Breeding Science 69: 545–563 (2019)
doi:10.1270/jsbbs.19070

Review

Climatic changes and potatoes: How can we cope with the abiotic stresses?

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Climate change triggers increases in temperature, drought, and/or salinity that threaten potato production, because they necessitate specific amounts and quality of water, meanwhile lower temperatures generally support stable crop yields. Various cultivation techniques have been developed to reduce the negative effects of drought, heat and/or salinity stresses on potato. Developing innovative varieties with relevant tolerance to abiotic stress is absolutely necessary to guarantee competitive production under sub-optimal environments. Commercial varieties are sensitive to abiotic stresses, and substantial changes to their higher tolerance levels are not easily achieved because their genetic base is narrow. Nonetheless, there are several other possibilities for genetic enhancement using landraces and wild relatives. The complexity of polysomic genetics and heterozygosity in potato hamper the phenotype evaluation over abiotic stresses and consequent conventional introgression of tolerance traits, which are more challenging than previous successes shown over diseases and insects resistances. Today, potatoes face more challenges with severe abiotic stresses. Potato wild relatives can be explored further using innovative genomic, transcriptomic, proteomic, and metabolomic approaches. At the field level, appropriate cultivation techniques must be applied along with precision farming technology and tolerant varieties developed from various breeding techniques, in order to realize high yield under multiple stresses.

Key Words: combined abiotic stress, heat, drought, salinity, genetic resources, genetic engineering, tolerance.

Global climatic changes and abiotic stresses

Climate change is an inevitable and unavoidable phenomenon globally, which affects all aspects of human life, including food security. Direct effects of climate change include temperature increase of the earth surface, drought in arid and semi-arid areas, uneven precipitation and unpredictably high precipitation (Andjelkovic 2018, Trenberth 2008). In 2016, the global temperature was 0.99°C warmer than in the middle of the 20th century (NASA 2018). Whereas in the late 21st century, the global mean surface temperature is projected to increase 1–3.7°C relative to the end of the 20th century (IPCC 2014). In terms of uneven precipitation, an increase of annual mean precipitation is predicted in the high latitudes, equatorial pacific regions and some mid-latitude wet regions, while many mid-latitude and sub-tropical dry regions are expected to experience a decrease in annual mean precipitation by the end of this century (IPCC 2014).

When plants are exposed to any kind of unfavorable environmental condition that causes reductions in growth and yield, they suffer abiotic stress. The conditions could be high temperature, low temperature, drought, metal toxicity, or salinity stress. In relation with climate change, high temperature (heat), drought and salinity are the most serious abiotic stresses. The increasing average global temperature triggers increases in heat stress events, whereas the decreasing annual mean precipitation in some mid-latitude and sub-tropical regions leads to water deficits (IPCC 2014). The low precipitation, together with high surface evaporation, weathering of rocks, seawater intrusion, and poor cultural practices, increases the problem of land-salinity (Duan 2016, Shrivastava and Kumar 2015).

Challenges for potato under climatic change with abiotic stresses

Potato is the third largest food crop in the world after wheat

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Communicated by Kenji Katayama
Received May 8, 2019. Accepted September 10, 2019.

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and rice based on food supply quantity (FAO 2019a). Potato is a staple food with wide agro-climatic zones, a harvesting area of over than 19 million hectares, where more than 388 million tons were produced in 2017, and with consumption of more than 239 million tons (FAO 2019b). Mainly consumed as a fresh food, potatoes also provide raw material for food processing (e.g., chips and French fries) and specific industries (e.g., starch and ethanol) (Birch *et al.* 2012, Watanabe 2015). In addition to high carbohydrate and low fat, the potato tuber has balanced nutritional value with vitamins and minerals, making this crop ideal for the human diet and important for food security worldwide (Birch *et al.* 2012, White *et al.* 2009).

As a typical task on plant breeding, higher plants depend on their environment to complete the life cycle, which is generally reagreed as Genotype-by-Environment interaction (G × E). When plants are exposed to an exotic or variable environmental condition which may negatively affect their growth and decrease the yield, they are said to have encountered an abiotic stress (Cramer *et al.* 2011). Even though potato has been grown around the world under various environments and seasons, cultivated potatoes originated from the highlands of Andes in South America (Hawkes 1994), a region characterized by a cool temperate climate and short photoperiod. Today the distribution of potato plants covers almost all the world, from 47°S to 65°N, but 90% of total potato production takes place in a narrower band from 22°N to 59°N (Hijmans 2001). Potatoes can be grown in both subtropical and tropical zones, such as in the highlands of Southeast Asia. Nonetheless, despite the wide distribution and adaptability of this plant to various environmental and climatic conditions, potato growth is not entirely unaffected by environmental problems. Water stress (drought and flooding), extreme temperature (low and high), and ion toxicity (salinity and heavy metal) are the abiotic constraints that potato plants face in their habitats (Bohnert 2007). The following discussion will focus on high temperature, drought and salinity, which are equally weighted in terms of their impact on potato production. In addition, more awareness should be paid to the combination of these abiotic stresses. When drought combined with the heat wave, the effect would create huge losses in the agricultural sector (Mittler 2006). In 2016, the potato yield in Ontario decreased 35% to 50% in response to heat and drought (Banks and VanOostrum 2016).

Heat stress

In the potato crop, the optimum temperature for vegetative growth is 24°C, but the maximum total biomass would be produced at 20°C, as well as the maximum final tuber yield (Fleisher *et al.* 2006, Timlin *et al.* 2006). Potato is highly sensitive to high temperature (Levy and Veilleux 2007), presenting an obstacle to cultivation in tropical and sub-tropical areas. Potato plants that are exposed to high temperature from the beginning of the growing period risk a higher reduction in tuber yield compared to those with later exposure to high temperature, due to a delay in tuber initiation and shorter bulking duration, as well as a lower net assimilation rate (Aien *et al.* 2016). Climate change has been predicted to decrease the global potato yield from 18% to 32% without adaptation or from 9% to 18% with adaptation (Hijmans 2003). In this context, adaptation is considered in the narrow sense of the "autonomous" adaptations made to the farmer field, such as adjusting the planting time or using adaptive cultivars (Hijmans 2003).

Drought stress

With respect to water, the potato is known as an efficient water-use crop, yielding more food per unit of water than other main crops (Vos and Haverkort 2007). However, the potato is extremely sensitive to water deficits, due to the shallow and low density of root architecture of this crop species (Wishart *et al.* 2014, Yamaguchi and Tanaka 1990). Potato requires 400 mm to 800 mm of precipitation for complete growth, and this is also dependent on other factors such as meteorological conditions, soil and other management factors (Ekanayake 1989). The low precipitation caused by climate change in the mid-latitude and sub-tropical dry regions induces drought stress on the potato crop. The deficiency of water negatively affects plant growth and tuber yield and quality (Aliche *et al.* 2018, Mackerron and Jefferies 1988, Soltys-Kalina *et al.* 2016). Yield losses per year due to drought reach 117 kg tuber per hectare for each millimeter of water deficit and result in smaller tubers in the Netherlands (Vos and Groenwold 1987). In a simulated model, climate change was predicted to reduce rain-fed potato-cultivation areas in England and Wales by 74% to 95% by the 2050s (Daccache *et al.* 2012). This would greatly decrease potato production or shift it to irrigated fields, which in turn would compete with the water supply in other sectors, such as the water used for direct human consumption.

Salinity

In addition to drought, salinity—either salinity of the soil or salinity of the water applied to it—is another stress that can restrict the potato crop in the semi-arid and arid zones. Salt stress induces severe senescence and nutritional imbalance in potato plants, which reduces the plant growth and tuber yield (Aghaei *et al.* 2009, Ghosh *et al.* 2001, Jaarsma *et al.* 2013, Levy *et al.* 1988).

Cultivation approaches to alleviate abiotic stresses on potato

At a certain level, we can protect potato crops from adverse effects by abiotic stresses. Cultivation technologies such as mulching, shading plants, water-saving irrigation strategy by creating wet and dry areas in the root zone at the same time or partial root zone drying (PRD), applying rhizospheric bacteria, and nano-hormones scaling have been used to reduce the negative impact of environmental stress

Table 1. Mitigation to alleviate the abiotic stresses on potato

Abiotic stress	Technology aspects	Main roles	References
Heat	Mulch	Maintain soil temperature, reduce evapotranspiration	Paul *et al.* (2017)
	Intercropping	Cool soil temperature, conserve soil moisture, reduce irradiance	Midmore *et al.* (1988)
	Nutritional treatment: Calcium and Nitrogen	Keep stomatal function, maintain cell membrane thermo-stability	Kleinhenz and Palta (2002), Tawfik *et al.* (1996)
	Hormone treatment: paclobutrazol (PBZ)	Increase chlorophyll a and b content, increase net photosynthesis	Tekalign and Hammes (2005)
Drought	Irrigation scheduling	Maintain water use efficiency (WUE)	Kang *et al.* (2004), Kashyap and Panda (2003)
	Drip irrigation	Maintain WUE Conserve soil moisture	Kumari (2012), Onder *et al.* (2005)
	Partial root-zone drying (PRD)	Increase WUE	Jovanovic *et al.* (2010), Posadas *et al.* (2008)
	Mulch	Enhance soil fertility properties, conserve soil moisture, reduce evapotranspiration	Kar and Kumar (2007)
	Application of Plant Growth Promoting Rhizobacteria (PGPR)	Enhance the ROS scavenging enzymes	Gururani *et al.* (2013)
	Plastic film mulching	Increase temperature and soil moisture, enhance WUE	Jia *et al.* (2017), Zhao *et al.* (2012)
Salinity	Irrigation management	Increase water productivity	Nagaz *et al.* (2016)
	Application of silicon nanoparticle	Increase the activity of antioxidant enzymes	Gowayed *et al.* (2017)
	Application of PGPR	Enhance the ROS scavenging enzymes	Gururani *et al.* (2013)
	Soil amendment using biochar	Adsorb Na^+ and reduce Na^+ uptake	Akhtar *et al.* (2015)

on potato plants (**Table 1**). Mulching can be applied in order to reduce soil temperature and conserve soil moisture, under high temperature and/or water deficit stress (Ghosh *et al.* 2006, Kar and Kumar 2007). Use of organic mulch such as rice straw has many benefits in potato cropping under a water deficit, such as reduction of the soil temperature, conservation of the soil moisture, and increase of the availability of phosphorus, potassium and organic carbon (Kar and Kumar 2007). All these effects can improve the plant growth and tuber yield compared to plants without mulch. In arid and semi-arid agroecosystems, mulching with plastic film can reduce drought in the spring season by preserving snow from the winter season (Jia *et al.* 2017). In addition, to maintain the microenvironment above the ground, shading plants are also commonly used. However, the soil temperature plays a greater role in potato tuberization than the air temperature (Reynolds and Ewing 1989a).

Irrigation is another cultivation practice that alleviates environment stress (Levy *et al.* 2013, Pavlista 2015). In potato cultivation, water-saving irrigation strategies using scheduled irrigation during drought-sensitive growth stage or deficit irrigation (DI) and PRD can save from 20% to 30% of the water used in full irrigation (Jensen *et al.* 2010). Partial root zone drying provides additional advantages, such as increased content of starches and antioxidants (Jensen *et al.* 2010, Jovanovic *et al.* 2010). Application of the drip irrigation method under salinity conditions could maintain a lower level of soil salinity in the root zone (Nagaz *et al.* 2016), while the effects of heat stress could be mitigated by watering to lower the soil temperature (Dong *et al.* 2016).

As a complement to these measures, rhizospheric bacteria can be applied, based on the finding in some crops that application of plant growth-promoting bacteria (PGPB) isolated from plant roots in a harsh environment enhanced the plant biomass under a drought condition (Gururani *et al.* 2013, Mayak *et al.* 2004, Naseem and Bano 2014, Timmusk *et al.* 2014). Scaling up of nano-hormones in the field should also be considered, since abiotic stress tolerance is related to certain specific hormones (Egamberdieva *et al.* 2017, Tekalign and Hammes 2005). A combination of cultivation treatments would seem to be more efficient and more likely to achieve a significant effect: e.g., mulching with scheduled irrigation and application of micronutrients will reduce the soil temperature and maintain the soil humidity, thereby promoting optimal absorption of the nutrition.

Breeding approaches for potato abiotic stress tolerance

Cultivation practices could be applied to modify the microenvironment to suppress the adverse effects of abiotic stresses on plant. However, many areas do not have access to such technologies, which in any case are expensive and labor intensive. Use of a tolerant variety is the most reasonable solution. Breeding activities have been widely conducted. Genetic diversity is the basic principal in breeding programs (Govindaraj *et al.* 2015, Hawkes 1991). Such diversity can be obtained from germplasm collection, plant introduction, landraces, hybridization, or modifications by mutation and genetic engineering. Landraces and wild relatives are the best genetic resources for breeding plants with biotic and abiotic stress tolerance (Hawkes 1991), since they have been adapted in a wide range of habitats with harsh environments (Dwivedi *et al.* 2016, Hawkes 1994, Watanabe *et al.* 2011).

To utilize the diversity of genetic resources in plant breeding, the potentially useful resources must be screened, selected and evaluated. A tolerance evaluation method with consideration of plant phenotypes is the key to stress breeding. The International Potato Center (CIP) has developed a guide for drought phenotyping and drought stress investigation (Ekanayake 1989). Some screening and evaluation protocols for abiotic stress tolerance have been studied and developed (**Table 2**). Basically, screening methods have been conducted under three environmental conditions: *in vitro*, in a growth chamber or green house, and in the field. For the drought stress screening and evaluation, either Poly Ethylene Glycol (PEG) 6000 or 8000 (Anithakumari *et al.* 2011, Barra *et al.* 2013, Gopal and Iwama 2007, Hassanpanah 2009, Huynh *et al.* 2014) or sorbitol (Albiski *et al.* 2012, Gopal and Iwama 2007) is used, mostly at various concentrations that result in a water potential of media between –1.10 and –1.80 Mpa, which induces osmotic stress that represents a drought condition. Potted plants in the greenhouse are also commonly used in drought stress screening, since drought conditions can be replicated simply by withholding watering. Whereas in the salinity stress tolerance screening, NaCl is added to the *in vitro* or *in vivo* planting medium (Aghaei *et al.* 2008a, Khrais *et al.* 1998, Queirós *et al.* 2007, Shaterian *et al.* 2008, Zhang and Donnelly 1997). High temperature was used in the *in vitro* culture room and growth chamber to expose the plant to heat stress (Ewing and Wareing 1978, Khan *et al.* 2015, Nowak and Colborne 1989). Since an *in vitro* environment is different from the actual field condition, it needs to be validated using a method that is close to an actual dry environment (Bündig *et al.* 2017, Hassanpanah 2010, Khan *et al.* 2015). Screening at the *in vitro* level seems to be a reproducible method, since it is less affected by environmental factors and many studies have been done with this phenotyping technique. *In vitro* screening also has good predictability of the result under *in vivo* condition (Bündig *et al.* 2017, Khan *et al.* 2015). One factor that must be considered in *in vitro* assay is the tuberization ability under a stress condition.

In order to run screening and selection effectively, tolerance phenotype indices based on yield or other relevant traits are used to measure the level of tolerance to abiotic stress (Cabello *et al.* 2013). These indices are obtained from the relationship of yield or other traits under non-stress and under stress conditions. The tolerance indices that have been proposed include average yield of stress and non-stress conditions or Mean Productivity (MP) (Rosielle and Hamblin 1981), Geometric Mean Productivity (GMP) that used when breeder is interested in relative performance under various conditions (Fernandez 1992), differences of yield between stress and non-stress environment or Tolerance (TOL) (Hossain *et al.* 1990), the Stress Tolerance Index (STI) to identify genotypes with high yield under both stress and non-stress condition (Fernandez 1992), the Stress Susceptibility Index (SSI) to measure relative yield loss in stress condition (Fischer and Maurer 1978), and the proportion of yield in stress to yield in non-stress condition or Yield Stability Index (YSI) (Bouslama and Schapaugh 1984). Potato drought stress tolerance selection based on tolerance indices revealed that MP, GMP and the Drought Tolerance Index (DTI, comparison of yield under stress and non-stress condition to the yield of all genotype under non-stress condition) (Cabello *et al.* 2013) and MP, GMP, STI and modified STI (Hassanpanah 2010) were effective to

Table 2. Screening techniques for abiotic stress tolerance on potatoes

Screening techniques	Abiotic stress	References
In vitro tuberization	heat	Khan *et al.* (2015), Nowak and Colborne (1989)
Internodal elongation	heat	Nagarajan and Minhas (1995)
Nodal cutting tuberization assay	heat	Ewing and Wareing (1978), Reynolds and Ewing (1989b), Van den Berg *et al.* (1990)
Seedling assay	heat	Levy *et al.* (1991), Sattelmacher (1983)
Pulling resistance of root (PR)	drought	Ekanayake and Midmore (1992)
In vitro assay	drought	Albiski *et al.* (2012), Anithakumari *et al.* (2011), Barra *et al.* (2013), Gopal and Iwama (2007), Hassanpanah (2009), Huynh *et al.* (2014)
Electrolyte leakage bioassay	salinity, drought, cold and heat	Arvin and Donnelly (2008)
In vitro assay	salinity	Aghaei *et al.* (2008), Khrais *et al.* 1998, Queirós *et al.* (2007), Zhang and Donnelly (1997)
In vitro recurrent selection	salinity	Ochatt *et al.* (1999)
Hydroponic sand-based system	salinity	Shaterian *et al.* (2008)

identify genotypes with high yield under both conditions, irrigated and water stress. The Geometric Mean also gave comparable tolerance indication when used in heat stress tolerance selection (Lambert *et al.* 2006).

The effect of abiotic stress can be observed visually and directly on plant morphology and physiology—that is, by phenotyping. Some of phenotypes correlate with abiotic stress tolerance (**Table 3**). The use of these variables as selection criteria could assist in the development of a potato cultivar tolerant to abiotic stress. The leaves are the part of plants most directly affected by high temperature (Berry and Bjorkman 1980). Therefore, the photosynthesis process and some of its apparatus could be used to assist in the process of heat-tolerance breeding. However, to develop a heat-tolerant potato, at least three physiological processes need to be considered: photosynthetic efficiency and haulm growth, tuber initiation, and photosynthate partitioning (Vayda 1993). Root architecture is related to drought tolerance (Khan *et al.* 2016, Koevoets *et al.* 2016), since root depth contributes positively to drought tolerance (Lahlou and Ledent 2005, Zarzyńska *et al.* 2017). In addition, Wishart *et al.* (2014) proposed that high numbers or high length of stolon roots contributed to drought tolerance. The drought-tolerant potato genotype increases the mass of roots under a stress condition induced by water deficit (Schafleitner *et al.* 2007b). It is also known that water deficit stress tolerance is associated with high Water Use Efficiency (WUE). High WUE is regulated by a low transpiration rate, which means low stomatal conductance (Blum 2005, Levy *et al.* 2013, Li *et al.* 2017). It is important to determine the main traits related to stress with high variability, heritability and genetic advance under stress condition (Gastelo *et al.* 2017, Luthra *et al.* 2013). However, because there is a Genotype × Environment interaction (G × E) on several desirable traits, we should consider conducting the selection at multiple time points and different locations (Benites and Pinto 2011, Gautney and Haynes 1983). Recurrent selection is commonly used to improve the targeted traits by increasing the frequency of desirable alleles in a population.

These abiotic stress-related traits could be utilized for selection criteria, but only when investigating one stress at a time. A problem arises when we work with combined abiotic stresses. The response to combined abiotic stresses is unique and different from the response to each stress individually (Mittler 2006, Pandey *et al.* 2015, Shaar-Moshe *et al.* 2017, Zandalinas *et al.* 2018). Thus drought stress and heat stress result in very different effects (**Table 3**).

Cultivars having tolerance to a single abiotic stress have been identified and developed. Recently, the heat-tolerant cultivar Kufri Lima was released in India (CIP 2017). Kufri Surya, another heat-tolerant cultivar, had previously been released in India approximately a decade earlier (Minhas *et al.* 2006). Both cultivars were derived from crossing between local cultivar and heat-tolerant lines developed for lowland tropics at the International Potato Centre, Lima Peru. In Japan, conventional breeding by crossing two commercial potato cultivars, Irish Cobbler (the Japanese name is Danshakuimo) and Konafubuki, resulted in a drought tolerant cultivar, Konyu (Iwama 2008). This cultivar has been developed using high root dry weight as a selection criterion. However, the heritability of these traits is still in question to be applied widely to stress tolerance in different cultivars.

The use of stress-related traits with high heritability and genetic advances for selection criteria could assist in the breeding steps required to obtain stable tolerance. Three factors must be considered in order to develop drought stress tolerances in plants: membrane stability, the photosynthesis system and the root system (Farooq *et al.* 2009). The integrity of the cell membrane ensures that cellular activities will proceed in an optimal fashion. On the other hand, the photosynthetic reaction is correlated with plant growth and yield under stress conditions.

With respect to abiotic stresses, the cell membrane plays many important roles, such as providing a protective barrier, sensing and transducing various external signals, and

Table 3. Physiological and morphological traits associated with abiotic stress tolerance in potato

Abiotic stress	Target traits	References
Heat	High net photosynthesis	Dou *et al.* (2014), Reynolds *et al.* (1990), Wolf *et al.* (1990)
	High stomatal conductance	Reynolds *et al.* (1990), Wolf *et al.* (1990)
Drought	Low stomatal conductance	Moon *et al.* (2015)
	Low transpiration rate High WUE	Coleman (2008)
	High cell membrane stability	Rudack *et al.* (2017)
	Stay green	Ramírez *et al.* (2014), Rolando *et al.* (2015), Schafleitner *et al.* (2007a)
	High root mass system	Ahmadi *et al.* (2017), Iwama (2008), Wishart *et al.* (2014)
	High Leaf Area Index (LAI)	Iwama (2008), Romero *et al.* (2017)
	High biomass	Schafleitner *et al.* (2007a)
	High photosynthesis per leaf area unit	Romero *et al.* (2017)
Salinity	Growth index	Shaterian *et al.* (2008)
	Root growth	Murshed *et al.* (2015)

Table 4. Genetic resources for abiotic stress in landraces and wild species of potato

Abiotic stress	Source (Ploidy, EBN level)	References	Traits associated with tolerance
Heat	*S. commersonii* (2x, 1 EBN), *S. demissum* (6x, 4 EBN)	Arvin and Donnelly (2008)	Membrane stability
	S. juzepczukii (3x)	Havaux (1995)	High PS II activity
	S. gandarillasii cardenas (2x, 2 EBN)	Coleman (2008)	Membrane stability
	S. chacoense (2x, 2EBN), *S. bulbocastanum* (2x, 1 EBN), *S. demissum* (6x, 4 EBN), and *S. stoloniferum* (4x, 2 EBN)	Reynolds and Ewing (1989b)	Shoot growth and tuberization ability
	S. acaule (4x, 2 EBN) *and S. circaefolium* (2x, 1 EBN)	Midmore and Prange (1991)	High dry matter content
	S. phureja (2x, 2 EBN)	Hetherington *et al.* (1983)	High chlorophyll fluorescence
Drought	*S. juzepczukii* (3x)	Vacher (1998)	Stomatal tolerance and high net photosynthesis
	S. gandarillasii Cardenas (2x)	Coleman (2008)	Water use efficiency
	S. acaule (4x, 2 EBN)	Arvin and Donnelly (2008)	Membrane stability
	S. chillonanum (2x), *S. jamesii* (2x, 1 EBN), and *S. okadae* (2x)	Watanabe *et al.* (2011)	Rooting system
Salinity	*S. chacoense* (2x, 2 EBN)	Bilski *et al.* (1988)	Survival and shoot growth
	S. acaule (4x, 2 EBN) *S. demissum* (6x, 4 EBN)	Arvin and Donnelly (2008), Daneshmand *et al.* (2010)	Membrane stability

activating the mechanisms to maintain cell homeostasis (Barkla and Pantoja 2011). Membrane stability and photosynthetic activity are the traits that built the abiotic stress tolerance in some landraces and wild types of potato (**Table 4**). In chili pepper, membrane thermostability has high heritability and genetic advance values and has a positive genetic correlation with yield (Usman *et al.* 2014).

Techniques for evaluating water stress in potato

a. Physiological variables

As the main mass component in the growing plant tissue (90%), water is highly required for physiological processes and associated physical function in the plant (Araya and Garcia-Baquero 2014). Evaluation of the potato response and the tolerance of potatoes to drought stress could be done using physiological analyses.

Gas exchange

Gas exchange analysis is the most frequently performed evaluation in relation to drought stress, because it is closely related to the main physiological traits, such as stomatal conductance, net photosynthesis, internal leaf CO_2, water use efficiency and transpiration rate (Fandika *et al.* 2014). In response to a water deficit condition, the leaf stomata will close to maintain the water potential in leaf cells by reducing the transpiration rate; however, the CO_2 input will decrease and affect the net photosynthesis (Yan *et al.* 2016). Genotypes with efficient photosynthesis under low stomatal conductances are considered to be drought tolerant. Gas exchange analysis is usually conducted using a portable photosynthesis system (Fandika *et al.* 2014, Romero *et al.* 2017).

Chlorophyll fluorescence and chlorophyll content

Chlorophyll fluorescence is a measure of photosynthetic performance, particularly for photosystem II (PS II), which is highly sensitive to environmental changes (Murchie and Lawson 2013). Potato genotypes that have high PSII performance under drought stress show tolerance to drought (Boguszewska-Mańkowska *et al.* 2018). Leaf chlorophyll content is used to assess senescence or loss of greenness caused by water deficit, and is measured using a portable chlorophyll meter (SPAD from Konica Minolta, Japan) (Ramírez *et al.* 2014, 2015, Rudack *et al.* 2017). Stay-green character has been correlated with extension of photosynthesis activity, which translates to high yield under drought conditions (Tuberosa 2012), and is used as a drought tolerance indicator in potatoes (Rolando *et al.* 2015).

Water relative content (RWC)

Leaf RWC is a key indicator of plant water status—specifically, it estimates water status in the leaf resulting from a disparity between the leaf water supply and the transpiration rate (Soltys-Kalina *et al.* 2016). Potato genotypes that can maintain high RWC under a drought condition are considered tolerant to drought stress (Shi *et al.* 2015, Soltys-Kalina *et al.* 2016).

Cell membrane stability (CMS)

Drought stress induces a high accumulation of reactive oxygen species (ROS) on the cell wall, resulting in a shift in the cell wall composition and a decrease in cell wall integrity (Zhu 2016). The high stability of the cell membrane keeps all cellular processes going properly. Measurement of the leakage of ions from the cell with a conductivity-meter is commonly used to evaluate the CMS. Increasing membrane stability is one strategy for the adaptation of potatoes to drought (Arvin and Donnelly 2008, Rudack *et al.* 2017).

Low photosynthetic rate values and mesophyll conductance

The photosynthetic process is affected by water restriction, and this relation is associated with stomatal closure in the beginning and mesophyll conductance afterward (Flexas and Medrano 2002, Schapendonk *et al.* 1989). The variance of photosynthetic rate value and mesophyll conductance were revealed among potato cultivars, even could distinguish cultivars tolerant to water deficit from cultivars susceptible to this stress (Schapendonk *et al.* 1989, Vasquez-Robinet *et al.* 2008).

Canopy spectral and vegetation spectral indices

Since physiological traits analysis requires a large number of samples and a large amount of time, reflectance information could be useful in phenotyping under a water limitation condition (Gutierrez *et al.* 2010, Romero *et al.* 2017, Sun *et al.* 2014). Canopy spectral reflectance measurement is a non-destructive form of analysis, and some indices derived from canopy spectral reflectance data have been highly correlated with physiological traits (Romero *et al.* 2017). Vegetation indices calculated from the hyperspectral reflectance data, such as the Normalized Difference Vegetation Index (NDVI), the vegetation quantification by measuring the difference of vegetation reflectance and Soil Adjusted Vegetation Index (SAVI), the modification of NDVI with account variations in soil, have also been shown to discriminate potato crops under different irrigation regimes, and are highly correlated with the projected leaves surface area overground area or Leaf Area Index (LAI) (Ray *et al.* 2006).

Leaf chlorophyll and leaf nitrogen contents

Moderate water deficit increases the chlorophyll contents in potato leaves, and leaves of the susceptible genotype exhibit a higher chlorophyll concentration than those of the tolerant genotype (Ramírez *et al.* 2014, Rolando *et al.* 2015). However, a lower rate of chlorophyll degradation was detected on a drought-tolerant cultivar (Rolando *et al.* 2015). Nitrogen content also increases in response to drought stress, and genotype-related differences in this variable have also been investigated (Meise *et al.* 2018).

b. High-throughput phenotyping supporting potato breeding

Appropriate phenotyping techniques are essential, given the phenotypic plasticity of plants in response to environmental conditions (Araus and Cairns 2014, Gratani 2014). We need to understand shifts of phenotype in response to abiotic stress, but phenotypic characterization performed by manual visualization and measurement is prone to subjectivity, destructive to certain properties of the samples, expensive, and time and labor intensive (Rahaman *et al.* 2015, Romero *et al.* 2017). Such problems are especially relevant when we are in a screening or selecting step, which involves a huge number of accessions or breeding lines. Choice of a proper screening technique coupled with high throughput phenotyping is thought to be useful for rapid and accurate identification of the best line, and subsequent improvement of the breeding efficiency (Araus and Cairns 2014). Various phenotyping tools have been developed and studied in potato plants in relation to environmental conditions, such as digital RGB (an additive color modelling using visible light red, green and blue) imaging to determine chlorophyll content (Gupta *et al.* 2013), thermal imaging to measure stomatal conductance (Prashar *et al.* 2013), spectral reflectance to assess physiological traits under drought stress (Romero *et al.* 2017), and chlorophyll fluorescence imaging to determine photosynthesis efficiency (Prinzenberg *et al.* 2018). Some of the other techniques used are related to biotic stress, i.e., field phenotyping using RGB imagery from an unmanned aerial vehicle (UAV) (Gibson-Poole *et al.* 2017, Sugiura *et al.* 2016), multispectral imaging from a UAV (Duarte-Carvajalino *et al.* 2018), and imaging with a camera sensor on-the-go (Dammer *et al.* 2016).

The dynamic development of high throughput phenotyping technology is expected to permit broad application to potato crops in the future. For instance, Light Detection and Ranging (LiDAR) estimates aspects of plant growth that are affected by abiotic stress, such as plant height, ground coverage, and biomass, and has already been applied to wheat (Jimenez-Berni *et al.* 2018) and cotton (Sun *et al.* 2018). Field-based phenotyping using mobile multiple imaging sensors, including thermal and hyperspectral sensors, has been developed and successfully used to differentiate plant growth parameters in several wheat cultivars under various growth conditions (Svensgaard *et al.* 2014) and in cotton (Jiang *et al.* 2018).

Exotic genetic resources support abiotic stress tolerance breeding and introgressiomics

Commercial potatoes (*Solanum tuberosum*) are generally sensitive to abiotic stresses. In addition, because of its narrow genetic variation, we need to explore and identify other resources, which has tolerance attributes to improve the traits of cultivated potato against abiotic stresses. Such resources could include exotic cultivated potatoes, landraces or wild relatives of potato. The wild relatives have been examined primarily for biotic (pest and diseases) stress resistance, rather than abiotic stress (Jansky *et al.* 2013, Prohens *et al.* 2017). However, in the case of the potato, many investigations have been done and have provided evidence of abiotic tolerances in the above-mentioned kinds of genetic resources (**Table 4**). For example, *S. acaule* and *S. demissum* have multi-tolerances, and thus could be used to breed a combined-abiotic stress tolerant potato cultivar (Arvin and Donnelly 2008). The polyploid nature of the potato germplasm often inhibits the use of potatoes in breeding work, and therefore we should apply the genetic rules of potatoes to enhance the potential for such applications (Watanabe 2015).

Even though the wild relatives of potato may provide great advantages for improving the traits of potatoes, it remains highly challenging to incorporate the desired traits into cultivated varieties in conventional ways. There are genetic barriers to crossing among them, due to differences in ploidy and the endosperm balance number (EBN) (Hanneman 1999, Jackson and Hanneman 1999, Johnston and Hanneman 1982, Novy and Hanneman 1991). To overcome these barriers, ploidy manipulation, somatic fusion and bridge crossing strategies have been used (Bidani *et al.* 2007, Jansky 2006, Jansky and Hamernik 2009).

Based on the composition of the potato gene pool as described by Bradeen and Haynes (2011), genetic resources that are included in the primary gene pool could be directly utilized by breeders, which would involve cultivated potatoes and landraces (2n = 4x = 48, 4EBN). With some manipulations, sexual crosses could also be made between cultivated potato and wild relatives in the secondary gene pool (2n = 2x = 24, 2EBN, 2n = 4x = 4EBN). On the other hand, for tertiary gene pool species that consist of wild *Solanum* species (2n = 2x = 24, 1EBN), which are sexually isolated from cultivated potato, specific techniques are needed to transfer the target traits into cultivated potato (Watanabe *et al.* 1995).

Various studies have been performed to manipulate the incorporation of desired traits from wild species into cultivated potato. The strategies have included somatic hybridization (Helgeson *et al.* 1998, Symda *et al.* 2013), the use of 2n gametes (Ortiz *et al.* 1997, Watanabe *et al.* 1992), bridge crossing (Yermishin *et al.* 2014, 2017) and gene cloning followed by transformation (Oosumi *et al.* 2009, Song *et al.* 2003), and most of them used for diseases resistance breeding (**Table 5**). From these cases, we can study the possibility of incorporating abiotic stress-tolerance genes from wild relatives into cultivated potatoes.

A new concept, the introgressiomics approach, was proposed relates with using the crop wild relatives (CWRs). This combines hybridization-backcrossing of crops with the wild relatives to generate a number of introgression lines and a genomic approach (Prohens *et al.* 2017). This approach was inspired by the fact that pre-breeding activities are needed to incorporate desired traits from CWRs into commercial varieties, since CWRs cannot be used directly in commercial breeding (Longin and Reif 2014). Conventional pre-breeding work is thought to be ineffective, as it takes a long time before readily for breeder (Sharma *et al.* 2013). The main idea of introgressiomics is to develop introgression generation massively by utilizing CWRs, for future needs (Prohens *et al.* 2017). Because potato wild relatives provide gene resources for abiotic stress-tolerance breeding and various approaches to overcome the crossing barrier between cultivated and wild relatives are available, it is possible to develop a number of potato lines carrying introgressions of genome fragments from wild relatives to answer the needs of abiotic stress breeding. Combined with a genomic approach, in introgressiomic full genome sequencing could be performed on targeted wild relatives to provide functional subsets of germplasm diversity (Warschefsky *et al.* 2014). Then, molecular markers could be used to trace the introgressed fragments from the wild species and characterize the introgressiomics individuals using less time, cost and human resources (Prohens *et al.* 2017).

Status of biotechnology application—transgenic technology

Some landraces and wild species are attributed with abiotic stress tolerances, however, in any cases, they cannot be directly used in a breeding program at the present time; on the other hand, almost daily progress is being made in genomic information. Reflecting on cv. Kufri Surya and Konyu, which were developed using conventional breeding, and

Table 5. Strategies for overcoming the genetic barriers in potato

Strategies	Genetic resources involved	Target traits	References
Somatic hybridization	*S. bulbocastanum* and *S.* × *michoacanum*	late blight resistance	Helgeson *et al.* 1998, Symda *et al.* 2013
	S. tarnii	potato virus Y (PVY), late blight and root knot nematode	Austin *et al.* 1993, Thieme *et al.* 2008
	S. brevidens	tuber soft root and early blight	Austin *et al.* 1986, Tek *et al.* 2004
	S. commersonii	bacterial wilt	Laferriere *et al.* 1999
	S. verrucosum	potato leafroll virus (PLRV)	Carrasco *et al.* 2000
2n gametes	*S. chacoense* and *S. sparsipilum*	bacterial wilt resistance	Watanabe *et al.* 1992
	S. vernei and *S. sparsipilum*	potato cyst nematode	Ortiz *et al.* 1997
Bridge crossing	*S. verrucosum* (as bridging species), *S. bulbocastanum*, *S. pinnatisectum*, *S. polyadenium*, *S. commersonii* and *S. circaeifolium*	–	Yermishin *et al.* 2014, 2017
Gene cloning followed by transformation	*S. bulbocastanum*	late blight resistance gene	Song *et al.* 2003, Oosumi *et al.* 2009

which required 13 and 16 years, respectively, from crossing to release (and note that parental material already existed in these cases) (Iwama 2008, Minhas *et al.* 2006), we need other tools to accelerate the breeding work in cases of complex traits and/or low heritability. Indeed, aside the enhancement difficulty, the sources of eminent tolerances in natural variation are limited or difficult to evaluate based on phenotypic selection. Although numerous genes related to abiotic stress in potato have been identified (Gangadhar *et al.* 2014, Gong *et al.* 2015, Schafleitner *et al.* 2007b, Zhang *et al.* 2017a), many challenges remain before these genes can be efficiently transmitted and effectively utilized.

Genetic engineering by inserting or manipulating desired genes associated with abiotic stresses from other species or organisms into cultivated potatoes is ongoing. **Table 6** reviews the genes that have been identified and used to develop transgenic potatoes. The potential for development of transgenic potato plants tolerant to abiotic stress engenders hope that we will be able to continue planting potatoes even under suboptimal conditions. The aforementioned transgenic

Table 6. Genes and transcription factors related to abiotic stress tolerance in potato

Abiotic stress	Gene	Source	Function	References
Heat	nsLTP1	*S. tuberosum*	Enhance cell membrane integrity under stress conditions Enhance activation of antioxidative defense mechanisms Regulate expression of stress-related genes	Gangadhar *et al.* (2016)
	HSP17.7	*Daucus carota*	Improve membrane stability	Ahn and Zimmerman (2006)
	CuZnSOD; APX; NDPK2	*Manihot esculenta; Pisum sativum; A. thaliana*	Increase levels of the antioxidants superoxide dismutase, ascorbate peroxidase and catalase, which are responsible for ROS scavenging	Kim *et al.* (2010)
	CBF3	*Arabidopsis thaliana*	Induce expression of genes involved in photosynthesis activities and antioxidant defense	Dou *et al.* (2014)
Drought	CBF1	*A. thaliana*	Modulate the abiotic stress-responsive genes expression, maintain high photosynthetic activity	Storani *et al.* (2015)
	DREB 1B	*A. thaliana*	Preserve cell water content	Movahedi *et al.* (2012)
	BZ1	*Capsicum annuum*	ABA-sensitive stomata closure and reduce water loss, up-regulate stress related genes	Moon *et al.* (2015)
	MYB1R-1	*S. tuberosum*	Reduce water loss transcription factor involved in drought-related genes activation	Shin *et al.* (2011)
	BADH	*Spinacia oleracea*	Membrane stabilization	Zhang *et al.* (2011)
	DHAR1	*A. thaliana*	Maintain membrane integrity, protecting chlorophyll against degradation, allowing faster removal of H_2O_2	Eltayeb *et al.* (2011)
	codA	*Arthrobacter globiformis*	Maintain the osmotic equilibrium of cells by inducing glycine betaine production as osmoregulator	Cheng *et al.* (2013a)
Salinity	DREB1	*S. tuberosum*	Activate stress-inducible genes, accumulate proline osmoprotectant	Bouaziz *et al.* (2013)
	DREB1A	*A. thaliana*	Transcription factor involved in abiotic stress-related genes activation	Celebi-toprak *et al.* (2005), Shimazaki *et al.* (2016), Watanabe *et al.* (2011)
	MYB1	*Ipomoea batatas*	Regulate the metabolism of secondary metabolites	Cheng *et al.* (2013b)
	SOD; APX	*Potentilla atrosanguinea; Rheum australe*	Enhance lignin deposition and scavenging capacity	Shafi *et al.* (2017)
	BADH	*Spinacia oleracea*	Membrane stabilization	Zhang *et al.* (2011)
	NHX1	*A. thaliana*	Enhance the capacity of vacuolar compartmentation of extra Na^+	Wang *et al.* (2013)
	DHAR1	*A. thaliana*	Membrane integrity, protect chlorophyll against degradation, allowing faster removal of H_2O_2	Eltayeb *et al.* (2011)

studies employ genes involved in membrane stability, i.e., *nsLTP1*, *HSP17.7*, *BADH*, and *DHAR1*, and other physiological processes, such as *CBF1* (*DREB3A*) and *CBF3* (*DREB1A*), which are involved in photosynthesis activity. Both type of genes play roles in determining plant growth under stress conditions. However, it should be noted that the potato is unique among crops in that the tuber is its main economic value. Therefore, the tolerance of potatoes developed by biotechnology should cover not only the physiological traits, but also the tuber yield parameters, as shown in a potato transgenic line harboring the gene *CaBZ1*, which confers drought-tolerance without sacrificing tuber yield (Moon *et al.* 2015). Continuing the strict transgenic plant assessment, field testing is required to ensure the yield potential. The potato transgenic field assessment conducted by Nichol *et al.* (2015) did not find that any of the transgenic lines showed superior drought resistance.

Status of biotechnology application—genome editing

Genome editing (or gene editing) is another biotechnological tool that could provide an alternative for the creation of potato tolerance to abiotic stress. Unlike transgenic technology, genome editing does not involve genes from a donor, but works precisely at a specific pin-pointed site in the genome. Four important genome editing (or gene editing) technologies are ribonucleic acid interference (RNAi), zinc finger nucleases (ZFNs), transcription activator-like effector nuclease (TALENs); and clustered regularly interspaced short palindromic repeats and CRISPR-associated protein-9 (CRISPR/Cas9) (Zhang *et al.* 2017b). Although work handling with RNAi is the simplest among the other tools, it has a high off-targeting issue (Boettcher and McManus 2015). This technique did lead to an important success story: in 2014, the US Department of Agriculture approved an RNAi product in potato with less bruising and low acrylamide (Waltz 2015). Off-target events also become an issue in ZFN besides the complexity to engineer ZFNs, on other side, it has binding specificity in the genome and high repairing ability (Gupta and Musunuru 2014). TALEN produces fewer off-targeting effects; however, it has a high cost and high complexity of work (Boettcher and McManus 2015). With its simplicity of design, combined with its low cost and less off-targeting effects, CRISPR/Cas9 (Boettcher and McManus 2015, Kadam *et al.* 2018) could be an appropriate tool for supporting plant breeding. The establishment of plant tolerance to abiotic stress using gene editing technologies, particularly CRISPR and CRISPR-associated protein-9 (CRISPR/Cas9), has already been accomplished in some plant species (Kim *et al.* 2018, Osakabe *et al.* 2016, Shi *et al.* 2017). In the potato itself, genome editing is also being studied even though this work does not yet involve the adaptation to environmental stresses (**Table 7**). Those studies focused on herbicide resistance, as well as tuber quality traits, by employing CRISPR-Cas9 and TALENs. For example, Andersson *et al.* (2017, 2018) developed mutated lines which are high in amylopectin starch content by knocking-out the Granule-Bound Starch Synthase (GBSS) gene using a CRISPR-Cas9 technique. By utilizing the information of genes related to abiotic stress, gene editing technology may also contribute to the breeding of abiotic stress-tolerant potatoes. Moreover, candidate genes for tuberization have been reviewed (Dutt *et al.* 2017), such as *StSP6A*, *StPOTH1*, *StBEL5*, etc. We need to have sufficient information on the response of these genes to abiotic stress, both singularly and when combined. Then, the integrative molecular work between many genes involved in cellular, physiological and tuberization processes might be gradually harnessed to achieve a broad portfolio of stress tolerance.

Table 7. Study of genome editing (or gene editing) in potato

Tool	Trait	Gene target	References
CRISPR-Cas9	High amylopectin content (waxy potato)	granule bound starch synthase (GBSS)	Andersson *et al.* (2017)
CRISPR-Cas9 RNP	High amylopectin content (waxy potato)	granule bound starch synthase (GBSS)	Andersson *et al.* (2018)
CRISPR-Cas9	Steroidalglycoalkaloids (SGAs) free	St16DOX	Nakayasu *et al.* (2018)
TALENs	Reducing sugar and acrylamide levels in cold-stored Processing quality in the cold storage	vacuolar invertase gene (*VInv*)	Clasen *et al.* (2016)
TALENs	No data	1,4-alpha-glucan branching enzyme (SBE1) gene StvacINV2	Ma *et al.* (2017)
TALENs	Herbicide resistance	acetolactate synthase gene (ALS)	Forsyth *et al.* (2016), Nicolia *et al.* (2015)
TALEN and CRISPR-Cas9	Herbicide resistance	StALS1	Butler *et al.* (2016)
RNAi	Less bruising and browning; lower acrylamide	Polyphenol oxidase-5 (PPO5); Asparagine synthetase-1 (Asn1)	Waltz *et al.* (2015)

Abiotic stress and transcriptomics, proteomics and metabolomics studies in potato

Because abiotic stress tolerance is multi-genic, the development of abiotic tolerant potato varieties, either with traditional breeding or genetic engineering approach, will require a basic understanding of the physiology, biochemical and molecular responses to each stress (Hancock *et al.* 2014). Thus, comprehensive information from integrated studies will be needed to develop cultivars tolerant to abiotic stress. Environmental stress affects the alteration of transcriptomics and proteomics in plants (Batista *et al.* 2017), as well as secondary metabolites (Yang *et al.* 2018). Understanding such alterations will be key to revealing how plants respond to and tolerate abiotic stress.

Transcriptomic studies in potato have identified a number of abiotic stress-related genes, providing new candidate genes for future studies of abiotic stress responses in potato (Gong *et al.* 2015, Pieczynski *et al.* 2018, Resink *et al.* 2005). Analysis using potato genotypes with contrasting heat-tolerance revealed that genes associated with photosynthesis, hormonal activity, sugar transportation and transcription factors were expressed differentially (Singh *et al.* 2015). Recently, Sprenger *et al.* (2018) proposed twenty transcripts as drought-tolerance markers, with the transcript annotated as glucosyl transferase being the most important. Knowledge regarding these gene functions can be used to generate potato cultivars that are tolerant to unfavorable conditions. Following the transcription factor, proteins, as the product of gene expression, have the important role of defining the plant response to abiotic stress. As studied by Aghaei *et al.* (2008b), up-regulation of some defense-associated proteins (e.g. osmotine-like protein, TSI-1 protein, heat-shock protein and calreticulin) and novel proteins could be considered involved in salt stress tolerance of potato plants. On the other hand, the metabolic features that explain variation of yield under stress condition also become a strong instrument in breeding program to abiotic stress tolerance (Evers *et al.* 2010). Various secondary metabolites are known to be increased in response to drought stress, such as galactose, inositol, galactinol, proline and proline analogues (Evers *et al.* 2010), and a number of drought-tolerance metabolite markers have also been proposed, such as ribitol, arbutin (4-hydroxyphenyl-b-D-glucopyranoside), dopamine and tyramine (Sprenger *et al.* 2018).

Conclusion and future perspectives

Potatoes are one of the world's main food crops, and their production is threatened by abiotic stress, which in turn is exacerbated by global warming. Various cultivation techniques have been applied to reduce the negative impact of abiotic stress on potato yield. To apply the available cultivation techniques effectively and precisely, potato growers should adopt precision agriculture in their field. Setting the planting time is helpful in relation to the abiotic stress period in the field. Potato growers can rely on weather forecasts to decide the proper time to start planting, avoiding periods of low humidity and/or high temperature during plant growth. In addition, various environmental conditions could be monitored by drone during plant growth, such as air temperature, soil temperature, soil moisture, and soil nutrient status. The growers could then refer to this collective database to decide the timing of the appropriate action, such as irrigation, fertilization or mulching.

In addition to good cultivation techniques, potato cultivars with stable tolerance to abiotic stress must be planted in order to ensure high production. Various traits correlated to abiotic stress have been evaluated and utilized as selection markers in the breeding process, including both morphological and physiological traits. Physiological variables have been widely used to distinguish tolerant genotypes from those susceptible to a water-deficit condition—e.g., analyses have been performed based on gas exchange variables, photosynthetic rate values, mesophyll conductance, relative water content, and chlorophyll content. However, these approaches were used to examine only a single stress condition (drought, heat, or salinity stress), and in some cases they would not work for the assessment of a combination of abiotic stresses.

Phenotyping plays an important role in breeding work. High-throughput phenotyping provides phenotype datasets that can be integrated with genotyping data and utilized in the breeding process. However, phenotyping with digitalizing study remains some crucial traits related to abiotic stress in potato. Root architecture is highly correlated with drought tolerance in potato (Deguchi *et al.* 2010, Lahlou and Ledent 2005, Wishart *et al.* 2014). Because the roots are underground, root phenotyping by destructive sampling is laborious and not reliable for a large number of accessions. RGB imaging and hyperspectral imaging could be useful for potato root phenotyping, as this method was developed and practiced on other species (Bodner *et al.* 2017, 2018). Measurement of water use efficiency, another main trait related to drought stress, could be done by multispectral drone imaging (Thorp *et al.* 2018).

Wild relatives provide us gene resources for abiotic stress tolerance, although there are some obstacles to their direct use in breeding programs. An introgressiomic approach provides a great opportunity to utilize wild relative in abiotic stress-tolerant breeding. Here, genomics is incorporated in some of the steps, from identifying the wild relatives and selecting the backcross cycle till introgressiomics population. Anticipating the dynamic plant breeding needs that are highly influenced by environmental changes, we will require large amounts of breeding material availability that can be directly used for the development of tolerant varieties. For this challenge, introgressiomics approach would be reliable.

Genetic engineering studies on abiotic stresses in potato plants continue to develop, either by transgenic or genome editing techniques. One important problem is that a potato plant may exhibit good tolerance to an abiotic stress, on the other hand tuber production has not been noticed. In the future, it will be important to consider gene stacking, so that not only genes that contribute to abiotic stress tolerance physiologically, but also those that promote tuber yield might be adopted simultaneously. In addition, advances in omics studies will provide us with various biological markers to be used in the potato breeding program, such as genes and metabolites related to abiotic stress. Such markers could be applied either singly or in combination.

Recommendations

The use of appropriate cultivation techniques and a tolerant cultivar will greatly determine the sustainability of potato production under abiotic stress. To practice proper cultivation, potato producers could be assisted by precision agriculture through the support of many high throughput phenotyping techniques; such technologies may first be supported by public institutions on an experimental basis and then later developed as commercial services. This is needed to ensure that every cultivation action is carried out exactly on the right target, at the right time, using the right dose, and that it is used optimally by the crop plant. For example, the irrigation of potato fields (with respect to time, block, and volume) should be carried out based on the results of monitoring of soil moisture levels and plant physiological responses, through satellite imagery or soil and plant analysis tools affixed to an unmanned aerial vehicle. On the other hand, abiotic stress-tolerant cultivar development needs to be accelerated by utilizing biotechnology tools on a wide range of potato genetic resources. Introgressiomics is a more acceptable approach than genetic engineering, particularly in relation to transgenic issues in many countries, by incorporating markers evaluated by transcriptomics, proteomics, and metabolomics approach and engaging high throughput phenotyping in certain steps.

Author Contribution Statement

T. Handayani assembled and analyzed the supporting information and wrote a major part of the manuscript. S. A. Gilani verified the assembled information and edited the manuscript. K. N. Watanabe planned the review, collected major information and finalized the manuscript.

Acknowledgments

This paper was made in part by the support of Plant Transgenic Design Initiative, Tsukuba Plant Innovation Research Center, University of Tsukuba, Japan.

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