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
and rice based on food supply quantity (FAO 2019a). Potato is a staple food with wide agro-climatic zones, a harvesting area of over 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.
Climate change and potatoes

**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 thermos- 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 greenhouse, and in the field. For the drought stress screening and evaluation, either Polyvitro). Basically, screening methods have been conducted under three environmental conditions: in vitro, in a growth chamber or greenhouse, and in the field. For the drought stress screening and evaluation, either Poly

| 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), Hassapanah (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 these traits can be used to assist in the process of heat-tolerance breeding. To develop a heat-tolerant potato, at least three physiological processes need to be considered: photosynthetic efficiency and haulm growth, tuber initiation, and photosynthetic 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, Zarzynska 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 1980). 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

| 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 | Coleman (2008) |
|               | Low transpiration rate | Rudack et al. (2017) |
|               | High WUE | Ahmadi et al. (2017), Iwama (2008), Wishart et al. (2014) |
|               | High cell membrane stability | Ahmadi et al. (2017), Iwama (2008), Wishart et al. (2014) |
|               | 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 | Schafleitner et al. (2007a) |
| Salinity      | Growth index | Shaterian et al. (2008) |
|               | Root growth | Mushedy et al. (2015) |
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).

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) | Hetherington et al. (1983) | High dry matter content |
|                | *S. phureja* (2x, 2 EBN) | Vacher (1998) | High chlorophyll fluorescence |
| Drought        | *S. juzepczukii* (3x)     | Coleman (2008) | Membrane stability |
|                | *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) | Arvin and Donnelly (2008), Daneshmand et al. (2010) | Membrane stability |
|                | *S. demissum* (6x, 4 EBN) | Midmore and Prange (1991) | High PS II activity |

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 (Ramirez 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 (UVAGibson-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 introgression**

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, Nový and Hanneman 1991). To overcome these barriers, ploidy manipulation, somatic fusion and bridge crossing strategies have been used (Bidani et al. 2007, Jansky and Hamernik 2009).

Based on the composition of the potato gene pool as described by Braden 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 introgressomics 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 introgressomics 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 introgressiomc 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 introgressomics individuals using less time, cost and human resources (Prohens et al. 2017).

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. barnii                                                                               | 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. circraefolium | –                                                          | Yermishin et al. 2014, 2017     |
| Gene cloning followed by    | S. bulbocastanum                                                                       | late blight resistance gene                                | Song et al. 2003, Oosumi et al. 2009 |

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
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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 | Gangadhar et al. (2016) |
|               |      |         | Enhance activation of antioxidative defense mechanisms | |
|               |      |         | Regulate expression of stress-related genes | |
|               | HSP17.7 | *Daucus carota* | Improve membrane stability | Ahn and Zimmerman (2006) |
| 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 H2O2 | 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 atroruginae*; *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 H2O2 | Eltayeb et al. (2011) |
studies employ genes involved in membrane stability, i.e., \textit{nsLTP1}, \textit{HSP17.7}, \textit{BADH}, and \textit{DHAR1}, and other physiological processes, such as \textit{CBF1} (\textit{DREB3A}) and \textit{CBF3} (\textit{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 \textit{CaBZI}, 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 ribonuclease 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 \textit{SiSP6A}, \textit{StPOTH1}, \textit{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 (\textit{VInv}) | Clasen et al. (2016)       |
| TALENs                | No data                            | 1,4-alpha-glucan branching enzyme (SBE1) gene \textit{StvacINV2} | Ma et al. (2017)            |
| TALENs                | Herbicide resistance               | acetolactate synthase gene (ALS)           | Forsyth et al. (2016), Nicolaia et al. (2015) |
| TALEN and CRISPR-Cas9 | Herbicide resistance               | \textit{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 introgressomic 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 introgressomics 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, introgressomics 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. Introgroessomics 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.

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