

**Climate change and consequences for potato production: A review of tolerance to emerging abiotic stress**

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## Abstract

Potato is a major global crop that has an important role to play in food security, reducing poverty and improving human nutrition. Enhanced atmospheric CO<sub>2</sub> concentrations provide an opportunity to increase potato yields in the future, but this will only be possible if the potato crop can cope with the other consequences of climate change caused by this rise in CO<sub>2</sub>. While climate change may impact biotic stress either positively or negatively, abiotic stresses are likely to be greatly increased and become a major threat to potato production. Increasing heat, drought and salinity stress will drive the need for greater understanding of genes, traits and management techniques that allow potato to cope with these stresses. In this review we identify some of the key physiological and molecular adaptations of potato to these stresses and propose an ideotype which should include 1) optimal stomatal regulation to balance water loss and heat stress in leaves, 2) production of metabolites and transporters to scavenge reactive oxygen species and partition toxic elements, 3) enhanced root systems to maximise water capture, 4) maintenance of tuberisation under stress conditions and 5) stress avoidance by accelerating crop development and reducing time to yield. We discuss potential ways to achieve this ideotype, emphasising the need to benefit from genetic diversity in landrace and wild material by screening for traits in combined stress environments appropriate to future agroecosystems.

**Keywords:** Heat, drought, salinity, root:shoot signalling, maintaining photosynthesis, roots

## Introduction

Potato (*Solanum tuberosum* L.) is an important global food source and the world's most important non grain food crop (FAO, 2009). Potato is the world's third largest food crop with 383 million tonnes produced per annum (FAOSTAT 2014, Dreyer et al. 2017; Goyer et al. 2017). It is grown on 19 million ha worldwide (FAOSTAT 2014) and China and India are responsible for over a third of the total world potato production (FAO 2009), while the greatest average yields are achieved in North America at 43.7 t ha<sup>-1</sup>. While potato is often cultivated in large scale commercial enterprises, it is also cultivated in remote, high elevation areas on marginal soils by resource-poor farmers with limited access to inputs (Scott 1985). In these regions, it contributes greatly to dietary daily energy intake (Scott et al. 2000) and is a staple for these communities (Thiele et al. 2010). Potato is also becoming more popular in rainfed agriculture as it can produce many more calories per volume of water used, producing around twice as many calories as cereals for the same water used (Monneveux et al. 2013). Moreover, since potato is traded locally, not on global commodity markets, it is a good candidate to contribute to regional food security and poverty reduction.

Potato was domesticated over 7000 years ago in South America (Hawkes 1992), where it was cultivated at moderately high altitudes in regions characterized by short day length, high light intensity, cool temperatures and relatively high humidity. Introduction to Europe and breeding for greater tuber yields under longer day lengths led to the development of what is today termed the Irish potato, which became the staple food source for many Europeans (de Ferrière le Vayer 2017). The long days and moderate temperatures of the temperate regions of Europe allowed longer periods of photosynthesis, efficient translocation of assimilates from haulm to tubers and low transpiration rates during the cool nights, turning the potato into a high-yielding crop. From Europe, the potato then spread to much of the rest of the world during the 18th and 19th centuries, including substantial tropical and subtropical production over the last few decades (Simmonds 1971; International Potato Center 1984; de Ferrière le Vayer 2017). Potato is now grown in approximately 150 countries from latitudes 69°N to 50°S all the way from sea level to 4000 m altitude (Hijmans 2001). This spread suggests that potato is either a particularly adaptable crop or that in most places it is grown under sub-optimal conditions. Climate change is likely to make these conditions less optimal or shift the zone of optimal conditions from geographical regions where agriculture is optimized for potato growth to regions where it is not. Thus some regions are likely to see improvements in the yield and sustainability of potato crops while in others they are likely to decline (reviewed in Raymundo et al. 2014).

This review aims to discuss the potential for maximising climate change benefits: from increased CO<sub>2</sub> concentrations and extension of the productivity range for potatoes due to climate change, by mitigating the impacts of increased abiotic stress that also come with climate change. We emphasize how improved genotypes

could achieve this if the interactions between different, co-occurring stresses are better understood, and describe an ideotype for future production systems.

### **Impacts of abiotic stress on potato production and quality in current climates**

Where potato is grown in summer, heat and drought stress are critical and will tend to occur at the end of the growing season when tuber bulking occurs. In such situations, insufficient water likely limits yield (Harris 1978; Burton 1981; van Loon 1981), requiring irrigation to maintain production. As potato production increasingly moves more into arid regions with high day and night temperatures combined with a comparatively dry atmosphere, irrigation is essential for successful cropping. However, irrigated agriculture, enhances salinity due to rising saline water tables (Rhoades et al. 1992). Developing crops with increased heat, drought and salt tolerance is important to cope with these prevalent conditions.

Potato is particularly susceptible to both drought (Monneveux et al. 2013) and heat (Levy and Veilleux 2007). Drought susceptibility of potato has been mainly attributed to an inability to capture water due to a shallow root system and an inability of the photosynthetic machinery to recover following water and heat stress (Iwama and Yamaguchi 2006). Drought on its own decreases plant growth (Deblonde and Ledent 2001), shortens the growth cycle (Kumar et al. 2007), and reduces the number (Eiasu et al. 2007) and size (Schafleitner et al. 2007) of tubers. The timing, duration, and severity of the stress (Jeffery 1995; Schafleitner 2009) dictate the magnitude of drought effects and are most critical to final yield at emergence and tuberization (Martínez and Moreno 1992). Often occurring with drought, heat stress also critically affects potato production (Gregory 1965; Slater 1968, Ahn et al. 2004). Moderate soils temperatures, greater than 18°C, substantially reduce tuber yield. Heat stress creates imbalances in source-sink relations, delays tuber initiation and bulking, and causes quality issues such as malformation and necrosis of tubers (Levy and Veilleux 2007). The ability to tolerate heat stress is not only important to cope with climate change effects, but also for further development of potato production in regions marginal to potato production such as subtropical India (Gaur and Pandey 2000), the semi-arid Middle East (Levy et al. 2001), and the tropics (Minhas et al. 2011) including Sub-Saharan Africa (Asfaw et al. 2015).

General information regarding optimal conditions for heat, drought and salinity for growth, yield and quality parameters and the effect of shifts outside these optimal conditions on yield and quality are reviewed in Table 1, along with information on some of the key physiological and molecular adaptations of potato to changes in these environmental conditions. The key observations are 1) the environmental conditions of heat, water availability and salinity do not have to be particularly extreme to affect potato detrimentally and could be experienced in most of the world's potato growing regions; 2) potato yield and quality are particularly affected at the tuberization stage; 3) all abiotic stresses have major impacts on production and quality by affecting photosynthesis, which should be maintained to sustain marketable yields 4) many physiological and some molecular responses are common between all three environmental stresses, so a universal stress response could be harnessed; 5) some of the stress responses to individual abiotic conditions are unique and may exacerbate the effects of other stresses; and 6) many of the stresses will interact in the field and plants may experience heat, drought and salinity stress at the same moment in space and time along with a range of other stresses including biotic stress and nutrient stress. We examine some of these issues in more detail in later sections, but it is clear that producing a new adapted genotype for abiotic stress requires an understanding of plant physiological and molecular adaptations to multiple stress environments.

### **Potential effects of climate change on potato production**

Climate change is predicted to increase global average temperature by between 1 to 7 °C by the end of this century, with impacts on global weather patterns and precipitation (IPCC 2007 a,b). Climate change is expected to increase the frequency of drought events in many regions, affecting drought susceptible crops like potato (Schafleitner et al. 2011; Simelton et al. 2012). This is likely to affect potato yields, but could also affect tuber quality by reducing dry matter and increasing reducing sugar concentration (Haverkort and Verhagen 2008). Increasing temperatures also enhance crop water demand, which along with changing rainfall patterns, will lead to greater potential for periods of critical drought to the crop. Notwithstanding this, increasing temperature is likely to have the largest

impacts on potato production as the current regions of production are those with the largest predicted increases in temperature (Schafleitner et al. 2011). At high latitudes, the increasing temperatures are likely to alleviate the limiting impact of minimum temperature for growth, while increases maximum temperatures above optimal levels for growth will limit yields in subtropical regions, although the mitigating effects of elevated CO<sub>2</sub> are usually not considered. Globally, the average expected change in potato production due to climate change is positive (+1.3%), but these gains will occur in places where the yield of crop is constrained by minimum temperature (Schafleitner et al. 2011) and there will be extreme losses in production in other regions.

From their analysis, Schafleitner et al. (2011) predict that the most significant losses in suitability of land for potato production occur in tropical highlands and in southern Africa. Likewise, India, currently the second largest producer of potato in the world after China, is likely to suffer adverse impacts of climate change causing losses in yields of 11% by 2080 (Naresh Kumar et al. 2015). The predicted impact of climate change on potato production in South Africa and India likely differs in different regions of the country with some areas having large losses in yield and others having marginal gains (Franke et al. 2013, Naresh Kumar et al. 2015). The reaction to climate change in South Africa is predicted to lead to increased planting in the cool winter season and increased planting earlier in the summer season (Franke et al. 2013). In India, the potential benefits of improved abiotic stress tolerance were evaluated, and genotypes with improved heat tolerance would allow 15.5 million new hectares of productive land, while improved cold tolerance would increase growing area by 8.7 million hectares (Naresh Kumar et al. 2015). Enhanced drought tolerance would have a smaller effect, opening up only 2.8 million hectares with much of this overlapping with areas that would benefit from heat tolerance (Schafleitner et al. 2011).

As well as changing the incidence and severity of abiotic stresses, climate change will also affect pest and disease incidence, with the numbers of beneficial organisms, insect pests and pathogens being influenced by changes in temperature, relative humidity and soil water availability. These interactions between abiotic and biotic stress will have severe implications on crop yield and quality (Newton et al. 2011). However, many of the impacts of climate change on pest and pathogens and vectors of those diseases are likely to be beneficial. Many biotic stress vectors will be negatively affected by climate change (temperature and drought) in their current range, for example late blight (Gaucher et al. 2017; van der Waals et al. 2013), aphids (Kruger et al. 2017) and rhizoctonia (Bouček-Mechiche et al. 2017) in France, South Africa and Algeria, respectively. However, other diseases/pathogens will become more prevalent such as soft rot, black leg and root-knot nematode in South Africa (van der Waals et al. 2013). Regardless of the impact on biotic stresses in their current range, climate change is also likely to open up new geographical regions where it is optimal for potato growth and for these pests and pathogens, assuming they are able and allowed to move into these zones. Therefore, on balance there may be little change in the impact of these biotic factors with climate change. Notwithstanding this, the perceived threat to potato production following climate change will be dependent on in which region the production occurs, as it is known that the relative perception of risk associated with abiotic and biotic stress is different in different environments (van der Waals et al. 2016).

### ***CO<sub>2</sub> fertilisation and other potential benefits of climate change***

Since the middle of 20<sup>th</sup> century, concentrations of atmospheric CO<sub>2</sub> have increased from 318 to 395 µmol mol<sup>-1</sup> and, depending on anthropogenic emission rates, are predicted to exceed 1000 µmol mol<sup>-1</sup> by the end of this century (Ziska et al. 2012). Importantly, increased CO<sub>2</sub> concentrations have the potential to enhance yield (Fleisher et al. 2008a), because most crop species (i.e. those with the C<sub>3</sub> photosynthetic pathway) currently lack optimal levels of CO<sub>2</sub> for photosynthesis. As a C<sub>3</sub> plant, potato is likely to benefit from greater atmospheric CO<sub>2</sub> concentrations through yield stimulation, improved resource use efficiency, more successful competition with C<sub>4</sub> weeds, and in some cases better pest and disease resistance (Fuhrer 2003). However, many of these benefits may be lost due to interactions with a range of other biotic and abiotic stresses that will be altered with climate change. Moreover, to fully benefit from elevated CO<sub>2</sub> levels, since the requirement for mineral elements for key metabolic processes is increased by enhanced carbon fixation, future potato genotypes may need to better acquire nutrients or be tolerant of mineral nutrient deficiency.

Temperature, along with day length, is a major determinant of the rate of development of plants including potatoes. Under climate change scenarios, warmer temperatures will shorten the development time and time to flowering of determinant crops and potentially reduce yield (Craufurd and Wheeler 2009). In fact, earlier flowering and maturity has been documented in recent decades and this has been associated with warmer springs (Menzel et al 2006; Estrella et al. 2007). In potato, warming of the atmospheric and soil ambient temperature in Scotland has led to earlier emergence and canopy closure increasing the growing period in the Scottish crop by almost 4 days in the north of the crop growing region and has translated to an increase in yield of 2.8t ha<sup>-1</sup> decade<sup>-1</sup> since the 1960's (Gregory and Marshall 2012). This benefit may also be threatened by greater abiotic stress.

Thus, for potato to take advantage of the potential benefits of elevated CO<sub>2</sub> and more amenable climate for crop development, it is paramount that future genotypes have the ability to cope with the range of abiotic and biotic stress predicted in future agricultural systems.

### **Manifestation of climate change in changed abiotic stresses**

As plants are sessile, they cannot escape stress, so they must adapt to abiotic stresses to survive (Atkinson and Urwin 2012). Many annual plants align their development cycle with environmentally favourable seasons, while perennial plants will either invest in year round protection from abiotic stress or become dormant and protect meristematic tissue to avoid the seasonal stresses. Abiotic stresses tend to be related to seasonality and seasonal fluctuations in temperature, water availability and irradiance or through impacts of the underlying geology and soil type, such as nutrient deficiencies and salinity. As already discussed, some of these stresses will be directly affected by climate change, including those associated with temperature and precipitation patterns, while others will be affected indirectly such as irradiance, salinity and availability of mineral elements.

### ***Impacts of elevated heat stress on potato***

As a cool temperate climate adapted species, elevated temperature affects multiple processes in potato plant physiology. Tuber development is sensitive to elevated temperature since the tuberization signal is inhibited at higher temperatures (Ewing 1981; Hancock et al. 2014). Carbon transport to sink organs in the potato plant is temperature-sensitive, with less assimilated carbon incorporated into starch in the tuber at elevated temperature (Wolf et al. 1991). This causes accumulation of sucrose at the phloem unloading sites, thus reducing sucrose transport to the tuber thereby decreasing sink strength. Excessive temperatures decrease photosynthetic performance, with heat sensitive tuber-bearing *Solanum* species exhibiting more severe inhibition of CO<sub>2</sub> fixation and chlorophyll loss than heat tolerant species (Reynolds et al. 1990). High temperature causes several tuber disorders, including irregular tuber shape, chain tuberization or secondary tuber formation (often associated with excessive stolon elongation and branching). Additionally, elevated temperature is related to negative impacts on potato skin finish (Moletberg 2017). Elevated temperatures of tubers at tuber filling had large impacts on the regulation of genes involved in the anthocyanin and steroidal glykoalkaloid pathways in the phelloderm (tissue just below the skin) of red-skinned potatoes. The reduced accumulation of anthocyanins observed may diminish the relative human health value of tubers produced (Ginzberg et al. 2017). Additionally, high temperatures during tuber maturation impact on tuber dormancy and can result in pre-harvest sprouting. Thus there is a complex array of heat stress responses that may impact on overall tuber yield and quality. Wide variation in heat tolerance has been identified in screening potato germplasm (reviewed in Levy and Veilleux 2007), but heat tolerant ideotypes should not only maintain yield, but also aesthetic and processing quality and nutritional and health promoting qualities.

Recently a tuberization signal has been shown to be an orthologue of the Arabidopsis protein FLOWERING LOCUS T (FT) termed StSP6A (Navarro et al. 2011). At elevated temperature, when tuberization is inhibited, StSP6A transcript level declines (Morris et al., 2014). The mechanism of regulation of StSp6A is complex, involving interactions with circadian clock components and the light receptor pathway. It is now clear that the phytochrome B photoreceptor also functions as a temperature sensor integrating light and temperature signals (Legris et al. 2016; Jung et al. 2016). Phytochrome B exists as dimers in inactive Pr and active Pfr forms. Red light drives the conversion of Pr to Pfr, whereas far-red light converts it back. Pfr can also be converted to Pr in the dark by a light independent thermal reversion process. The dark-reversion light independent reaction was also

shown to be accelerated by elevated temperature. Thus, in the dark, the amount of active Pfr is temperature dependent. Downstream of PhyB, two interconnected signalling networks have been shown to operate in the control of plant growth; the PHYTOCHROME INTERACTING FACTOR 4 branch and another branch involving CONSTITUTIVE PHOTOMORPHOGENESIS 1 and ELONGATED HYPOCOTYL 5 (reviewed in Legris et al. 2017). These signalling networks exert major control over many processes in plant development and are likely involved in regulating tuberization. However, as pointed out by Ewing (1981), heat tolerance requires vigorous shoot growth, indicating the ability to produce biomass at high temperatures as well as the ability to tuberize. Heat shock proteins may protect shoot growth at high temperatures (Trapero-Mozos et al. 2017). Recently, allelic variation of *HSc70* corresponding to heat tolerance was demonstrated, and *HSc70* expression level identified as a significant factor influencing tuber yield stability under moderately elevated temperature. The potential for specific allelic variants of *HSc70* for the induction of thermotolerance via conventional introgression or molecular breeding approaches has been discussed (Trapero-Mozos et al. 2017).

### ***Impacts of drought on potato***

Soil drying alters the potato root system morphologically (Wishart et al. 2013, 2014) including increased lateral root proliferation, decreased root elongation, increased root thickness and the production of root hairs that maintain root-soil contact in soil which shrinks away from roots during drying (Schmidt et al. 2012; Haling et al. 2013). Additionally, greater hydraulic resistance of the root system related to smaller xylem vessels increases drought tolerance of plants by decreasing the rate of extraction of water from the soil without rapidly reducing the amount of available water. Hydraulic conductivity varies along the root according to tissue age and among root types (Doussan et al. 1998) and can be controlled by cell membrane permeability and aquaporin expression. Soil drying initially increases root hydraulic conductivity (to maintain water uptake), but continued water extraction later decreases root hydraulic conductivity (to prevent losses to the soil) and these changes are ascribed to aquaporin activity and regulation (Maurel et al. 2010). In the long term, root hydraulic conductivity is further decreased by increased suberization of root endodermis/exodermis (Vandeleur and Mayo 2009). After longer periods of drought, root hydraulic conductivity can be further reduced in the plant by xylem embolism, a process by which air enters the xylem vessels interrupting the sap flow (Cruziat and Cochard 2002).

Bigger root systems in potato genotypes, particularly those roots associated with stolons, lead to better ability to cope with drought and allow maintenance of yield under drought conditions (Wishart et al. 2013, 2014; Puertolas et al. 2014). Interestingly, genotypes with bigger roots systems also achieved quicker canopy closure, which will extend the duration of maximal photosynthetic potential and more rapidly reduce the amount of water lost from the soil by evaporation rather than transpiration through the plant. It has been suggested that breeding for greater numbers of seminal roots, root hair length, and increased root hydraulic resistance is possible (Bengough et al. 2011). Recent observations also point to a rhizospheric effect on the water relations at the soil-root interface of mucilages, root exudates and possibly solute accumulation (Stirzaker and Passioura 1996; Read et al. 2003; McCully et al. 2009; Carminati and Vetterlein, 2013), which would modulate soil-root contact, soil physical conditions and water uptake with variations in dry or moist soil (White and Kirkegaard, 2010; Koebernick et al. 2017).

Plant roots are also postulated to detect soil drying biochemically, stimulating synthesis of the phytohormone ABA, which can be transported in the xylem to the shoot to inhibit leaf expansion and induce stomatal closure (Dodd 2005). More recently, this root-sourced ABA paradigm has been challenged, with reciprocal grafting experiments between ABA-deficient mutants and wild-type plants revealing that the shoot genotype regulates root ABA concentration (McAdam et al. 2016). Irrespective of the ABA source, soil moisture gradients (that typically occur due to vertical gradients in root length density and thus water uptake) induce pronounced spatial variation in root ABA concentration (Puertolas et al. 2015). When the entire root system is allowed to dry the soil in containerized plants, increased xylem ABA concentration precedes any change in leaf water relations and coincides with partial stomatal closure (Liu et al. 2005). Although xylem ABA concentration was inversely correlated with stomatal conductance (Liu et al. 2005; Puertolas et al. 2014), it is uncertain whether there is sufficient ABA in the xylem sap to initiate stomatal closure, or whether hydraulic signals such as decreased leaf turgor are also important.

Decreased transpiration rates in response to drying soil may also be induced by decreased stomatal density (Yan et al. 2012; Sun et al. 2014). Drought resistant varieties have around five times fewer stomata in the upper surface of the leaf than drought sensitive varieties and also larger root systems (Boguszewska-Mankowska et al. 2017). Drought resistant varieties were also more heat-resistant, despite their diminished transpirational cooling. This, along with the maintenance of chlorophyll fluorescence in the resistant varieties under stress, suggests that they are able to counteract the production of detrimental metabolites and reactive oxygen species (ROS) more effectively.

### ***Impacts of greater salinity on potato***

Salinity increases the osmotic pressure of soil pore water restricting root water uptake and adversely affects soil structure, reducing water infiltration, soil aeration and oxygen supply to the roots. Greater uptake of some elements associated with salinity such as sodium, chloride and boron induces toxicity (Levy and Veilleux 2007). Genetic variation in salinity tolerance tends to correlate with the ability to cope with drought, or at least ephemeral availability of water through irrigation with often scarce and poor quality (i.e. brackish) irrigation water. Thus potatoes must be able to cope with drought and reduced transpiration leading to greater heat stress, by limiting the impact of these stresses on photosynthesis. In addition, salinity tolerant genotypes must cope with ion toxicity in the form of elevated sodium and boron concentrations and general nutrient imbalances (Koyro et al. 2012). One of the key consequences of salinity is severe osmotic stress in the tissues leading to detrimental changes in cellular function, that impair amino acid synthesis, protein metabolism, respiration and photosynthesis (Koyro et al. 2012). These effects can be counteracted by the producing osmoprotectants including proline and glycine betaine, which enhance osmotic adjustment and act as chaperones to proteins preventing their denaturation (Rontein et al. 2002; Koyro et al. 2012). Another consequence of the combined impact of salinity and drought is reduced CO<sub>2</sub> assimilation, enhancing the production of ROS which are extremely damaging to nucleic acids, lipids and proteins (Huchzemeyer and Koyro 2005; Koyro et al. 2012). Plants counter the effects of ROS by producing antioxidants including compounds and specific enzymes (Blokhina et al. 2003) such as glutathione, superoxide dismutase and catalase.

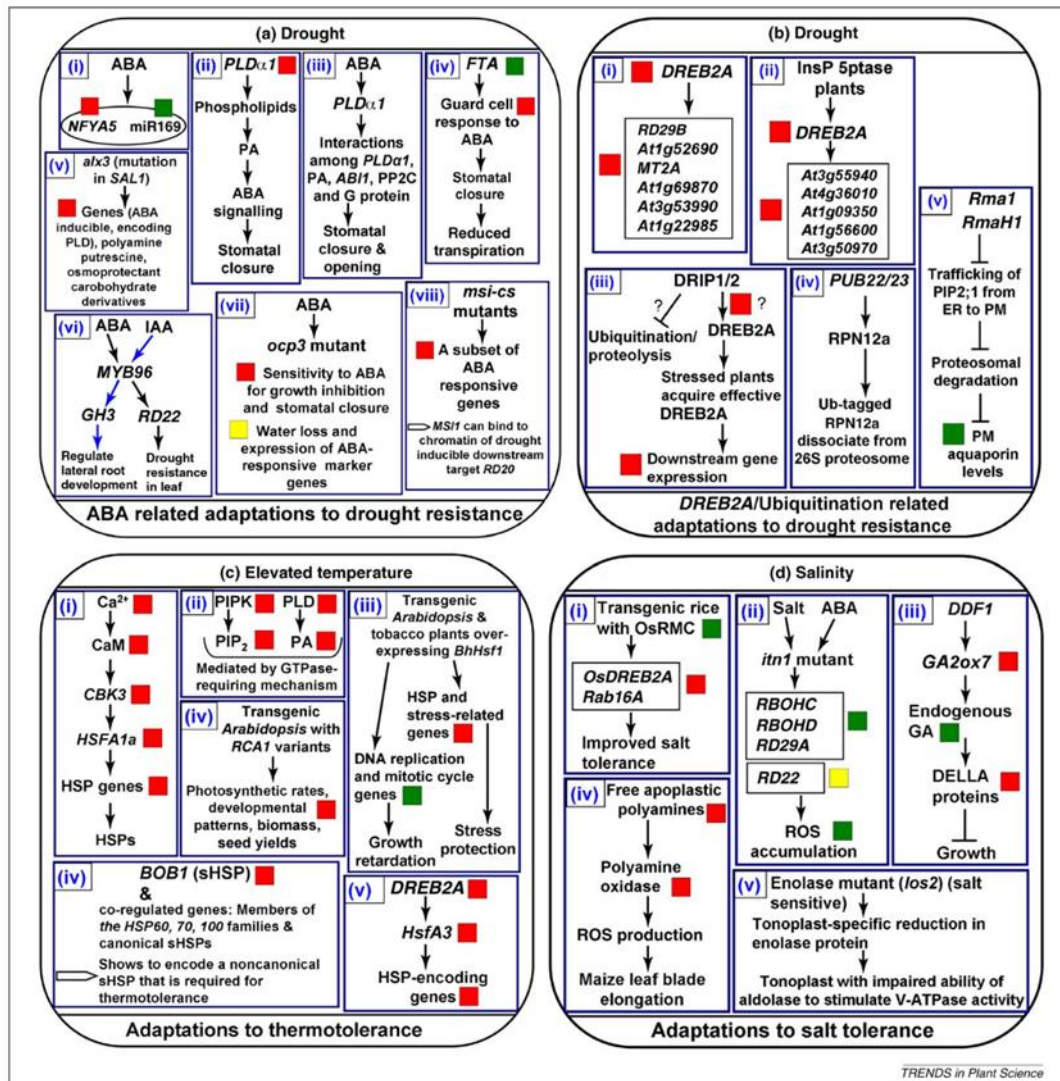
Another way for plants to cope with saline environments is to avoid taking up the toxic ions in the first place, through a range of root related traits including down-regulation of membrane transporters, or by removing the ions from the functional part of the cells once taken up by up-regulating ion specific transporters at the tonoplast and shunting the toxic elements to the vacuole (Munns and Tester 2008; Querios et al. 2009; Munns et al. 2012). Salt-tolerant and salt-sensitive varieties showed pronounced differences in Na<sup>+</sup> homeostasis, with tolerant cultivars accumulating Na<sup>+</sup> in the stem thereby reducing foliar Na levels (Jaarsma et al. 2013). Many of the negative impacts of salinity, particularly those associated with the production of ROS, will be mitigated by greater atmospheric CO<sub>2</sub> concentration and more photosynthesis (Koyro et al. 2012).

Recent research has demonstrated 29 gene homologues in the potato genome for LEA Dehydrin proteins, which are involved in osmoprotection and ROS scavenging. These genes exhibit key differences in the promoter regions, suggesting differences in the stress triggers and response to different stresses. One specific LEA gene was expressed in all tissues of the plant when exposed to salinity and only in the roots when exposed to drought; its expression was also repressed by exogenous ABA application (Charfeddine et al. 2015, 2017a,b). Whether expression levels of this gene can be biotechnologically modified to improve salt tolerance has yet to be tested. Overproduction of such osmoprotectants has been extensively used in several target crops in an attempt to improve tolerance to abiotic stress (Reguera et al. 2012). Overexpression of genes involved in polyamine expression in plants (Roy and Wu 2002; Capell et al. 2004), including tuber bearing crops (Kasukabe et al. 2006), enhanced tolerance to a range of abiotic stresses. Similarly, glycinebetaine overproduction was a promising approach in developing abiotic stress tolerant plants (Lv et al 2007). Overexpression of ROS scavenging proteins such as Mn-superoxide dismutase (Mn SOD3.1), in a range of crops, including potato (Waterer et al. 2010), increased tolerance to abiotic stress and improved yields under field conditions (Reguera et al. 2012). Expression of ascorbate peroxidases and catalases in crops, including other *Solanum* species such as tomato, improved tolerance to exposure to direct sunlight under field conditions and improved growth and yield under salt stress (Reguera et

al. 2012). Expressing multiple antioxidant enzymes could be a promising strategy to enhance abiotic stress tolerance (Zhao and Zhang 2006), but such a pyramiding approach has not yet been tried in potato.

### The importance of considering interactions of stress

There are a large range of responses in plants to abiotic stresses in plants and many of these are common to a range of stresses. In addition to these common responses, there are many that are unique to the particular stress. The common molecular adaptations of arabidopsis to individual stresses in isolation are summarised in Fig. 1. What this figure does not show is what the impact of combinations of abiotic stresses are on the molecular response cascade.



**Fig. 1** Schematic representation of plant adaptations to abiotic stress. (a) ABA-related adaptations to drought resistance, (b) DREB2A and ubiquitination-related adaptations to drought resistance, (c) Plant adaptations towards heat stress. (d) Plant adaptations to tolerate salt. Red square symbolizes activation/upregulation/induction/accumulation/elevated, green square symbolizes knockdown/downregulation/suppression/reduced, and yellow square symbolizes unaffected/not-impaired. This figure is taken with permission from Ahuja et al. (2012).

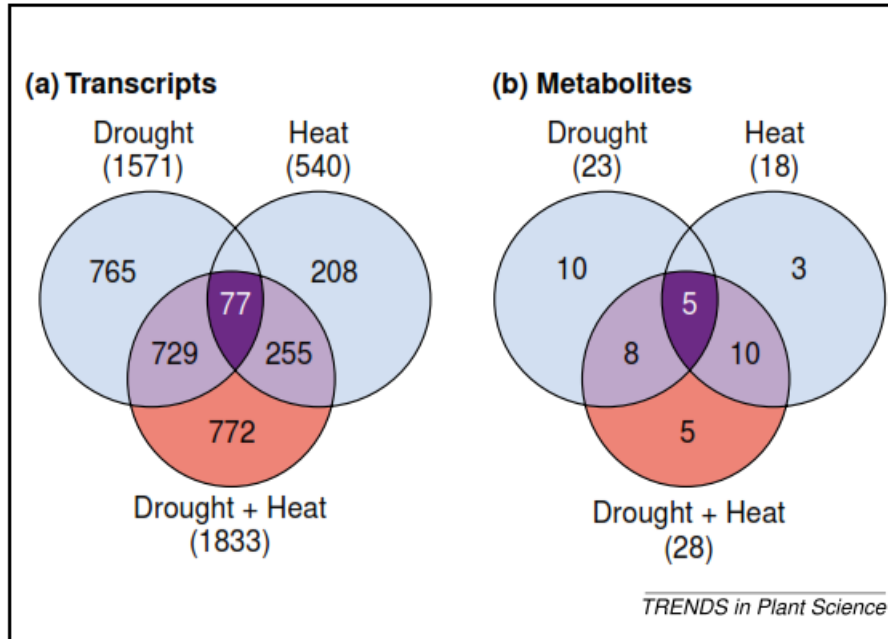
In field conditions, abiotic stresses often occur in combination, with effects that are often additive, if not synergistic, further diminishing yield and quality parameters. Few studies have investigated combinations of abiotic stresses, especially for crop species such as potato. For heat stress alone, studies on arabidopsis have



identified four major thermotolerance types (Yeh et al. 2012). These responses include basal thermotolerance, short- and long-term acquired thermotolerance, and thermotolerance to moderately high temperatures. This diversity in thermotolerance response suggests that phenotypic assays accounting that take account of all these types of heat stress are required to fully assess gene function. Considering the impacts in response to single and combined stresses at different crop development stages is also essential. For example, screening 3 potato varieties in 32 environments across France demonstrated that tuber yield was most affected by the combination of heat and drought stress at tuber initiation (Pruedhomme-Zub et al. 2017).

Plant responses to combined abiotic stresses are often unique and are not the same as the responses of the plant to the stresses applied individually, with key (mostly abiotic) stresses interacting in different ways, all of which are potentially affected by climate change (Mittler 2006). They produce a stress matrix which demonstrates that most of the interactions are antagonistic, while only a few show complementary interactions. These complementary responses include the production of antioxidative compounds to combat the impact of ROS, which may be part of a universal response in plants to abiotic stress in general. Notwithstanding this potentially universal response, many of the responses to individual stresses will be antagonistic to one another when stress is combined. For example, drought-induced stomatal closure to conserve water will reduce a plant's ability to regulate leaf temperature under high ambient temperatures (Rizhsky et al. 2002). In addition, nutrient deficiency could further limit plants attempting to cope with heat, drought or salinity stress. Energy and resources are often required for plant acclimation to abiotic stress, for example the synthesis of heat shock proteins or production of larger root systems, while key micronutrient elements are often required for the function of different defence enzymes, such as superoxide dismutase or ascorbate peroxidase (Mittler 2006). The acclimation of plants to a combination of different abiotic stresses will, therefore, require an appropriate response customized to each of the individual stress conditions involved, as well as tailored to the need to compensate or adjust for some of the antagonistic aspects of the stress combination.

Plants subjected to drought or heat stress or their combination show that the stress combination has several unique characteristics where enhanced respiration is combined with reduced photosynthesis, closed stomata and high leaf temperature (Rizhsky et al. 2002). Transcriptome profiling studies of arabidopsis undergoing combined drought and heat stress shows that the stress combination invokes a unique acclimation response involving several hundred transcripts that are not altered by drought or heat stress alone (Rizhsky et al. 2004; Figure 2). Similar changes in metabolite accumulation were also found, with several unique metabolites, mainly sugars, accumulating specifically during the stress combination (Fig. 2). Figure 2 further illustrates that plant acclimation responses to heat or drought stress differ, with only a small overlap in transcript expression and metabolite production found between these responses. Importantly, the ability of a plant to coordinate its response to combined stress is likely to involve cross-talk between biochemical pathways involved in the response (Atkinson and Urwin 2012). Such cross-talk is likely to include 1) integration between different networks of transcription factors and mitogen-activated protein kinase (MAPK) cascades (Cardinale et al. 2002; Xiong and Yang 2003); 2) different stress hormones such as ethylene, jasmonic acid and abscisic acid (Anderson et al. 2004); 3) calcium and/or ROS signalling (Bowler et al. 2000); and 4) cross-talk between different receptors and signalling complexes (Casal, 2002). It is critical that these transcriptional and metabolomics responses and the coordination of this response to combined abiotic stresses are understood in potato.



**Fig. 2** Unique molecular characteristics of drought and heat stress combination in *Arabidopsis*. Venn diagram showing the overlap between a) transcripts and b) metabolites during individual and combined stress. Total number of transcripts and metabolites is indicated in parenthesis. Taken with permission from Mittler (2006).

In the absence of a universal response to combined stress, another approach would be to use crop phenology to identify varieties that perform well under the combined stress conditions of climate change. Identifying early varieties that avoid stress, by completing their developmental cycle in advance of late summer stress periods, could be valuable. Early Serbian potato varieties have tolerance to heat and drought stress in the field when subjected to a 20 day period of minimal precipitation and maximum temperatures of  $>40^{\circ}\text{C}$  towards the end of the growing season. In contrast late varieties showed susceptibility to the combined stress (Postic et al. 2017). Similarly, early season drought delayed canopy closure and reduced yield in early varieties, but had no impact on late varieties in South Korea (Chang et al. 2017). This highlights the difficulties of trying to identify an ideotype for a changing and variable climate. Due to large inter-seasonal variation in precipitation it would be difficult to establish whether an early variety would be the best option to avoid late season stress, when drought can occur at any time in the crop's development.

### Designing better agronomy and genotypes

There are a number of opportunities to improve the ability of potato cropping systems to cope with the impacts of climate change on abiotic stress levels. These include both agronomic solutions, such as plant, soil and water management options, and genotypic solutions by breeding better cultivars or ideotypes for the new climatic conditions. In reality, combining both approaches may offer the best solutions. For example, crop models suggest that the best options for coping with potential yield losses of potatoes due to climate change in India include the use of new adapted varieties along with a change in sowing time and the addition of more inorganic nitrogen (Naresh Kumar et al. 2015).

#### *Better agronomy for potato production*

Many management practices can alleviate the negative effects of drought and heat stress, including soil management practices, irrigation management, crop residues management application of growth regulators as foliar sprays.

#### *Soil management*

Changes in the soil surface affect soil water and heat balance including soil water evaporation and infiltration and heat exchange between soil and atmosphere (Ferrero et al. 2005; Sekhon et al. 2010). Soil surface roughness can be manipulated by tillage, residue management and mulching. These are effective by changing surface-energy interactions, gradients in temperature, rainfall infiltration, the amount of water stored in the soil and water uptake by plants (Lipiec et al. 2006; Sekhon et al. 2010). Soil tillage can have a large impact on the availability and accessibility of water to crops. However, tillage management is limited for potatoes due to the need to aggressively manipulate the soil to produce hills for growth. Using surface organic mulches also reduces soil temperature by reducing thermal conductivity, enhancing the water content by controlling evaporation from the soil surface and absorbing water vapour onto mulch tissue, and aggregating of soil particles which affects the quantity of rainwater entering the soil and evaporation and crop yield (Lipiec et al. 2013).

### *Irrigation*

Supplemental irrigation during the growing season can significantly increase water use efficiency (WUE) and yield. Modern targeted irrigation techniques are more effective in terms of water saving water (up to more than 50%), compared to surface irrigation (Lipiec et al. 2013). Potatoes are especially responsive to irrigation during tuber initiation and bulking, although this is often to control incidence of potato scab (*Streptomyces scabies*). Nevertheless, there has been much interest in the irrigation technique of partial rootzone drying (PRD), which seeks to exploit the concept of root-to-shoot ABA signalling (discussed earlier) by irrigating only part of the rootzone. Theoretically, sufficient irrigation is applied to part of the rootzone to satisfy crop water requirements and prevent any leaf water deficits, while synthesis of ABA by roots in drying soil stimulates root-to-shoot ABA signalling to affect partial stomatal closure thereby increasing WUE (Liu et al. 2006). Commonly, the wet and dry parts of the rootzone are frequently swapped, to promote root growth and root-to-shoot ABA signalling (Dodd et al. 2015). Whether the physiological and agronomic effects of PRD differ substantially from applying less water to the entire rootzone (conventional deficit irrigation - DI) has been investigated in many species (Dodd 2009) including potato (Saeed et al. 2008; Shahnazari et al. 2008; Ahmadi et al. 2010; Xie et al. 2012; Yactayo et al. 2013; Ahmadi et al. 2014; Sun et al. 2015). Only two of these studies showed substantial yield differences between PRD and DI in potato. Irrespective of whether irrigation was limited 6 or 8 weeks after planting, applying 50% less water via PRD enhanced average yields by ~50% compared to DI, which was associated with greater leaf water content at a given level of osmotic adjustment (Yactayo et al. 2013). Conversely, in a much drier environment, applying 25% less water via PRD decreased average yields by ~50% compared to DI, apparently due to severe water deficits occurring during long soil drying cycles (Ahmadi et al. 2014). The magnitude of these yield differences between PRD and DI plants suggests that additional research is needed to understand their mechanistic basis, and optimise irrigation to maximise its benefits.

### *Applying growth regulators*

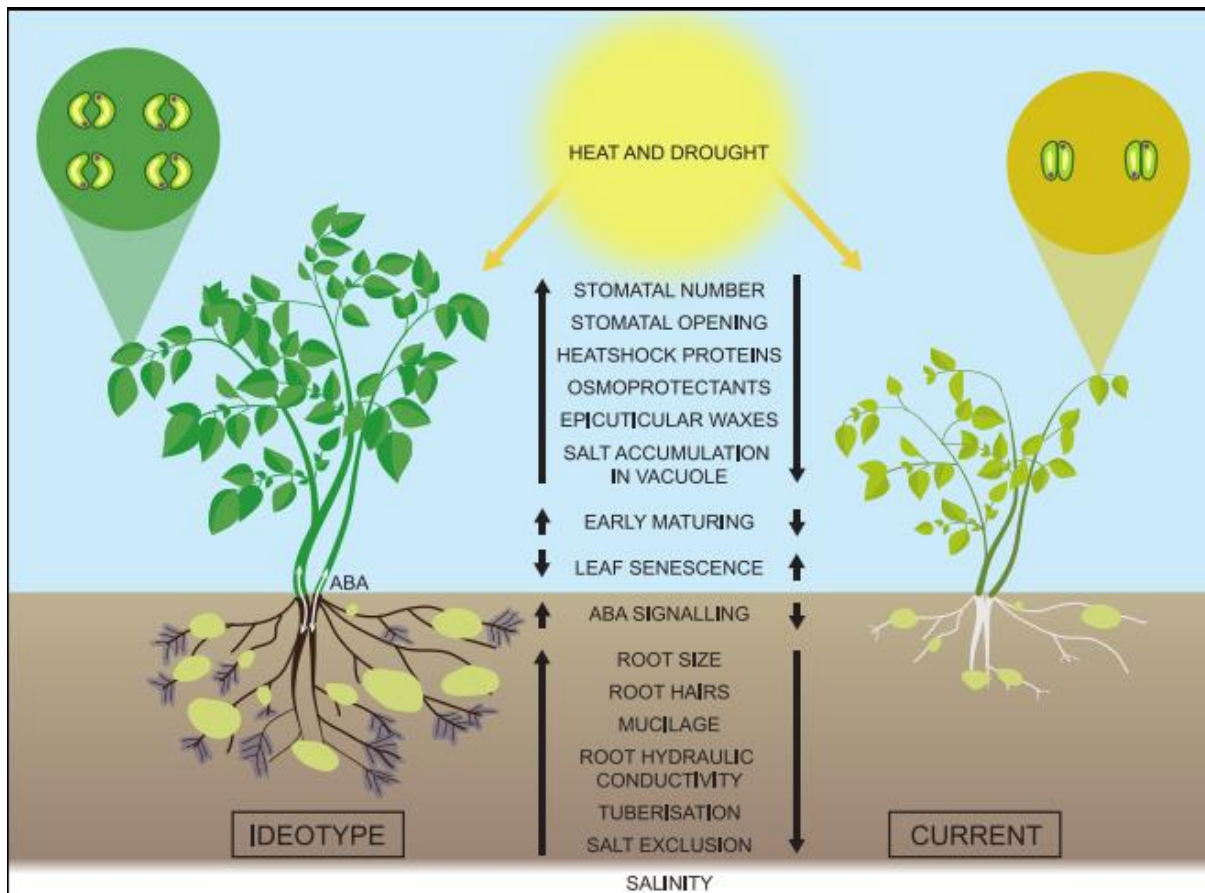
The adverse effects of abiotic stresses can also potentially be mitigated by foliar application of natural and synthetic growth regulators. Application of gibberellic acid (Taiz and Zeiger 2006), 1-aminocyclopropane-1-carboxylic acid (Brownfield et al., 2008), and glycinebetaine (Farooq et al., 2009) can all reduce the effects of drought stress. Exogenous application of ABA regulates water flow at the root level by modulating aquaporin activity (Beaudette et al. 2007; Parent et al. 2009), with small concentrations stimulating root hydraulic conductivity ( $L_p$ ), while higher concentrations ( $> 10 \mu\text{M}$ ) decrease  $L_p$  (Dodd 2013). Whether foliar ABA applications affect  $L_p$  is less certain, but rapid ABA metabolism *in planta* may result in only transient physiological effects of ABA application. This is an emerging area of agronomy that needs greater scientific understanding to become part of an effective management practice.

### *Adapted crop ideotypes*

As highlighted above, the key stresses that will be impacted by climate change will be heat, drought and salinity. An ideotype which copes with these three in combination via an integrated stress response, that is not antagonistic

to any one of the stresses or to other aspects of the production system, while at the same time maintaining carbon fixation and photosynthesis, should be pursued.

It is possible to propose a shoot, root or whole plant ideotype and the traits for these are highlighted in Fig. 3. The ideal potato genotype for combined stress tolerance will likely be early maturing to avoid the late season stress of the drought and heat, will achieve rapid canopy closure to maximize photosynthesis, be effective at utilising available water by accessing more water and fixing more carbon per unit of water taken up, and be able to maintain tuberization under conditions of high temperature, water deficit and salt toxicity. To maintain photosynthesis and carbon fixation under stress conditions, it should maintain density and opening of stomata under water deficit and salinity and protect the photosynthetic machinery of the chloroplasts from toxic elements and ROS by producing heat shock proteins, osmoprotectants and antioxidants and delay the onset of senescence for as long as possible. Understanding and manipulating ABA signalling pathways to optimise stomatal opening before critical wilting point should also be targeted. Ways of maintaining membrane integrity under high temperature and reduced water potential, such as saturation of fatty acid lipids in membranes and protecting the cells against desiccation by producing epicuticular waxes should be included in the ideotype. As discussed, keeping the stomata open as long as possible is a critical way to maintain photosynthesis, carbon fixation and heat dissipation at the leaf surface. This may be achieved by enhancing the size and water uptake capacity of the root system when water is available for uptake. This will also have the added advantage of maximising nutrient acquisition which is critical for the effective metabolism of carbon fixed by photosynthesis and reduce accumulation of sugars and sink strength feedback issues. However, maximising water uptake and water use by the crop will also increase the exposure of the crop to potentially toxic elements in saline conditions. A root ideotype should target an increased root system size, most notably the stolon roots, and root penetration ability by the production of root hairs and root mucilage. Root mucilage also confers the benefit of altering the soil physical conditions to increase the ease of extraction of water which is critical when saline conditions disperse soil particles. Water uptake will be enhanced by increasing root hydraulic conductivity by altering xylem vessel diameter, reducing xylem embolism and increasing the abundance of aquaporins in root plasma membranes. To counter the potential detrimental impacts of water uptake on the uptake of toxic elements such as sodium, chloride and boron in saline conditions, an ideotype should select against these elements without reducing the uptake of other essential elements. If toxic ions are taken up, their effects should be minimised by limiting their transport to the shoot and/or selectively exporting them from cells either to the external environment or to the vacuole by the expression of antiporters or tonoplast transporters. To achieve this ideotype, it is important that genetic and phenotypic variation in these traits is assessed and ways of bringing this multitude of traits into a single genotype considered.



**Fig. 3** Potato ideotype for combined heat, drought and salinity stress tolerance in the warmer dryer conditions predicted following climate change. This ideotype is compared to current genotypes not selected for abiotic stress tolerance

### Approaches and opportunities for producing a potato ideotype for climate change

Since breeding currently focuses on improving yield under optimal conditions, there has been little progress breeding for tolerance to specific or combined abiotic stress. For example, despite centuries of breeding of potatoes, little gain has been made in traits such as temperature tolerance (Parent and Tardieu 2012). Currently, numerous genes related to plant responses to abiotic stress have been identified (see Fig. 11 and 22, Table 1), however there has only been limited success in producing abiotic stress tolerant crop cultivars through genetic engineering (Peleg et al. 2011; Reguera et al. 2012). Many studies report abiotic stress resistance in model species tested under extreme and artificial conditions, usually involving assessment of recovery from near-fatal stress conditions (Umezawa et al. 2006; Ashraf and Akram 2009; Pardo 2010). How useful these studies are for improving crops grown under field conditions in response to the stresses imposed by climate change, which occur as small incremental changes in conditions over a number of decades, is a moot point. Under field conditions, crops must cope with multiple abiotic stresses which vary in space, time, duration and intensity (Mittler and Blumwald, 2010).

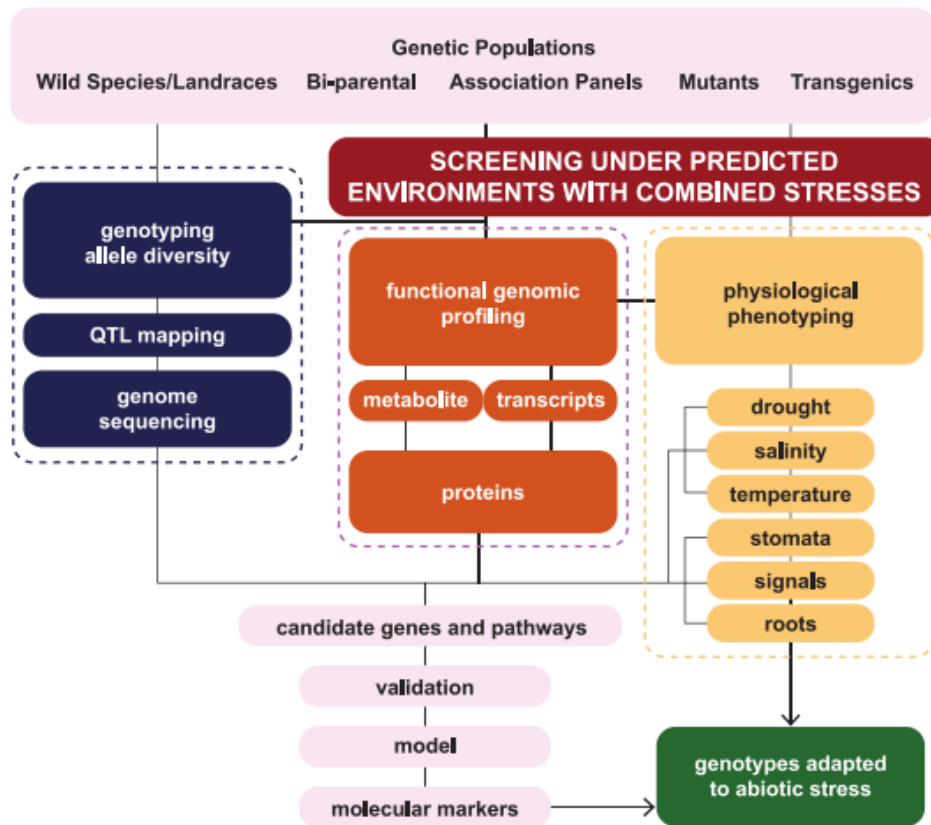
There are a number of approaches that could be taken to produce an ideotype (Reguer et al. 2012; Bitá and Gerats 2013) including targeting single genes in specific tissues under the promotion of signals from developmental or environmental cues, through to the targeting of entire biosynthetic pathways with hormone homeostasis (ABA) or epigenetic and post-transcriptional control. The single gene approach for drought and salinity has been less successful than targeting pathways and regulatory networks (Cominelli et al. 2013) such as DREB (Dehydration Responsive Element Bindings) proteins (Lata and Prasad 2011). Approaches targeting regulatory pathways in this way are likely to provide the second generation of abiotic stress tolerant transgenic plants, which may be more successful and applicable to a wider range of environments than approaches targeting single genes.

Epigenetic approaches also have potential in a clonal species like potato, where seed tubers could be epigenetically imprinted with a “stress memory” from exposure of the mother plant to such conditions (Monneveux et al. 2013). Activation of genes that take part in ABA biosynthesis metabolic pathways, heat-shock proteins and other antioxidants have been modified epigenetically. Stress memory is manifest by epigenetic changes such as modification of DNA activation by methylation or acetylation, histone alteration and chromatin remodelling that result in gene silencing and/or gene activation (Bruce et al. 2007). Drought stress memory studies have been carried out in potato to test and compare water response and tolerance of some varieties with varying success (Watkinson et al. 2006; Vasquez-Robinet et al. 2008).

How we bring together the traits of interest and make sure they are appropriately expressed is probably less important than identifying the relevant variation in the potato germplasm. To source relevant variation, it is critical to exploit untapped genetic resources in the form of landraces and wild relatives of potato, which must be appropriately conserved and protected. It is also imperative to screen genotypes under appropriate conditions. In Fig. 4 we present a conceptual model of how the process of gene, metabolite and trait discovery could be approached. The key concept here, which will allow it to contribute to our goal of obtaining climate change adapted ideotypes, is the screening of germplasm in appropriate environments and conditions. Critically, these appropriate conditions should include the target environments for which the ideotype is to be designed for, i.e. in the field in the agroecological zone of interest, in the climate conditions for which it is targeted, including elevated CO<sub>2</sub>, temperature, drought and salinity and where performed in controlled conditions should include combinations of stress as an absolute minimum requirement.

Landrace populations and wild relatives, which conserve a diversity of phenotypes and genotypes, have been selected through natural and human selection for specific adaptations to a range of environments (Redden 2013). Through their distribution across a large range of local environments, landraces reflect selection for changes in alleles at loci controlling fitness traits for that locality and that specific environment with its unique combination of stresses. In contrast to modern potato varieties, landraces of Andean potato species and wild potatoes occurring in the Americas, from Colorado (USA) to Chile and Uruguay, are better adapted to abiotic stress (Schafleitner et al. 2007). Genes from this germplasm could contribute to the improvement of potato for current and future needs (Monneveux et al. 2013). It is now possible to systematically explore the genetic variation in landraces and wild varieties by using our understanding of the selection environments for local adaptation along with genomics approaches to identify candidate genes/alleles from the germplasm for tolerances to specific abiotic stresses. Wild relatives of crops have largely untapped genetic variation for abiotic and biotic stress tolerances, and could greatly expand the available domesticated gene pools to assist crops to survive the predicted extremes of climate change (Redden 2013). For example, recent programmes cloning late blight resistance genes from potato wild relatives and expressing them in modern germplasm have successfully conferred biotic stress tolerance (Haverkort et al. 2016). Notwithstanding this, the relatively limited use of wild potatoes in breeding programs thus far is largely due to undesirable effects of genes linked to the introgressed trait and since some of the traits contributing to drought tolerance in wild potatoes are themselves associated with low yield potential (Cabello et al. 2012).

Targeted breeding approaches are also hampered by a lack of fundamental knowledge of the molecular mechanisms of how plants perceive and translate abiotic stresses into relevant acclimatory responses. For potato, resilience to combined abiotic stress can be achieved by maintaining shoot growth at the same time as tuber initiation and development. Understanding the interactions between below ground water uptake by the roots and above ground water loss from the shoot system is essential (reviewed in Obidiegwu et al. 2015). The development of high throughput precision phenotyping platforms could provide a tractable new tool for precision screening, aiding the selection and pyramiding of stress response genes appropriate for specific environments. Outcomes from genomics, proteomics, metabolomics, and bioengineering advances will undoubtedly complement conventional breeding strategies and present an alternative route toward development of abiotic stress tolerant potatoes. Moreover, the adoption of genomic selection strategies in breeding has the potential of greatly speeding up the selection of both single traits and quantitative traits (Slater et al. 2014, 2017; Caruana et al. 2017).



**Fig. 4** Research pipeline required for developing a potato ideotype which is adapted to the changed climate of 2050

## Conclusions

With increasing atmospheric CO<sub>2</sub> concentrations there is an opportunity to enhance potato yields in the future, but this will only be possible if the potato crop can cope with the other consequences of climate change caused by this rise in CO<sub>2</sub>. While climate change may impact biotic stress either positively or negatively, abiotic stresses are likely to be greatly increased in severity, becoming a major threat to potato production. Increasing heat, drought and salinity stress will drive the need for greater understanding of genes and traits in potato that are able to cope with these stresses. Here we have identified a range of key physiological and molecular adaptations of potato to these stresses and demonstrate that it is important to understand these responses under combined stress conditions. We have further identified an ideotype for potato that combines a number of root and shoot adaptations to environments with multiple stresses and sets a target for future breeding activities. It is also clear that there is a need to combine cutting-edge genomics and genetics approaches with the nascent genetic diversity in landrace and wild material to help identify and bring together some of the key elements of such an ideotype. If relevant phenotyping systems can be identified and such an approach made a priority today, we believe it would be possible to produce a range of potato genotypes with tolerance to the combined stress environments appropriate to the future agroecosystems.

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**Table 1** Definition of optimal and stressful conditions of three key abiotic stresses heat, drought and salinity and their impact on the yield and quality of potatoes and some information on the physiological and molecular response of the potato plant to these stresses

Stress and impact of climate change	Definition / Conditions	Effects on Yield and Quality	Physiological response	Molecular response	References
<p><b>Heat</b></p> <p>Extreme Heat Effects (Heat Waves)</p> <p>Basal temperature effects</p> <p>1) General effects on phenology</p> <p>2) Passing critical thresholds for optimal growth</p> <p>Shifts in temperature of particular seasons or night/day</p> <p>Interactions with water stress and salinity</p>	<p>6°C Required for spouting 18 to 20°C optimum for tuber growth, 27°C for Haulm growth</p> <p>Temperature optimum of 20°C for photosynthesis in potatoes, reducing rapidly above this point.</p> <p>Optimum soil temperature of 15 to 18°C.</p> <p>Soil temperature &gt;18°C combined with high atmosphere temp particularly detrimental</p> <p>Interaction with light intensity - low light intensity lower optimum soil temperature</p> <p>Irreversible loss of photosystem II seen at 38°C. But, if acclimated to sub-lethal high</p>	<p>High temp reduces tuber bulking rate</p> <p>Temperature outside the optimum reduces tuberization</p> <p>Low night temp increases number of tubers per plant. High night time temps reduces yield</p> <p>Internal Brown Spots or Chocolate Spots are increased at high temperature</p> <p>Heat necrosis occurs at high soil temperature</p> <p>High temperature cause irregular tuber shape, chain tuberization, secondary tuber formation, sprouting and reduced dry matter content.</p> <p>Tuber cracking noted after short periods of high temperature</p>	<p>Increased temperature leads to greater ET thus decreased WUE</p> <p>Tuberization inhibited at high temp</p> <p>Increasing temperature leads to quicker development and earlier flowering time.</p> <p>High temperature effects cell anatomy, changing shape of chloroplasts, swelling of stromal lamellae, clumpy vacuoles which effect thylakoid organization and produce antennae depleted PSII reducing photosynthesis and respiration.</p> <p>Heat sensitive genotypes have faster rates of dark respiration than tolerant.</p> <p>Temperature effects assimilate partitioning switching from tubers to roots and haulms above 20°C</p> <p>Conversion of sugar to starch is inhibited at high temperature leading to accumulation of sugar at phloem unloading sites and decline in sink strength and tuber bulking.</p> <p>Heat leads to production of ROS that may interfere with starch synthesis</p>	<p>Expression of Heat Shock proteins (HSPs, e.g. HSc70) which act as molecular chaperones to prevent protein denaturation and aggregation under heat stress</p> <p>Impacts of temperature on flowering genes</p> <p>Impacts on growth regulators e.g. high ratio of GA:ABA increases haulm growth (e.g. POTH1 transcription factor)</p> <p>High GA reduces activity of ADPG pyrophosphorylase stopping tuber growth</p> <p>Sucrose synthase depressed more in tubers in heat susceptible genotypes</p> <p>Enzymes involved in starch metabolism depressed at soil temperatures &gt;30°C</p> <p>Tuber sprouting increased by heat induced increase in GA</p> <p>Reduced ROS expression with heat</p> <p>Perturbation of circadian clock transcripts StSP6A (tuberization signal) under mild temperature stress</p>	<ol style="list-style-type: none"> <li>Levy and Veilleux 2007</li> <li>Kumar et al. 2015</li> <li>Ahuja et al. 2010</li> <li>Craufurd and Wheeler, 2009</li> <li>Hannapel et al. 2004</li> <li>Mares et al. 1981</li> <li>Lafta and Lorenzen 1995</li> <li>Krauss and Marschner 1984</li> <li>Hancock et al. 2014</li> <li>Lipiec et al. 2013</li> <li>Bitá and Gerats 2013</li> <li>Vollenweider and Gundhardt-Goerg 2005</li> <li>Hua et al. 2009;</li> <li>Tian et al. 2009</li> <li>Smertenko et al. 1997; Potters et al. 2008;</li> <li>Rasheed 2009</li> <li>Larkindale and Verlig 2008; Saidi et al. 2011</li> <li>Lang-Mladek et al. 2010; Pecinka et al. 2010</li> <li>Trapero-Mozos et al. 2017</li> </ol>

	temperature (e.g. 35°C) then >40°C is tolerated	<p>High temp increase level of steroidal glycoalkaloids and bitter taste</p> <p>Mild heat stress showed increased accumulation of amino acids in tubers, which may promote the Maillard reaction which effects colour, aroma, flavour and acrylamide accumulation upon cooking.</p> <p>Tuber quality issues exacerbated by interactions between heat and drought</p>	<p>Heat and drought stress impact the function of PSII by decreasing electron transport, removal of external proteins and release of Ca and Mg ions from binding sites.</p> <p>Extreme heat leads to physiological injury - scorching of leaves and stems, leaf abscission, shoot and root growth inhibition. Also elongation of hypocotyls and petioles similar to shade avoidance.</p> <p>By causing cell membrane damage heat leads to reorganization of microtubules and the cytoskeleton changing cell differentiation elongation and expansion.</p>	<p>Increased fluidity of membranes activates lipid based signalling cascades and increased Ca influx.</p> <p>5% of the transcriptome is upregulated by heat stress and only a small proportion is heat shock chaperones. Most proteins are involved in primary and secondary metabolism, translation, transcription and regulation of stress responses; calcium and phytohormone signalling, sugar and lipid signalling or protein phosphorylation.</p> <p>Heat stress leads to transient activation of repetitive elements or silenced gene clusters in centromeric regions by downregulating epigenetic gene silencing by remodelling the heterochromatin</p>	
<p><b>Drought</b></p> <p><i>Direct effects</i></p> <p>Water deficit for transpirational cooling</p> <p>Water deficit for cellular function</p> <p><i>Indirect effects</i></p> <p>Water deficit leading to soil strength</p> <p>Water deficit leading to osmotic stress</p>	<p>-45kPa soil matric potential is classed as severe water stress, -25kPa is adequate</p> <p>Water deficit for cellular function occurs when tissue water potential is -0.4- -2.0 MPa</p> <p>Water deficit leading to soil strength (&gt;1MPa)</p>	<p>Drought leads to reduced accumulation of dry matter and tuber yield</p> <p>Drought is most critical at emergence and tuberization</p> <p>Drought increases the tuber protein and ascorbate content</p> <p>Drought has detrimental effects on tuber shape producing dumbbell, knobby or pointy tubers</p>	<p>Water deficit leads to stomatal closure and reduced CO<sub>2</sub> fixation and transpiration which will have a knock effect on heat stress</p> <p>Production of larger and altered root system, changes in root length, targeting of wet zones of soil (depth). Suberization of roots in dry zones</p> <p>ABA production in roots and transport to shoots through xylem causing inhibition of shoot growth and stomatal closure.</p> <p>Root hydraulic conductance - cell permeability and aquaporin expression. Changes with root age, gradually declining</p>	<p>Antioxidant genes – superoxide dismutase, ascorbate peroxidase, catalase, glutathione peroxidase, peroxiredoxin</p> <p>NFYA5 and OCP3 are ABA sensitive transcript associated with stomatal closure</p> <p>SAL1 inactivation results in altered osmoprotectants, leaf RWC and maintenance of viable tissue during drought</p> <p>MYB96 involved in ABA Auxin crosstalk and impacts lateral root formation under drought</p>	<ol style="list-style-type: none"> <li>1. Levy et al. 2013</li> <li>2. Schafleitner et al. 2011</li> <li>3. Levy 1985</li> <li>4. Wang et al. 2007</li> <li>5. Martinez and Moreno 1992</li> <li>6. Lynch and Tai 1989</li> <li>7. Wang and Frei. 2011</li> <li>8. Monneveux et al. 2013</li> <li>9. Teixeira and Pereira 2007</li> <li>10. Andre et al. 2009</li> <li>11. Gander and Tanner, 1976;</li> <li>12. Ackerson et al. 1977;</li> <li>13. Shimshi et al. 1983</li> <li>14. Lipiec et al. 2013</li> <li>15. Kondrak 2011</li> </ol>

<p>Water deficit leading to reduced nutrient delivery</p>	<p>-0.8MPa is considered an intense drought stress</p>		<p>Production of aquaporins</p> <p>Change in rhizosphere conditions through production of root exudates and mucilage</p> <p>Greater proline and sucrose accumulation (reduced conversion to starch) in tubers</p> <p>Reduce leaf number and size</p> <p>Production of epicuticular waxes</p> <p>Cell wall elasticity</p> <p>Generation of toxic metabolites</p> <p>Heat and drought stress impact the function of PSII by decreasing electron transport, removal of external proteins and release of Ca and Mg ions from binding sites.</p>	<p>DREB2A involved in regulation of a number of drought related genes - overexpression led to enhanced drought tolerance - associated with post-transcriptional regulation of genes (ubiquitination)</p> <p>Transgenic expression of polyamines as osmoregulating compounds has shown enhanced tolerance to abiotic stress</p> <p>Overexpression of ROS scavenging enzymes has shown increased abiotic stress tolerance (likely effective for heat, drought and salinity)</p>	<ol style="list-style-type: none"> <li>16. Shin et al 2011</li> <li>17. Eltayeb et al. 2011</li> <li>18. Ahmad 2010</li> <li>19. Gawronska et al. 1992;</li> <li>20. Lafta and Lorenzen 1995</li> <li>21. Fleisher et al. 2008b</li> <li>22. Vos and Haverkort 2007</li> <li>23. Ahuja et al. 2010</li> <li>24. Reguera et al. 2012</li> <li>25. Koyro et al. 2012</li> </ol>
<p><b>Salinity</b></p> <p><i>Direct Effects</i></p> <p>Osmotic effects on plant cells</p> <p>Impact of toxic elements on cell function</p> <p><i>Indirect effects</i></p> <p>Impact on the hydraulic conductivity of roots</p>	<p>EC 6 to 9 dS/m produces salt stress</p> <p>30 to 200 mM NaCl</p> <p>40mM Na<sub>2</sub>SO<sub>4</sub></p>	<p>Reduced tuber yield due to impacts on photosynthesis</p> <p>Impact on yield reduced if salinity imposed well after establishment</p> <p>Browning and cracking of tuber surface</p> <p>Increased tuber protein content</p>	<p>Reduced relative leaf water content, leaf stomatal conductance and transpiration rate</p> <p>Thylakoid swelling and reduced grana stacking</p> <p>Changes in chloroplast structure</p> <p>Suppression of nitrate reductase</p> <p>Yellowing of leaves due to ion (Cl, Na, B) toxicity</p>	<p>Upregulation of ADP ribosylation factor-like proteins</p> <p>Proteins which were also upregulated by cold stress, drought and ABA</p> <p>Transgenic expression of glyceraldehyde 3 phosphate dehydrogenase gene conferred salt tolerance</p> <p>Expression of DREBIA gene conferred salt tolerance</p> <p>Upregulation of general stress and defence proteins</p>	<ol style="list-style-type: none"> <li>1. Shaterian et al. 2005</li> <li>2. Kim et al. 2003</li> <li>3. Ryu et al. 1995;</li> <li>4. Pruvot et al. 1996</li> <li>5. Teixeira and Pereira 2007</li> <li>6. Jeong et al. 2001</li> <li>7. Celebi-Toprak et al. 2005</li> <li>8. Aghaei et al. 2008</li> <li>9. Ahuja et al. 2010</li> </ol>

<p>Impacts on soil pH and physical conditions effecting nutrient availability and soil structure and water relations</p>		<p>Interactions with heat and light intensity impact salt tolerance</p> <p>Early maturing types more susceptible to salt stress</p>	<p>Restricted water uptake by roots due to osmotic potential</p> <p>Shift from protein and carbohydrate to proline production</p>	<p>Accumulation of ROS, salt-induced transcription factors, peroxisomes, appoplatic proteins, glycolytic enzymes</p>	
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