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Heat and drought stress and their implications on potato production under dry African tropics

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Abstract

The two most important abiotic factors affecting potato productivity in many areas of the world and especially in the dry African tropics are drought and high temperature. The situation is worsened by global warming. High temperature and drought reduce not only yields but also quality of potatoes. The effects of drought depend on the genotype, timing, duration and severity of the stress; plant emergence and tuberization are two critical periods when water stress most affects the final tuber yield. The susceptibility of potato crops to high temperature largely depends on genotype, development stage and stress duration; tuber initiation and bulking are critical stages. High temperature, particularly high night temperature, is reported to delay tuber induction, prolong tuber setting, and delay the onset of rapid tuber growth. The optimum soil temperature range for tuber initiation and tuber growth is 15–20 ^{0}C, and the colder the soil temperature, the more rapid the initiation of tubers and the greater the number of tubers formed. At high temperature more photoassimilates are partitioned to the vegetative parts than tubers resulting in acceleration of haulm growth and inhibition of tuber initiation and growth. In tropical Africa, potato production is moving to the dry mid and low altitudes due to high population pressure in the moist highlands. In these dry areas, potato production is facing the double tragedy of high temperature and water stress. This has led to low yields and poor quality since there is no available commercial potato variety which is tolerant to high temperature and water stress. Breeding for heat and drought tolerance in potatoes is hard because in most cases, especially in dry tropics, these two conditions occur concurrently. In addition, the two traits are polygenic with low inheritance making conventional breeding difficult; more progress could be achieved through molecular breeding and/or genetic engineering.

Keywords: Drought, Heat, Potatoes, Tolerance, Tropical Africa.

Introduction

Potato (*Solanum tuberosum* L. $2n=4x=48$) is the third most important food crop in terms of human consumption after rice and wheat (FAO, 2008, 2013; CIP, 2014); more than a billion people worldwide eat potato (CIP, 2014). The total world production was estimated at 388.2 million tonnes in 2017 grown on about 19.3 million ha (FAO, 2019). The total production was valued at around USD 92 billion, making it one of the most profitable crops for the farmer, just behind rice and maize (FAOSTAT, 2019). Potato is grown in more than 158 countries worldwide (FAO, 2019) from latitudes 65^0 N to 50^0 S (Acquaah, 2007) and can grow from sea level up to 4 700 metres above sea level; from Southern Chile to Greenland (CIP, 2014). More than half of global potato production comes from developing countries, where it is cultivated in marginal areas prone to environmental anomalies such as heat, drought, and salinity (Scott and Suarez, 2012). Potato is grown successfully in tropical and subtropical climates, with about 100 potato growing countries being located within the tropics and sub-tropical regions.

The primary center of genetic variability of cultivated potatoes is located in the Andean mountains of Peru and Bolivia. Here in the Titicaca plateau, 10 to 20^0 south and 3,000 to 4,600 meters above sea level, potato has been cultivated for over 2,400 years (Acquaah 2007; Sleper and Poehlman 2006). The secondary center of diversity of cultivated potatoes is in southern South America, particularly in Chile (Bukasov 1966). From here is spread to Europe, then Northern America and Africa (Hijmans 2001; Acquaah 2007; Sleper and Poehlman 2006). Potato was introduced into the tropical and subtropical Africa by the white settlers who grew it in the cool highlands. The principal areas of potato cultivation are concentrated in zones of the world with cool to medium temperatures during the growing season. These conditions are met both at low elevations in medium to high latitude countries as well as at high elevations in many tropical countries (Haverkort, 1989; Haverkort and Verhagen, 2008); in the tropics at latitudes below 20^0 N or S, the crop can only be grown at elevations of at least 2,000 masl. Potato production is the greatest in the temperate zones where mean yields of 20 ton/ha and above are reported. The high yields per unit area in these countries may be to a large extent caused by the favourable climate, i.e. moderate temperatures and long days with moderate light intensities. Consequently, most of potato breeding work was conducted in the temperate climates of Europe and North America as well at the International Potato Center (CIP) in Peru. From Peru, advanced potato clones were evaluated for adaptability in Africa and Asia by the CIP regional offices; successful clones were released in these countries. Potato performs best under cool climates and is generally adversely affected by high temperatures (Borah and Milthorpe, 1962; Hawkes, 1978). Potatoes require a cool growing season with an average daily temperature of 15-18^{0}C; temperatures above 21^{0}C have adverse effects of growth (Kabira et al., 2006). Optimal tuber yield for most commercial potato varieties is produced when potato plants are grown at average day temperatures between 14 and 22^{0}C (Van Dam et al., 1996). The susceptibility of potato crops to high temperature largely depends on genotype (Tang et al., 2018), development stage and stress duration (Ahn et al., 2004); tuber initiation and bulking are the most critical stages (Struik, 2007; Ghosh et al., 2000). In potato plants, minimum night temperature plays a crucial role during tuberization which is reduced at night temperatures above 20^{0}C with complete inhibition at above 25^{0}C. High night temperatures are more deleterious to the formation of tubers than day temperature. High temperature can disturb the relationship balance between source and sink, delay the process of tuber formation and bulking, and finally result in tuber deformities and necrosis (Levy and Veilleux 2007). At high night temperature, more of assimilated carbon is partitioned to vegetative parts while at lower night temperature most of the assimilated carbon is partitioned to the tubers (Wolf et al., 1990). Delayed tuberization has been linked to the high temperature-induced inhibition of tuberization signal StSP6A (an orthologue of Arabidopsis flowering *locus* (FT) (Navarro et al., 2011) at elevated temperatures (Ewing 1981; Hancock et al., 2014). The limits and optimal temperature for the growth of the above-ground parts of the potato plant and for the tubers are different; research has shown that haulm growth is fastest in the temperature range of 20–25^{0}C whereas the optimum soil temperature range for tuber initiation and tuber growth is 15–20^{0}C (Marinus and Bodlaender, 1975; Struik et al., 1989a; Struik et al., 1989b; Van Dam et al., 1996); the colder the soil temperature, the more rapid the initiation of tubers and the greater the number of tubers formed. Optimum soil and air temperatures lead to a good balance between vine and tuber growth (Griffin et al. 1993). The highest tuber yields can be gained at moderate temperatures, about 21^{0}C during the day and 18^{0}C at night (Kim and Lee, 2019). Soil temperature higher than 18^{0}C causes tuber yield losses when combined with high ambient air temperature (Monneveux et al., 2014); tuber growth is inhibited at temperatures above 25^{0}C and growth of above-ground parts is limited when temperatures reach above 39^{0}C (Donnelly et al., 2007). Potato is also sensitive to drought mainly due the crop's shallow root system and the low capacity of recuperation after a period of water stress (Iwama and Yamaguchi, 2006). Potatoes have sparse and shallow root system (Kashyap and Panda, 2003; Onder et al., 2005) with a depth ranging from 0.5 to 1.0 m (Vos and Groenwold, 1989). About 85% of the total root length is concentrated in the upper 0.3 m of soil (Opena and Porter, 1999). Due to this, potato extracts less of the available water from the soil compared to other crops (Weisz et al., 1994). These ecological constraints to potato production partly explains why this food crop has not attained the dominant role that major cereals have enjoyed in the tropics. Given the fast expanding population in the tropics, crops with high yielding potential could become increasingly important as a supplement if not a complete substitute to the staple grains. Potato is a prime candidate for this subsidiary role as it has high yield potential and yields more food on less land than any other major food crop. With a yield potential of more than 51,000 calories/ha per day in a short growing season, its productivity in terms of energy produced is the highest of all major arable crops, almost double that of wheat and rice (Sanginga, 2015). Potato's short cropping cycle of three to four months is well-suited to the double cropping seasons in the tropical African highlands, particularly in rain-fed systems; this is a significant advantage over grains which take six to nine months to mature. A hectare of potatoes could provide up to four times the calories of a grain crop and up to 85% of the plant is edible human food, compared to around 50% in cereals. Moreover, potato is nutritionally better balanced (Burlingame et al., 2009) contributing protein, vitamin C, zinc, and iron to the diet. The 'nutritional productivity' of potato is especially high: for every cubic meter of water applied, 5,600 calories of dietary energy are produced, compared to 3,860 in maize, 2,300 in wheat, and only 2,000 in rice. For the same cubic meter of water, potato yields 150 g of protein which is double that of wheat and maize, and 540 mg of calcium, double that of wheat and four times that of rice (Sanginga, 2015; Renault and Wallender, 2000). Potatoes also contain vitamins and minerals as well as important phytochemicals, many of which have antioxidant properties. These qualities make potato an important food security and cash crop for smallholder farmers with limited options as is the case in tropical Africa. For potato to create a significant impact on agriculture and industry in the African tropics, its range of adaptation should be widened to cover the vast hot and dry lowland areas. Because heat and drought stress occur concurrently in the dry African tropics, development of potato varieties with combined heat and drought tolerance could play an important role in expanding potato production in these areas. This review looks at the effects of heat and drought stress on potato and how this affects potato production in the dry African tropics.

Potato production in tropical Africa

In Africa, potatoes are grown under a wide range of conditions; from irrigated commercial farms in Egypt and South Africa to intensively cultivated tropical highland zones of Eastern and Central Africa, where it is mainly a small farmer's crop grown under rainfed conditions. Potato production is important in North Africa because of a huge export market to Europe. Potato is also grown under irrigation in Harmattan season in the Sahel Zones in West Africa (Sanginga, 2015). The 10 major potato producers in Africa are Algeria, Egypt, South Africa, Morocco, Tanzania, Kenya, Nigeria, Malawi, Ethiopia and Rwanda in that order (FAO, 2019). The hilly, fertile terrain of East, Central, West, and Southern Africa is home to more than seven million smallholder potato farmer households (Sanginga, 2015). High altitudes, a temperate climate and generally dependable rains make for near ideal growing conditions for potato. Potato is the fastest growing food crop in Sub-Saharan Africa (SSA). In SSA, 52% of the area harvested and 45% of the potato production is in East and Central Africa (Scott et al., 2013). Most potatoes are grown under rainfed conditions in the highlands of Sudan, Ethiopia, Kenya, Uganda, Congo, Rwanda, Burundi, Madagascar and Cameroon (Haverkort and Verhagen 2008). However, potato production in SSA is generally far behind that of other countries and regions in the world although potatoes are an important food and cash crop in this region (Witte, 2013). Potato yields in SSA range from 6 to 10 ton/ha, far below attainable yields of 25–35 ton/ha. Demand for potato is increasing in SSA and the trend is to increase the area under production (Sanginga 2015). In tropical Africa, potato is grown in the highlands at altitudes between 1500 and 3500 meters above sea level. However, the high population growth in the tropical African highlands is forcing the local small scale farmers to move to the hot and dry lowlands. Most of these small-scale farmers have retained the traditional land-use practices that evolved in the moister and therefore more productive highlands where they grew potato. However, the high temperatures and limited moisture in the lowlands areas may result in low yield and poor quality potatoes.

Africa is the most tropical of all continents; it is the only continent that straddles the equator and incorporates both the Tropic of Cancer and Capricorn. Rainfall is the most significant climatic factor in Africa; this is because most crop production activities are rain-fed. Temperature is high throughout the continent because of the continent's location relative to Equator and the range of temperature is quite small. In warm tropical areas, the negative effect of water stress is exacerbated by high temperature. These conditions are worsened by the global climate change. The main repercussions of climate change are a rise in temperature, an increase in CO_2 concentration in the air, an altered precipitation pattern, frequent frost and snow fall in high altitudes (IPCC, 2007; 2014). The global daily mean temperature is expected to increase by 1.0– 3.7^0C by the end of the 21st century (IPCC, 2013). It has been observed that the increase in minimum temperature during the night has been greater than the increase in maximum temperature during the day thereby reducing diurnal temperature range (DTR) on a global scale (Easterling et al., 1997; Harris et al., 2014). Reduced DTR has been shown to affect crop growth and development (Benoit et al., 1986; Yin et al., 1996; Bahuguna and Jagadish, 2015). Climate change is projected to increase median temperature by $1.4–5.5^0$C and median precipitation by −2 to 20% by the end of the 21st century (Adhikari et al., 2015). According to IPCC (2007), crop productivity is projected to increase slightly at mid to high latitudes for local mean temperature increases by up to 1 to 3^0C depending on the crop, and then decrease beyond that in some regions. At lower latitudes, especially in seasonally dry and tropical regions, crop productivity is projected to decrease for even small local temperature increases (1 to 2^0C). While the anticipated increase in the atmospheric CO_2 level may enhance yield potential in certain crop species (Deryng et al., 2016) the yield losses due to high temperature and water deficit may surpass the benefit achieved by any increase in CO_2 (Lobell and Gourdji, 2012). Moreover, the sub-optimal growth conditions are occurring at a time of predicted 30% increase in the world population by 2050 (UNDESA, 2011) thereby increasing food demand. It is estimated that by 2050, food and agriculture systems will need to produce 50% more food to feed the projected global population of close to 10 billion (FAO, 2017). Climate change will affect both food quantity and quality; protein content of crops may be reduced considerably in major staple crops such as barley (14.6%), rice (7.6%), and potatoes (6.4%) (FAO, 2017). Due to climate change, Africa will very likely (with > 90% probability) experience warming in greater measure than the global average in all seasons (Lobell and Burke, 2010). Temperature in Africa is projected to rise faster than the rest of the world, which could exceed 2^0C by mid-21st century and 4^0C by the end of 21st century (Niang et al., 2014). In tropical climates, excess solar radiation and high temperatures are often the most restrictive factors which affect crop development and yield. In SSA, many crops will be more affected by water stress, caused by increased evapotranspiration and variability in rainfall, rather than heat stress (Adhikari et al., 2015). As such, rainfed farming in SSA is typically limited to 3–6 months during the rainy season and the crop yields are subjected to weather- driven fluctuations (Burney and Naylor, 2012). The impact of heat and drought stresses on potato production will increase over the next decades due to climate change and the expansion of potato cultivation into hot and dry conditions (Hijmanns, 2003). Effects of global warming on potato production have been predicted to decrease yields by 10–19% in 2010-39, and by 18–32% in the 2050s; this is the time when more food is needed to feed the world's growing population (Hijmans, 2003; Hancock et al., 2014). For several countries, particularly in tropical Africa, potato yield declines are expected to reach upto 20–30% (InfoResources, 2008). Due to drought, it is estimated that potential potato yield will decrease by 18 to 32% between 2040 and 2069 (Hijmans, 2003). In addition, it is estimated that the average global potato yield could be increased by at least 50% if water supply to the crop could be optimised. Climate change is projected to increase temperature and precipitation variability in East Africa. Consequently, potato yield in most of East African countries (except Rwanda) will decrease due to heat and water stress (Adhikari et al., 2015). Haverkort et al. (2013) predicted that the positive effects of elevated CO_2 on water use efficiency and crop yield were more than adequate to compensate for the negative effects of increased temperatures and reduced water availability in 2050s. Similarly, IFPRI (Tenge et al. 2012) using the IMPACT model, predicted up to a 100% increase in potato yield and a 50% increase in cultivation area in Rwanda in 2050 compared to 2010; the authors predicted doubling or tripling the potato production by 2050. However, Jarvis et al. (2012) projected about 15% reduction in potato yield in Africa by 2030. Similarly, Tatsumi et al. (2011) projected a 17% decline in potato yield in eastern Africa in 2090s compared to 1990s. In adapting potato production to climate change, breeding is going to play a key role as well as adapted seed potato programmes and management of quarantine diseases and pests (Haverkort and Verhagen, 2008). Identification or development of potato cultivars with increased heat (Hijmans et al., 2003) and drought tolerance appears to be important to cope with climate change especially in the hot and dry African tropics.

Effects of heat and drought stress on potato growth and development

High temperatures (Midmore, 1983) and drought (Yuan et al., 2003) and are some of the major abiotic stresses that affect potato production worldwide affecting both yields and quality. Heat stress and drought stress, when imposed independently on the potato, may have contrasting effects on maturation: high temperatures enhance vegetative growth and may delay maturation (Bodlaender, 1963; Ivins and Milthorpe, 1963), whereas drought inhibits growth and enhances maturation (Deblonde and Ledent, 2001; Van Loon, 1981). When these stresses occur concomitantly in the field, the high temperature commonly associated with increased evapotranspiration aggravates the drought stress, leading to growth inhibition and enhanced maturation (Levy, 1986). For the early maturing genotypes which accomplish yield accumulation in a relatively short period of time, shortening of the growth period by stress was relatively small compared with the later maturing cultivars (Levy, 1986). This is because the later maturing genotypes are exposed to the increasing stress constraints for longer periods. Consequently, this situation could explain the relatively small yield loss of the early maturing genotypes. High temperatures delay, impede or even inhibit tuber initiation (Minhas et al., 2006). Minimum night temperature is very important for potato crop; whether or not potato will tuberise depends largely on the minimum night temperature and not on the average daily temperature (InfoResources, 2008). Tuberisation is reduced by night temperature of 20^0C and there may not be any tuberisation at night temperature of 25^0C and above even though potato plants can tolerate day temperature of about 35^0C without much deleterious effects (Wolf et al., 1990; InfoResources, 2008). Night temperatures above 20^0C severely depress both tuber initiation and bulking and temperatures above 25^0C effectively stop tuber production (Minhas et al., 2001). Potato can give good yield even at day temperatures of 30-35^0C provided night temperatures are below 18^0C (Minhas and Kumar, 2005).

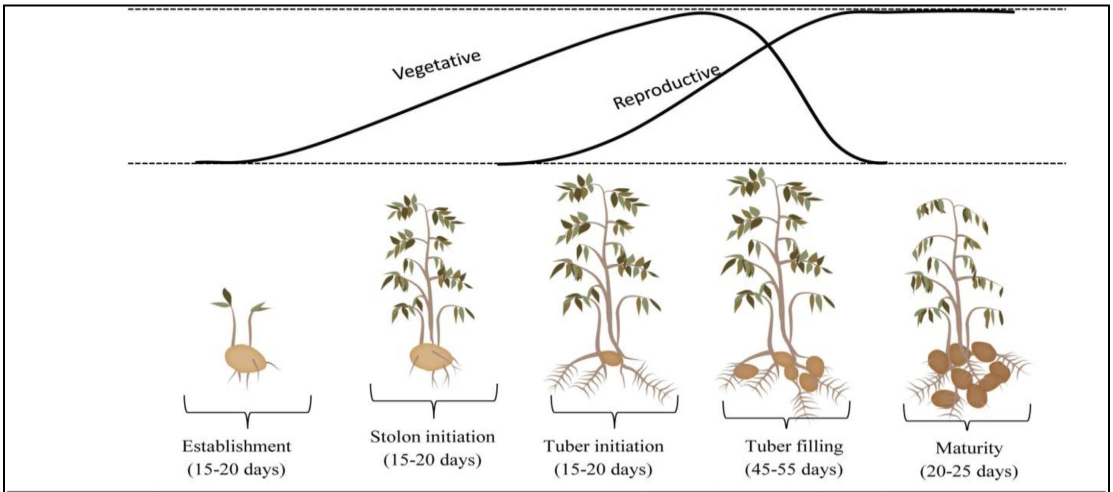
The magnitude of drought effects depends on phenological timing, duration and severity of the stress (Schafleitner 2009). Sensitivity of potato to water stress varies with the developmental stage of the crop; plant emergence and tuberization are two critical periods when water stress most affects final tuber yield (Martínez and Moreno, 1992). Water shortage during the tuber bulking period decreases yield to a larger extent than drought during other growth stages. Drought after planting may delay or even inhibit plant emergence while insufficient water supply between plant emergence and beginning of tuber bulking may lead to slow growth rate of the foliage, small leaves and small plants (Figure 1).

Effects of heat and drought stress on potato yields and quality

Moisture stress can reduce potato yields, produce misshapen tubers, negatively affect processing quality and increase common scab incidence (Mane et al., 2008). Moisture stress results in reduced number (Eiasu et al., 2007) and size (Schafleitner et al., 2007a) of tubers produced. Drought events occurring early in the growing season reduce the number of tubers per plant (Haverkort et al., 1990). Furthermore, a single, short-term drought event during tuber bulking stage can inhibit future bulking of those potatoes already set and result in initiation of new tubers. This not only decrease potato grade (i.e. tuber size and quality) but lowers overall yield. Minhas and Bansal (1991) showed that tuber initiation is the most sensitive stage to water stress; drought during this period can reduce the number of tubers produced per plant (King and Stark, 1997). Tuber shape, dry matter and reducing sugars contents can be influenced by water stress during the vegetative period. Shape defects such as dumb-bell shaped, knobby or pointed end tubers can be caused by short periods of moisture stress during the tuber bulking stage (MacKerron and Jefferies, 1988). Secondary growth symptoms and tuber malformation could occur when soil moisture is replenished after a drought period. Misshapen tubers can also occur due to secondary growth which mainly occurs in dry soils when temperatures rise (Lugt et al., 1964). Hot and dry conditions may also result in poor cooking quality (glassiness) of the tubers, jelly end or translucent tuber ends. They also result in high content of reducing sugars in tubers which cause difficulties during processing. High temperature stimulates conversion of starch to reducing sugars that triggers dark French fries (Minhas, 2012). High temperatures delay tuberization and result in a higher number of smaller tubers per plant and low specific gravity which is indicative of low dry matter contents (Haverkort, 1988). The average temperature during the growing season is the main determinant factor for final dry matter concentration at harvest: low temperatures lead to high dry matter concentrations and vice versa. The main reason that potato is not grown in warm areas is that the dry matter concentration is too low—lower than 17% is unacceptable due to poor storability and processing quality (Haverkort and Verhagen, 2008). Haverkort and Harris (1987) found a relation between dry matter concentration and altitude-dependent average temperature during the growing season: the dry matter concentration of tubers decreases by 0.446% per ^{0}C temperature increase with base value of 20% at an average daily temperature of 14^0C. In addition, they found that the number of tubers per plant increases by 1.68 tuber per ^{0}C increase in temperature (base value is 12 tubers, at 14^0C daily average temperature). Heat stress also results in secondary growth, internal brown spots (IBS), cracks, sprouting at harvest, short dormancy period, high glycoalkaloid content and high content of sugars in the tubers (Levy, 1986, Tai et al., 1994; Levy and Veilleux 2007). These disorders are mainly caused by elevated soil temperatures during the later stages of tuber growth and development (Stevenson et al. 2001; Struik and Ewing 1995).

Breeding potatoes for heat and drought tolerance

Breeding potatoes adapted to hot and dry climates is one of the main objectives of modern potato breeding programmes (Raymundo et al., 2014). To obtain cultivars adjusted to such conditions, wild potato germplasms are often used for the introgression of genes encoding heat-tolerance e.g. *Solanum chacoense* which contains genes encoding for heat-tolerance (Veilleux et al., 1997). Introgression of such germplasm directly into *S. tuberosum* would require sexual polyploidization or breeding at the diploid level with dihaploids of *S. tuberosum* followed by tetraploidization



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

Fig 1. *Effects of moisture stress at different growth stages of potato growth. Source:* Obidiegwu et al., 2015

through sexual polyploidization, somatic hybridization or artificial chromosome doubling. There are reports of the existence of genetic variability for heat tolerance (Tai et al. 1994, Menezes et al. 1999), which could be exploited in breeding programs. Heat-tolerant accessions of several diploid species including *S. berthaultii*, *S. chacoense*, *S. demissum*, and *S. stoloniferum*, among others, have been identified for utilization in breeding programs (Reynolds and Ewing, 1989). However, wild potato germplasms such as *S. chacoense* which contains genes encoding for heat-tolerance (Veilleux et al., 1997) also contain naturally high levels of total glycoalkaloids (TGA). Introgressions of such germplasm often cause increased levels of total glycoalkaloids (TGA) in the potato tubers; high levels of TGA may be toxic to humans and cause an undesirable taste (Storey and Davies, 1992). In addition to high levels of glycoalkaloids in the tubers, hybrids with a huge proportion of wild species can exhibit other undesirable wild attributes such as a large number of small tubers, excessive stolon growth and secondary growth among others (Veilleux et al., 1997). Previous study showed that TGA-content is controlled by a relatively low number of genes and is characterised by a relatively high heritability estimate; the minimum number of genes controlling TGA-content was estimated to be between 3 and 7 (Van Dam et al., 1999). Heat tolerance is not necessarily correlated with high levels of glycoalkaloid in tubers and thus it is possible to find tolerant clones with low content of glycoalkaloid when grown under conditions of high temperatures (Veilleux et al., 1997). Manuel et al (2017) found that broad sense heritability for glycoalkaloid content was 0.63 and its correlation with tuber yield was weak, r=0.33 and R^2=0.11 (P<0.01). Consequently, the high heritability and weak correlation will allow for selection of clones with high tuber yield and low glycoalkaloid content. It has been reported that heat tolerance in potatoes is controlled by several genes (Tang et al., 2018; Benites and Pinto, 2011; Rickey and Belknap, 1991) thereby making selection of tolerant plants in breeding programs rather difficult due to genotype-environment interactions while other reports indicate that in potatoes, response to temperature is oligogenic with low temperature reaction being dominant over reaction to high temperature (Mendoza and Estrada, 1979). In a typical breeding programme, selection for heat tolerance calls for extensive field trials and several years of testing a large number of potato clones. Despite advances made in breeding heat-tolerant potatoes, molecular mechanisms governing heat-tolerance is poorly understood. Multiple loci for heat tolerance have been identified in wheat (Paliwal et al., 2012) and maize (Messmer et al., 2009) whereas no QTL for heat tolerance in potatoes has been reported (Trapero-Mozos et al., 2018). Consequently, the first step towards understanding the heat-tolerance mechanism in potatoes is to identify the key genes involved in it (Gangadhar et al., 2014). Breeding for heat tolerance should focus on effect of high temperatures on tuberization, since potato tuber initiation and development are very sensitive to high temperatures (Muthoni and Kabira 2015). Since 2004, CIP has sought to improve the heat tolerance of its late-blight resistant population, B3, by developing the new late blight and temperature tolerant 'LBHT' population (Gastelo et al. 2015). The aim was to obtain potato clones with high levels of resistance to late blight, with high tuber yield under high temperatures, more than 20^0C at night, low glycoalkaloid content and early maturity (90 days), adapted to tropical mid-elevation environments. Aspects of heat tolerance that are considered important and should be taken into account in breeding programmes are: 1) ability of the plants to tuberise at night temperature of 22^0C and above, 2) low shoot/root ratio at high night temperature and 3) early maturity of the crop (Hijmans, 2003).

Recently, researchers have discovered a small RNA (about 19 nucleotides) that regulate tuber formation depending on temperature. The RNA is inactive at low temperatures. When temperatures rise, the RNA blocks the formation of StSP6A and thus the formation of tubers. The same researchers have created potato plants in which the effect of the small RNA was deactivated; this resulted in plants that continued to produce good quality tubers even at temperatures of over 29 degrees during the day or 27 degrees at night. (University of Erlangen-Nuremberg, 2019).

Drought tolerance is a quantitative trait under complex phenotypic and genetic control (McWiliam, 1989). The differential response of potato cultivars to water stress indicates that there is genetic variability for drought tolerance in cultivated potato (Harries 1978; Levy 1983). In addition, wild relatives of the potato have been identified that is drought tolerant, but linkage drag, incompatibility and different photoperiod requirements have hampered the introgression of the drought tolerance traits (Monneveux et al., 2013). Drought tolerance is a genetically complex polygenic trait with multiple pathways implicated (Obidiegwu et al., 2015). The complex phenotypic response of potato plants to drought is conditioned by the interactive effects of the plant’s genotypic potential, developmental stage, and environment. Effective crop improvement for drought tolerance will require the pyramiding of many disparate characters, with different combinations being appropriate for different growing environments. Selection efforts in areas which suffer from drought stress has not led to the development of highly drought tolerant cultivars due to low heritability and interactions with the environment (Cattivelli et al., 2008). Moreover, mechanisms which are advantageous for surviving severe drought might reduce tuber yield under mild drought. Breeding for drought tolerance is further complicated by the fact that several types of abiotic stress such as high temperatures, high irradiance and water deficit can challenge crop plants simultaneously. In addition, successful breeding requires exact information on effective tolerance traits, their heritability and their genotype x environment interaction as well as suitable selection tools for the traits of interest. The first step in the development of drought tolerant varieties is identification of drought tolerant traits that are available; this is not an easy task due to the complexity of the drought response. Molecular techniques might pose a solution to the problem by identifying the drought tolerance genes or QTLs and subsequent introgression of these traits by marker assisted selection or genetic engineering. However, knowledge about genetics of drought tolerance in potato is still limited and a few QTLs have been identified related to drought tolerance traits (Aksoy et al., 2015). Though many stress responsive genes are characterized in potato, commercial transgenic potato plants that are tolerant to drought have not yet been successful. This may be due to the quantitative nature and multiple loci of genes involved in plant stress tolerance, it is possible that crop growth and yield may not simply be improved through over expression of a single gene. The limited success of the physiological and molecular breeding approaches until now suggests that a careful rethink is needed of the strategies for better understanding and breeding for drought tolerance. Studies using transcriptome and metabolite analyses showed that *S. andigena* genotypes were more tolerant to drought than the *S. tuberosum* genotypes. They also reported several candidate genes, such as genes involved in osmotic adjustment, in changes in carbohydrate metabolism, membrane modifications and strengthening of cuticle and in cell rescue mechanisms (Schafleitner et al 2007b; Vasquez-Robinet et al 2008). Although these studies provide insights into potato response to water stress at the transcriptional level, the genetic regulation of these transcriptional responses is largely unknown.

Conclusion

Rain fed production of potatoes by small-scale farmers in the hot and dry parts of tropical Africa results in low yields and poor quality due to combined effects of high temperature and drought. The situation is worsened by the global warming. Breeding efforts have been going on to develop potato varieties that are drought tolerant and/or heat tolerant; there is need to develop potato varieties with combined heat and drought tolerance. Conventional breeding has not achieved much, more progress could be achieved through molecular breeding and/or genetic engineering techniques.

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