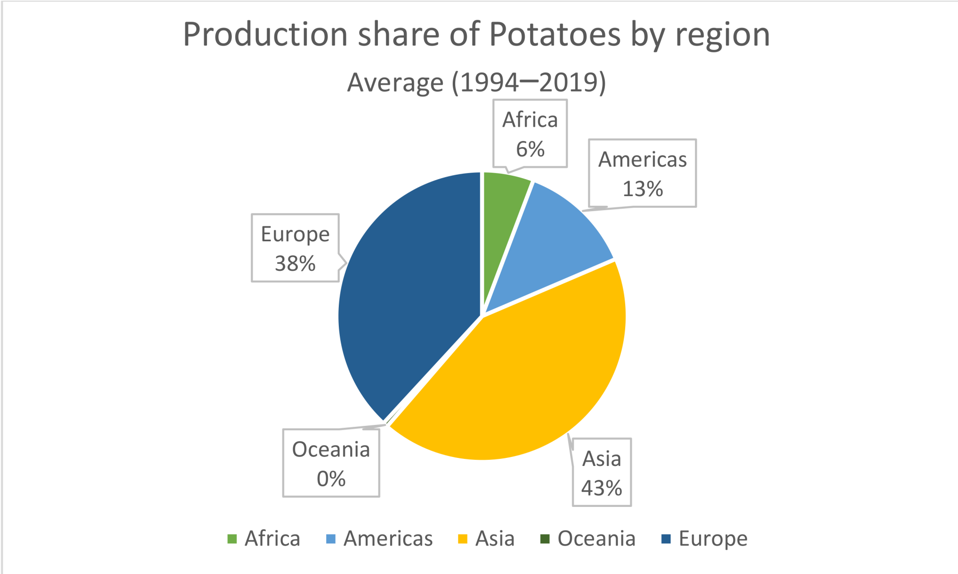

Figure 3. Regional share in potato production during 1994–2019 [4].

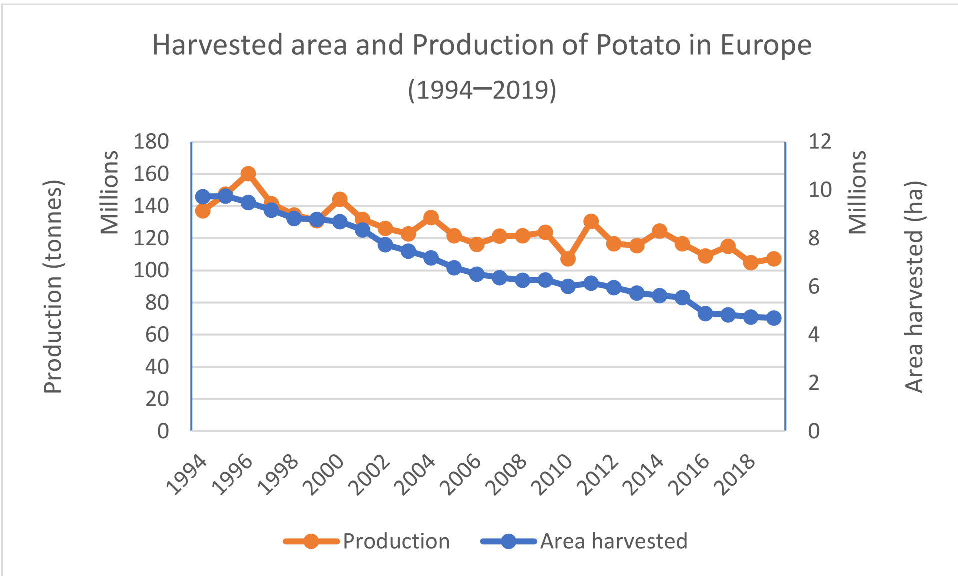

Figure 4. Potato production and area allocated for potato harvest in Europe during 1994–2019 [4].

Potato is considered an important crop in developed and developing countries because of its versatile utilization [2]. Approximately 85% of the biomass of a potato plant is edible: much higher than the 50% of edible biomass from cereals [2]. In Europe, potato is the fourth most important crop by production (107.26 million tonnes) 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).

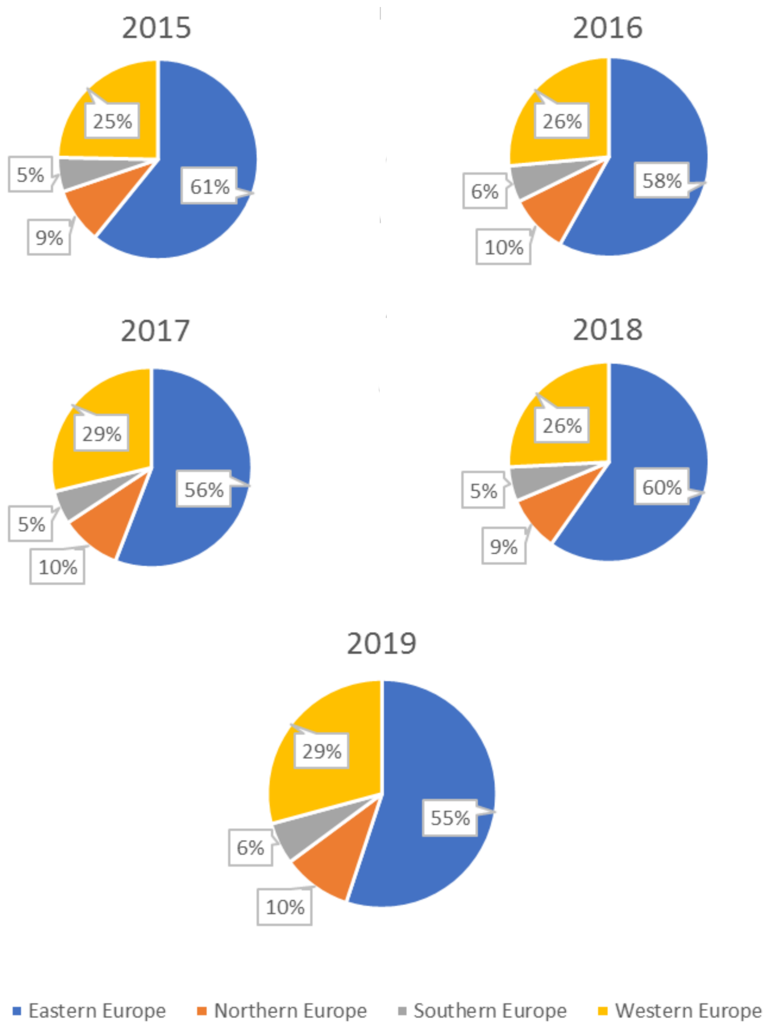

Figure 5. Potato production shares by different European regions during 2015–2019 [4].

Table 1. Area harvested and yield per unit land of the five most produced crops in Europe in 2019 [4].

Item	Production (Million Tonnes)	Area (Million ha)	Yield (kg ha^{-1})
Wheat	266.123	62.39	4265.8
Sugar beet	194.46	03.17	61,411.6
Maize	132.773	18.35	7234.3
Potatoes	107.265	04.69	22,840.1
Barley	95.634	24.22	3948.2

2. 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 [5] (Pieterse, Lukie; Judd, Julian (Eds.)) (2014). 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 [6]. 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 [6]. Seedbed preparation includes ploughing to a 20–35 cm depth followed by tillings [7]. In hot weather conditions, soil turning and keeping it fellow is also adopted to reduce soil-borne pathogen and weed problems [6]. Seed tubers are sown into ridges, and the furrow irrigation method is most popular for irrigation [8]. Depending on the cultivar, potatoes can grow up to 3.5 feet 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 [9,10]. 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 [6]. Tuber formation initiates after 20–25 days of sowing [11], 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 water during their life cycle [6]. 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 [6]. 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 [12], early blight [13], black scurf and stem canker [14], and powdery scab [15]. 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 [16], bacterial wilt [17], and blackleg and soft rot [18]. 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 Gudenie	53.74% 71.50%	[12]
Powdery scab	Diacol Capiro	30%	[15]
Black scurf and stem canker	Diamant	18.13%	[14]
Early blight	Nadinc	Up to 58%	[13]
Common scab	Kexin No. 1	24.58%	[16]
Bacterial wilt	Helan 7	34.9%	[17]
Blackleg and soft rot	BP1	39.57%	[18]
Potato leafroll virus (PLRV)	Victoria Kingi Sifra	91.8% 84.8% 22.1%	[19]
Potato virus Y (PVY)	Victoria Kingi Sifra	87.2% 85.1% 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 [20,21]. 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) [19] 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 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 [22].

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 [23]. Researchers discuss abiotic factors that influence potato productivity include temperature, solar radiation, photoperiod, soil salinity, and drought [24,25]. 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 [6]. 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 [26–28].

On the other hand, a decrease in temperature ($\leq$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 [26,29]. A further decrease in temperature (≥ -3 °C) can demolish the whole field of potatoes [30]. 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 [31]. Poor water management, irrigation practices, reduced rainfall, and high evaporation rate in hot climates enhance the chances of soil salinity [32]. Potato is a water-efficient crop, but its shallow root system makes it susceptible to drought stress [33]. Drought is one of the major abiotic constraints in potato productivity, affecting potatoes' physiology, biochemical process, and yield [34,35]. Therefore, the potato crop needs the optimum water to maintain its yield.

3. Potato Water Requirement and Climate Change

Potato is a comparatively water-efficient crop that produces more calories per unit of water utilized [33]. According to Renault and Wallender [36], 105 L water is required to produce a 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 a kilogram of rice, wheat, and maize, respectively. Despite high water use efficiency, potato is very susceptible to drought stress. One primary reason is the need for a large amount of irrigated water [37]. Depending upon agroclimatic conditions and soil available water, potato, on average, may require irrigation water between 143 mm to 313 mm [38]. Li et al. [39] and Vishnoi et al. [40] 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 to 154 mm [41]. Byrd et al. [42] 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 [38].

Most potato cultivars have a shallow root system [43], 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 [44]. Moreover, transpiration losses due to canopy characteristics also vary in potato cultivars from stem type canopy to leaf type canopy [45]. The stem-type canopy performs better under drought stress conditions [46]. 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 [47]. Therefore, potatoes are provided with additional water in the UK, USA [42,48], and some Mediterranean regions to obtain marketable yield [49].

Due to the high drought susceptibility of potatoes [37], 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 [50]. 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 crops production significantly [51]. 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 [52]. Although potato production is predicted to increase in some regions with increased temperature due to stretch in the growing season [48], 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 [53]. 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 [53].

4. 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 [54] as it affects the morphology, physiology, ecological, biochemical, and molecular traits of plants [55]. Drought is a broad term and is defined differently in different fields. In meteorology, a prolonged period of no rain or very little rain is called drought (meteorological drought) [56]. 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 [57]. 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 [57]. 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 [58]. 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 [59].

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 [60], and the food crisis in Russia and China in the 1920s (causing 4 million deaths) [61] 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 [62]. 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 [63,64]. Later on, the Amazon rain forest faced a lack of rain in 2005 and 2010, causing massive loss of vegetation [65]. The Iberian Peninsula faced a multi-year drought from 2008, affecting its groundwater level and reservoir storage [66]. At the beginning of the second decade, Russia also faced severe heat and drought stress during 2010 and 2011 [67], 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 [68,69]. In 2011, an enduring drought resulted in mass migration and deaths in Africa [70]. 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 [71,72]. The prolonged drought period is considered among the most destructive natural threats affecting economic costs and causing social problems [73]. From 1900 to 2010, drought-affected more than 2 billion people around the globe [74]. Therefore, it is imperative to tackle drought stress.

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 [75]. Arid and semiarid regions that represent 40% of the world's agricultural land [76] face serious water shortage challenges [77,78]. The water crisis is expected to increase due to climate change that negatively affects crop production [79,80]. Several climate models forecast reduced annual rainfall and increased temperature with frequent droughts that negatively affect worldwide crop productivity [81]. 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 [82]. Besides the frequency of extreme abiotic stresses, the magnitude of such stresses as drought is also predicted to increase with time [83], affecting food production around the globe [83]. Moreover, redistribution of rainfall is also expected due to climate change that will affect irrigated agricultural lands and rainfed areas [26,80]. With the ever-increasing drought threat, it is important to study the response of main crops to drought stress.

5. 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 [84]. 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 [85–88]. An increase in leaf tissue sugar concentration also leads to feedback inhibition of photosynthesis that affects plant growth and yield [89]. 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 [90]. 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 [91]. The effect of drought depends upon the severity of drought, stage of plant development, and susceptibility of the genotype to drought stress.

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 [31]. Drought may affect potato yield by affecting vegetative growth such as plant height, number, and size of leaves [91], 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 [92] or by reducing the size [37] and numbers of tubers [93] produced by plants. Moreover, drought may also affect the quality of tubers produced [94,95]. Therefore, drought stress on potatoes can be grouped in the effect of drought stress on above-ground parts, below-ground parts, and yield.

5.1. Effects of Drought on above Ground Growth in Potato

Canopy development is among the most drought-sensitive stages in plants [96]. 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 [97], production of new leaves [45], stem number [97], and individual leaf area [98] of potatoes. Canopy growth depends upon high turgor pressure that helps in cell expansion and thus growth [98]. 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% [99]. However, leaf growth in potatoes stops when available soil water is less than 60% [100], 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 [101]. 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 [45]. 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 [45]. Chang et al. [97] 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 [97]. A comprehensive investigation of 103 potato cultivars reported that late-maturing cultivars might be less affected by late drought than early maturing cultivars [45]. 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 [102]. On the other hand, potato stem numbers may be less affected as plants already produce optimum stem numbers before the start of late drought [103]. Similarly, Deblonde and Ledent [90] 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 [104]. 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 [105]. These results were also confirmed in another study where drought stress significantly reduced the LAI in Banba cultivar [106]. 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 [7,106,107]. The variation in LAI of potato cultivars under drought stress can be because of different canopy architecture [105]. 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) (Figure 6). Michel and others [105] 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 [97]. Jefferies and MacKerron [101] 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 [108].

Multiple effects of drought stress on canopy growth of potatoes lead to a reduction in photosynthesis [109]. 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 [107]. 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 [110]. 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 [111,112]. In some crops, such as soybean and sunflower, reduction in RuBP production has been mentioned as the main inhibitory effect of drought [111,113]. 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 [114]. A lower concentration of carbon dioxide in the mesophyll leads to substrate unavailability necessary for plant growth and respiration [112]. Bota et al. [115] 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 [115].

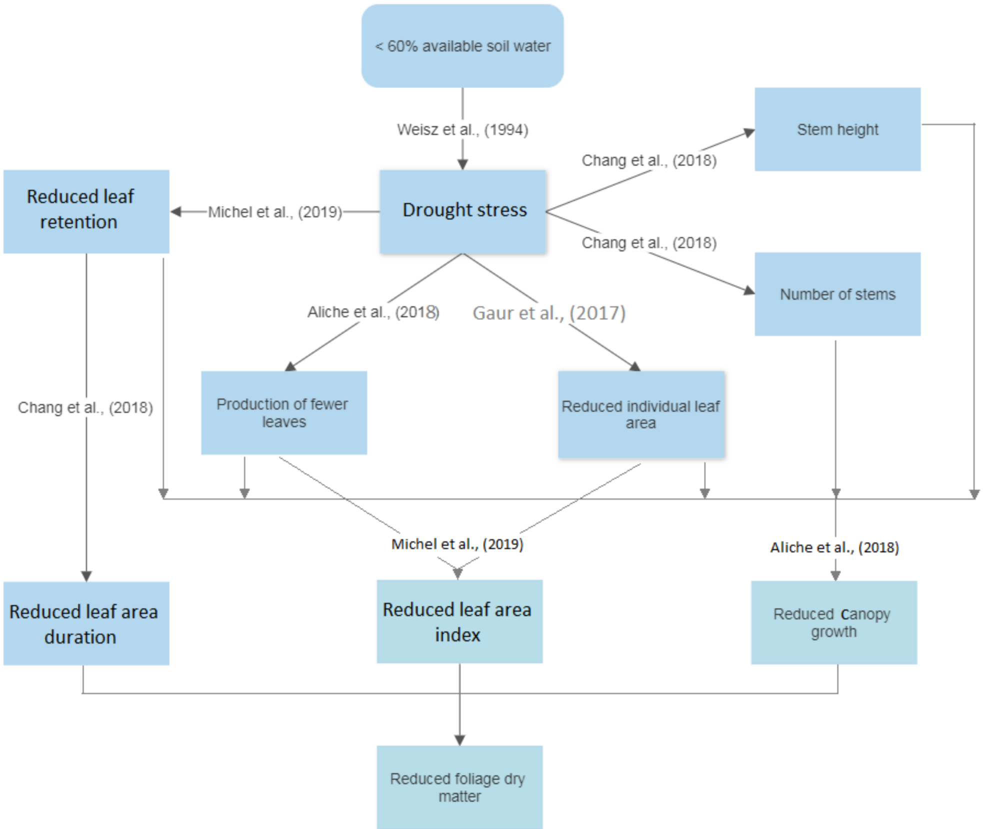

Figure 6. Schematic diagram of the effect of drought stress on above-ground growth of the potato [45,97,100,105,107].

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5.2. 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 [116,117]. 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 [118]. In contrast, some researchers reported an increase or no change in root length under drought stress [44,119,120].

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

Morphological Trait	Observation	References
Foliage cover	Reduction	[45,121]
Stem thickness	Reduction	[97]
Stem number	Reduction	[97,103,106]
Plant dry matter	Reduction	[97,106,120,122,123]
Shoot fresh weight	Reduction	[97]
Leaf area index	Reduction	[103,105,106,124,125]
Leaf size	Reduction	[126]
Leaf area duration	Reduction	[103,105,106,124]
Leaf water potential	Reduction	[126]
Number of leaves	Reduction	[45,91,97]
Relative water content	Reduction	[106,110,120,121,126]
Plant height	Reduction	[97,106,121,125,126]
Tuber fresh weight	Reduction	[31,45,97,103,123,127]
Tuber yield	Reduction	[97,120,125]
Tuber dry mass	Reduction	[97,103,106,123,125,128–131]
Number of tubers	Increase Reduction	[103,125] [45,47,93,103,106]
Stolon number	Increase Reduction	[44] [132]
Root length	Increase Reduction	[44,119,120] [118]
Root number and thickness	Reduction	[120]
Root biomass	Reduction	[133]
Root water potential	Reduction	[134]
Root dry matter	Increase Reduction	[44,135,136] [44,120,133]
Chlorophyll	Reduction Increase	[122,137] [126]
Carotenoids	Reduction	[122]
Antioxidants	Increase	[122]

Similarly, the root dry mass of potatoes has also been reported to decrease [44,133], increase [44,135,136], and remain constant [133] under water shortage. Moreover, opposing results were also reported for the stolon number due to drought stress [44,132]. Many arguments have been made to justify these variations in observations. Most studies discuss the variation in genotype and environment interaction [117,120,138–142]. Different cultivars respond differently to the specific intensity and duration of the drought [143]. 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 [144]. 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 [31,116,119]. The unpredictability of all these factors makes it more challenging to study the effect of drought stress on underground parts of potatoes.

5.3. Effects of Drought on Potato 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 [103,127], tuber number [91], tuber dry matter [145], and marketable tuber yield [49] have been studied in detail.

5.3.1. Effects of Drought on Fresh Tuber Mass

Fresh tuber yield depends upon dry matter allocation to tubers and water content of tubers [146], where water content contributes up to 80% in fresh tuber mass depending upon the cultivars [147]. Therefore, fresh tuber mass is highly affected by water shortage [31,127]. Jefferies and MacKerron [101] 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 [103]. A recent study [45] 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 [45]. In another study, Boguszewska-Mańkowska and others [120] 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 [148]. This deviation can be an adaptive response of potato cultivars to drought stress involving osmotic regulation [149]. 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 [101], 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 [97]. 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 [97]. Similar results were also reported in several other studies [55,150,151].

5.3.2. Effects of Drought on Number of Tubers

Besides fresh tuber weight, drought also affects the number of tubers produced by potato plants [93]. 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 [45]. Similarly, exposure to a single short-term early stress also exhibits an inhibitory effect on the tuber number produced by the plant [132]; however, late short-term drought stress showed a higher effect on tuber dry matter than on the number of tubers [152]. In another study, Chang et al. [97] 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 [153,154]. On the other hand, some studies have reported an increase in tuber number under drought stress [103,125]. This can be due to the adaptive response of cultivars to sustain the yield under drought stress [45] 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 [155]. Rykaczewska [125] 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.

5.3.3. Effects of Drought on Dry Tuber Mass

Potato yield and quality are also determined by the dry mass of tubers [156]. Total tuber dry mass depends upon substrate production by leaves [157] 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 [101]. 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 [158]. Assimilate translocation depends on tuber water content [101] and is used to describe tuber quality, particularly the quality of processing cultivars [159]. Due to the economic significance of total tuber dry mass and dry matter translocation into tubers, researchers have studied them extensively.

Steckel and Gray [119] 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 [119]. 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 [146] 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 [146]. Steyn et al. [160] 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 [103] 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 [125,128–131].

In several studies, reduction in net photosynthesis under water shortage stress has been argued as the main reason for total tuber dry mass reduction [124,137,161,162]. Drought stress affects the relative water content of leaves [110], which affects plants' metabolic activities. Stomatal conductance is reduced when leaf water potential reaches below -0.6 MPa [162], causing a reduction in carbon dioxide absorption [161] and reduced net photosynthesis rate [106]. Moreover, water stress also causes a reduction in chlorophyll content [137] and leaf area index and leaf area duration [124]. 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. [163] 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% [163]. 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 [97].

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 [164,165]. 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 [166]. Animal manure and other carbon-rich wastes can also improve the nutrient status of soils and the water-holding capacity of soils [167]. Biochar and compost have been reported to alleviate drought stress [168], improve the soil structure [169], and increase the water-holding capacity of soils [170]. However, the effectiveness of compost depends upon the type of compost, the frequency of treatment with compost, and the type of soil [171].

Nutrient management also affects soil health; thus, the water holding capacity of the soil. Several inorganic nutrients such as Zn, N, P, K, and Se have been reported to alleviate drought stress in wheat [172–174]. Pilon et al. also reported that foliar and soil application of silicon improves drought tolerance in potatoes [175]. 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 [176], 1-aminocyclopropane-1-carboxylic acid, ABA [177,178], 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 [166]. 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 [179]. Wastewater can be cleaned by activated sludge, membrane filtration, and bioreactors; however, it is expensive and unsuitable for a larger scale [180]. The Israeli government has set an example by reusing 85% of treated wastewater under the integrated water resource management (IWRM) policy [181].

Although 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.

7. Conclusions

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, this review has shown that canopy development and cultivar type also play a crucial role in the 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 producing fewer, larger, and thicker leaves can be a better option. This review also highlighted the variable response of different potato genotypes to different degrees of drought. It can help the breeders select promising genotypes to develop drought-tolerant potato cultivars.

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