Abiotic Stress Effects Associated with Climate Change on Yield and Tuber Quality of Potato Cultivars in New Zealand

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Allan Banasihan Siano

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Abstract

The recent weather anomalies in New Zealand, particularly the summer heatwaves of 2017/18 and 2018/19, hottest and third hottest on record, respectively, have seemingly affected potato production. The purpose of this research is to determine how abiotic stress commonly associated with climate change, e.g., drought and heat, is affecting the current potato production in New Zealand, define its effects on yield and tuber quality of commercial potato cultivars, and determine if cultivars exhibit differential susceptibility.

Secondary climate data in the past 60 years (1958–2018) during the potato growing months of October to March showed an increasing trend for temperature in Ohakune (+0.53 °C), Opiki (+0.36 °C), and Hastings (+0.28 °C) as well as a decreasing trend for rainfall in Ohakune (-24.8 mm) and Hastings (-48.7 mm). The increase in temperature also increased the number of days with supra-optimal atmospheric temperatures believed to delay (>25 °C) or inhibit (>30 °C) tuber growth in Hastings by 57 days (2017/18 season) and in Opiki by 103 days (2018/19 season). Baseline data from a preliminary study during the 2017/18 growing season showed that abiotic stress associated with the extreme weather conditions apparently affected the yield and tuber quality, with cultivars showing differential susceptibility. Up to 85% unmarketable tubers were recorded among the samples collected, which was attributed to the high incidence of a wide array of tuber physiological disorders.

The multi-environment trial in the 2018/19 growing season showed that abiotic stress had significant effects on the different morpho-agronomic and physiological functions of the potato crop and ultimately affected the yield and tuber quality. Abiotic stress increased the incidence of tuber physiological disorders, e.g., tuber malformation, growth cracks, and second growth, which reduced the total yield and marketable yield by up to 43.3% and 45.1%, respectively. Additionally, genotype × environment analysis showed that cultivar ‘Taurus’ is the most stable and adaptable cultivar across trial sites (wide adaptation). At the same time, cultivars ‘Hermes’ and ‘Snowden’ are tolerant to heat and drought stress (Opiki) and heat stress alone (Hastings) (specific adaptation), respectively.

The glasshouse and plant growth chamber trial revealed that drought stress (DS) generally reduced the plant height, number of leaves, and canopy cover but enhanced the formation of more but smaller stomata and glandular and non-glandular trichomes. DS also encouraged the closing of the stomatal aperture potentially to reduce water loss, thereby reducing the transpiration rate (E), stomatal conductance (g_S), and net photosynthesis (P_N), which potentially affected the final yield. Conversely, heat stress (HS) increased the plant height, canopy cover, and number of leaves and developed more and larger stomata. HS also stimulated stomatal opening, leading to enhanced E and g_S and improved P_N at the vegetative stage. On the other hand, in general, the combination of drought and heat stress exacerbated the adverse effects of each abiotic stress type on the different morpho-physiological parameters.

As established in the various component trials of this research, different abiotic stresses associated with climate change have a significant effect on the morpho-agronomic and physiological functions of potato crops and negatively impacts the yield and tuber quality. Breeding of new cultivars, and mass selection of existing cultivars should be conducted through multi-environment trials to identify adaptable cultivars that can be used to mitigate the effects of abiotic stresses associated with climate change on potato crops in the field and to increase the resiliency of the New Zealand potato industry.

Acknowledgments

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Dedication

This thesis is dedicated to my wife, Maria Liza Siano, who has been very supportive in my PhD undertaking, and to my two lovely daughters Elizabeth ‘Elliz’ and Katherine ‘Erin’, my inspiration.

I also dedicate this work to my father Artemio Siano, my late mother Rosita Siano and sister Rowena Fruto, and my other siblings Rosanna, Andre, Rina, Artemio, Raquel, and Regina.

CANDIDATE’S DECLARATION

I, **Allan Banasihan Siano**, declare that this thesis entitled *"Abiotic Stress Effects Associated with Climate Change on Yield and Tuber Quality of Potato Cultivars in New Zealand"* submitted to Massey University for the degree of Doctor of Philosophy is the outcome of my own research work. Acknowledgment is given where material from other resources was used. I also certify that the thesis has not been presented, in whole or partly, for any degrees or diplomas.

CANDIDATE’S NAME: Allan Banasihan Siano

STUDENT ID NO.: [redacted]

SIGNATURE:

DATE: August 27, 2021

SUPERVISOR’S DECLARATION

CHIEF SUPERVISOR’S NAME: **PROF. NICK ROSKRUGE**

SIGNATURE: _________________________

DATE: 27 August 2021

CO-SUPERVISOR’S NAME: **DR. HUUB KERCKHOFFS**

SIGNATURE: _________________________

DATE: 27 August 2021

CO-SUPERVISOR’S NAME: **DR. SVETLA SOFKOVA-BOBCHEVA**

SIGNATURE: _________________________

DATE: 27 August 2021

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List of Abbreviations

µmol	Micromole
^{0}C	Degree centigrade
AMMI	Additive Main effects and Multiplicative Interaction
ANOVA	Analysis of Variance
C	Control
CIP	Centro Internacional de la Papa (International Potato Centre)
CliFlo	The National Climate Database of New Zealand
cm	Centimetre
DAP	Days after planting
DHS	Drought and heat stress
DMC	Dry matter content
DS	Drought stress
E	Transpiration rate
FAO	Food and Agriculture Organization
GGE	Genetics and Genetics × Environment interaction
GHG	Greenhouse gas
g_S	Stomatal conductance
HI	Harvest index
hrs	Hours
HS	Heat stress
IPCC	Intergovernmental Panel on Climate Change
MET	Multi-environment trial
MHW	Marine heatwaves
mm	Millimetre
mmol	Millimoles per litre
NASA	National Aeronautics and Space Administration
NIWA	National Institute of Water and Atmospheric Research
NOAA	National Oceanic and Atmospheric Administration
PC	Pot capacity
PED	Potential evapotranspiration deficit
P_N	Net photosynthesis
RCP	Representative Concentration Pathway
RH	Relative humidity
RWC	Relative water content
SEM	Scanning electron microscope
SG	Specific gravity
SPAD	Soil plant analysis development (chlorophyll content)
TDR	Time-domain reflectometer
TPP	Tomato-potato psyllid
WMO	World Meteorological Organization
WUE	Water use efficiency
ψL	Leaf water potential

CHAPTER 1

General Introduction and Research Objectives

1.1 Background

1.1.1 Economic importance of potato

Potato (*Solanum tuberosum* L.) is an economically important vegetable crop in many regions of the world. As a food crop, potato ranks third after rice and wheat (FAO, 2018a), grown in over 150 countries and consumed daily by more than a billion people. In 2018, the global production of potato reached 368,168,914 MT from 17,578,671 ha of planted area (FAO, 2018a). The biggest production share of potatoes is in Asia (42.2%) and Europe (38.5%). Oceania, including New Zealand, contributes only a 0.5% share in potato production worldwide (FAO, 2018a). However, New Zealand is an important supplier of fresh, processing, and seed potatoes, especially in Asia. In 2019, the potato exports of New Zealand to Asia totaled $32M (Fresh Facts, 2019). The top potato producers (in volume) are China, India, the Russian Federation, the United States, Ukraine, Poland, Germany, Belarus, the Netherlands, and France in 2018 (FAO, 2018a). Despite the decline in the production area in the past few years, the yield and production volume have an increasing trend due to the introduction of high-yielding cultivars and improved production management systems. The majority of the production and consumption of potatoes used to be concentrated in Europe, North America, and the former Soviet Union, but in the 1990s, the production and demand increased significantly in Asia, Africa, and Latin America. About a third of potatoes in the world are now grown in China and India (FAO, 2018a). More than 80% of the potato plant is edible human food, compared with around only 50% in cereals. Potato is carbohydrate rich, and 60%–80% of its dry matter consists of starch (FAO, 2008a). On a dry weight basis, potato is similar to cereals in terms of protein content but has higher than other root and tuber crops (FAO, 2008a). Potato is also rich in vitamin C and is a good source of iron, niacin, thiamine, riboflavin, and minerals like potassium, phosphorus, and magnesium (FAO, 2008a). Potato also contains folate, pantothenic acids, dietary fiber, and oxidants, which play an essential role in preventing diseases. According to the Food and Agriculture Organization (FAO) of the United Nations, “Food security exists when all people, at all times, have physical, social and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life” (World Food Summit, 1996). Further, the FAO highly recommends potato as a food security crop because it produces more nutritious food in a shorter time and lesser land and in wide-ranging environments compared with other major crops (FAO, 2008b). The relatively high adaptability of potato to varied environmental conditions, ease of cultivation, and good nutritional value have led to a steady increase in its production in developing countries (Devaux, Kromann, & Ortiz, 2014). In this regard, potato plays a significant role in mitigating malnutrition and hunger worldwide. Moreover, in areas where potato production and poverty coexist, there is an immense prospect of utilizing potatoes as a means to reduce poverty (Devaux et al., 2014).

1.1.2 New Zealand potato industry

The New Zealand potato industry was valued at $1,088 million in 2019, with a 6% estimated annual growth (Potatoes New Zealand, 2020a). Potato is the fifth highest horticultural export crop, after kiwifruit, grape wine, apples, and onions, valued at $126 million in 2020 (Fresh Facts, 2020). Potato is one of the most important vegetable commodities, with Auckland, Waikato, Hawke's Bay, Manawatu-Wanganui, in the North Island, and Canterbury in the South Island (see map in Figure 1.1) as the major potato producing regions (Fresh Facts, 2019). Among the vegetable crops in New Zealand, potatoes had the highest consumer spending at more than $150 million in 2019 (Fresh Facts, 2019). The New Zealand potato production and area planted have increased for the past five to 10 years (FAO, 2018a). The production volume increased by about 7% from 2013 to 2019 (Potatoes New Zealand, 2020a). Recent increases are primarily attributed to the improvement of yield across the industry, increasing the volume and value of potato (Potatoes New Zealand, 2020b). In 2019, the production volume was estimated at 533,030 MT harvested from 10,471 ha, with 71% for processing, 28% for fresh market, and a very small percentage for seed potato production (Fresh Facts, 2020). About 80% of potatoes produced in New Zealand are consumed locally, while the rest is exported as fresh, processed, and seed potatoes. The major export destination of New Zealand's frozen processed potatoes is Australia, which accounts for over 75%. Other important markets are Japan, French Polynesia, and Papua New Guinea, accounting for about 6% of exports (Potatoes New Zealand, 2020c). The major processing varieties are Russet Burbank, Ranger Russet, and Shepody, with an average yield of 60 t ha^{-1} (Potatoes New Zealand, 2020c). The fresh export market is smaller than the processed export market due to the stringent phytosanitary requirements of importing countries (Potatoes New Zealand, 2020c).

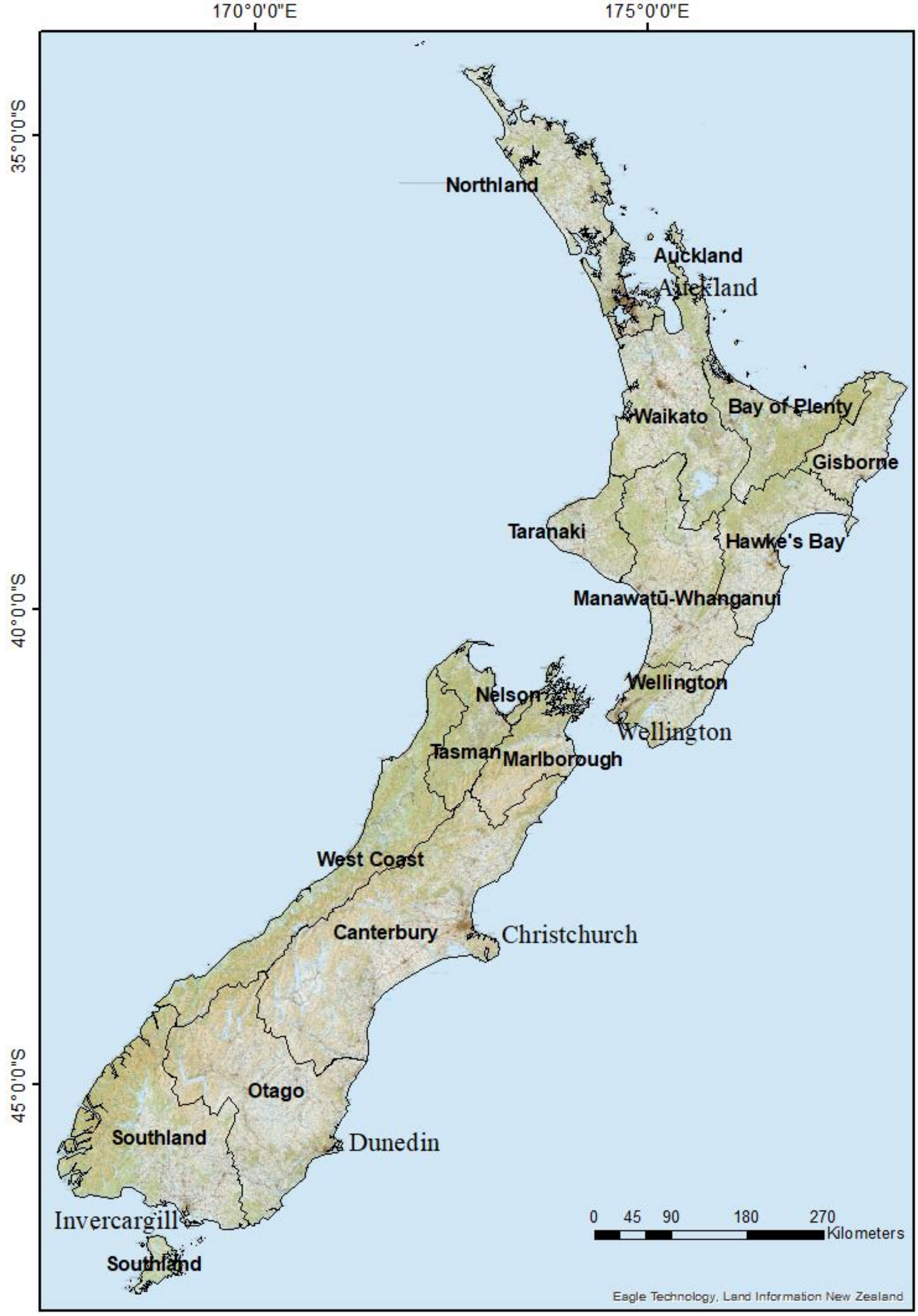


Figure 1.1 Regional map of New Zealand (Eagle Technology, 2021).

Fiji absorbs about 80% of the New Zealand fresh potato export market, while the rest are exported to Pacific and Asian markets (Potatoes New Zealand, 2020a). The entry of fresh potato products is currently prohibited to some potential markets, such as Japan and Australia, but has recently opened in Taiwan, South Korea, and Vietnam (Potatoes New Zealand, 2020a).

Despite the New Zealand potato industry's seemingly optimistic future, it is still constrained with production problems, such as pests and diseases, degrading soil quality, and soil nutrient leaching, which contribute to significant losses. One of the more recent issues the New Zealand potato industry faces is the incursion of the tomato–potato psyllid (TPP, *Bactericera cockerelli*), which became a serious threat to the industry when it was established in 2006. The pest harbors the bacterium *Candidatus Liberibacter solanacearum* (CLso), which causes sudden deterioration and subsequent death to the infected plant with a disorder in potato tubers called zebra chip (Ministry for Primary Industries, 2012). TPP damages are estimated at $25 million per year (Potatoes New Zealand, 2018a).

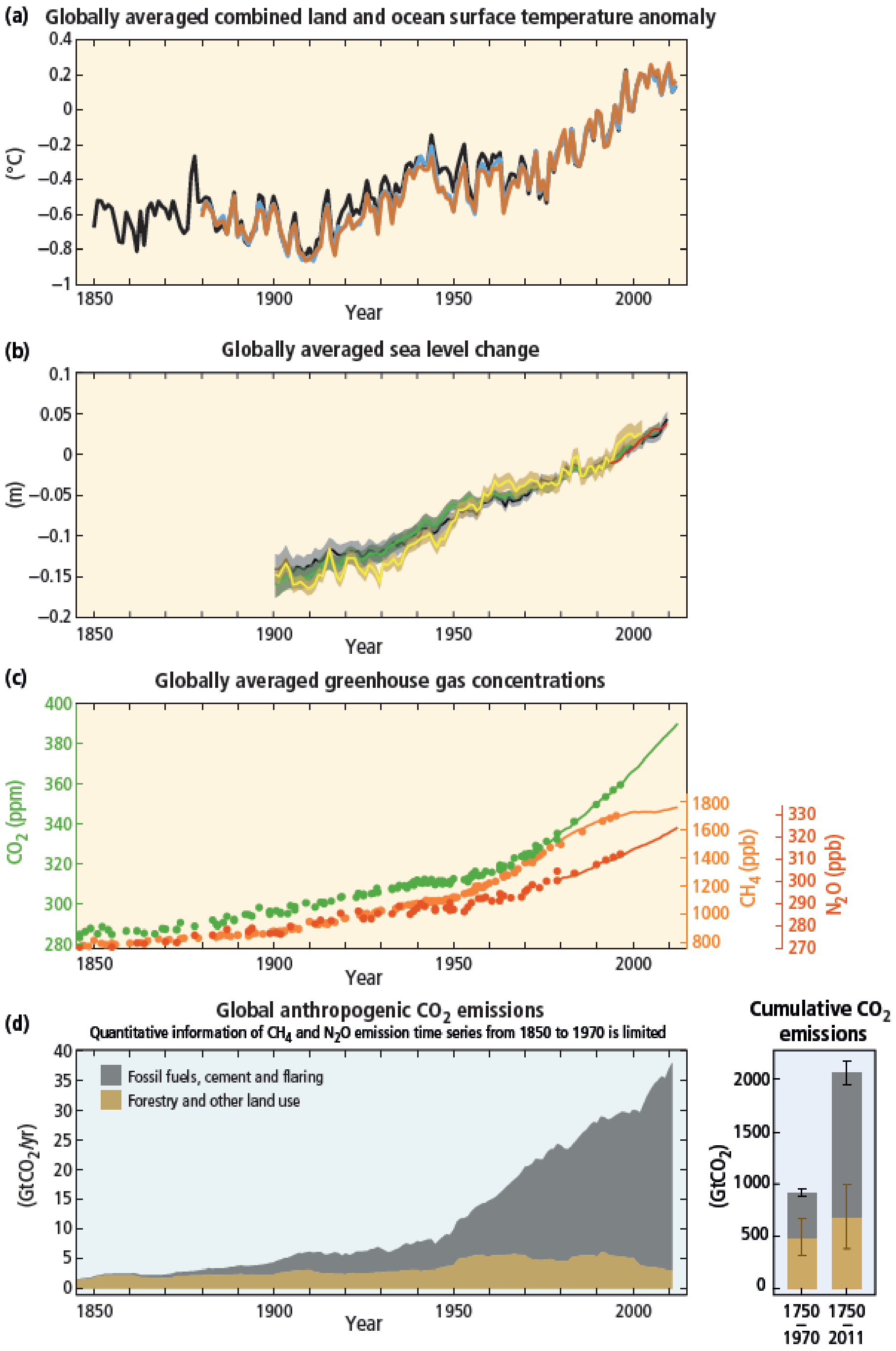
Another important emerging issue for the New Zealand's arable and horticulture industries, including the potato industry, is the changing weather and climate patterns attributed to climate change that adversely affects potato production. Experts project that the major potato production areas in New Zealand would significantly suffer from predicted extreme heat and water scarcity or excessive rain events in the coming years (New Zealand Climate Change Centre, 2014).

1.1.3 Climate change

Weather is short-term changes (minutes to months) in the atmosphere (NASA, 2021), while climate is the average weather condition for a location for a long period (WMO, 2021). Climate change is referred to as "a change in the state of the climate that can be identified (e.g., using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer. It refers to any change in climate over time, whether due to natural variability or as a result of human activity" (IPCC, 2007a). Climate can be influenced by natural and human factors. Natural factors may include solar output, volcanic activity, Earth's orbit around the sun, and ocean currents (IPCC, 2007b). On the other hand, human factors include fossil-fuel burning, deforestation, and agriculture (Mann & Kump, 2016). These human factors contribute to the dramatic increase in greenhouse gas (GHG) emissions, such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). For the last two centuries, the levels of CO_2, CH_4, and N_2O have increased by 40%, 150%, and 20% (Mann & Kump, 2016), respectively, and further increased by 147%, 259%, and 123%, respectively, in 2018 from pre-industrial levels (WMO, 2020), causing a significant greenhouse effect in the Earth's atmosphere. In the pre-industrial era, around 1750, the atmospheric CO_2 concentration was 280 ppm, which had increased constantly, reaching 367 ppm in 1999 (Prentice et al., 2001) and 379 ppm in 2005 (Le Treut, 2007). The greenhouse effect is "the warming of the earth's surface and lower atmosphere caused by substances such as carbon dioxide and water vapour which let the sun's energy through to the ground but impede the passage of energy from the earth back into space." (NIWA, 2018a). The Intergovernmental Panel for Climate Change or IPCC (2014) stated that "warming of the climate system is unequivocal." Both atmosphere and ocean have warmed, melting snow and ice, resulting in rising sea levels (Figure 1.2). Anthropogenic influence on the climate system is strong, with recent greenhouse gas (GHG) emissions being the highest in history. The rise in surface temperature over the 21st century will likely result in more frequent and longer heatwaves and more intense and frequent extreme precipitation events in many regions globally (IPCC, 2014).

Since the beginning of the 21st century, the recorded number of summer heatwaves have increased in many parts of the world (Barriopedro, Fischer, Luterbacher, Trigo, & García-Herrera, 2011; Karl et al., 2012; Sparnocchia, Schiano, Picco, Bozzano, & Cappelletti, 2006). This correlates with the increased frequency of both atmospheric and marine heatwaves recorded in Europe, Asia, and Australia since the 1950s (Perkins & Alexander, 2013; Salinger, Diamond, Behrens, Fernandez, Fitzharris, Herold, Johnstone, Kerckhoffs, Mullan, Parker, Renwick, Scofield, et al., 2020). In 2019, the global average temperature was 1.1±0.1 °C above the pre-industrial levels and considered the second warmest (WMO, 2020) after the all-time high record observed in 2016. Moreover, the past five years and 2010–2019 have been the warmest five years and decade on record (WMO, 2020). Furthermore, the projected increase in global mean temperature by the end of the 21st century is likely to be +0.3 °C to +1.7 °C, +1.4 °C to +3.1 °C, and +2.6 °C to +4.8 °C under stringent, intermediate, and high GHG emission scenarios, respectively (IPCC, 2014).

Climate change will continue to affect precipitation, with some areas experiencing extreme conditions like flooding and drought. Global temperature increases of 4 °C or higher later in the century coupled with increasing food demand due to increasing population size would pose significant risks to global food security.



(a) Globally averaged combined land and ocean surface temperature anomaly

(b) Globally averaged sea level change

(c) Globally averaged greenhouse gas concentrations

(d) Global anthropogenic CO_2 emissions

Quantitative information of CH_4 and N_2O emission time series from 1850 to 1970 is limited

Cumulative CO_2 emissions

Figure 1.2 Observations and indicators of climate change: (a) annual and average global land and ocean surface temperature anomalies (relative to 1986 to 2005); (b) yearly and global average sea-level change (relative to 1986 to 2005); (c) atmospheric concentrations of greenhouse gases; (d) global anthropogenic CO_2 emissions (adapted from IPCC, 2014).

1.1.4 New Zealand climate and climate change status and projections

1.1.4.1 Climate

New Zealand is an island country positioned in the southwestern Pacific Ocean. The total land area is 268,107 sq. km. (Statistics New Zealand, 2015), which is almost equally divided between its main two islands: the North Island and the South Island, and with around 600 smaller islands.

The New Zealand sea climate is complex, varying from sub-tropical in the far north and cool temperate in the far south. Mountain ranges extending down the narrow island nation provide a barrier for the predominantly westerly winds, separating the country into unique climate zones, making New Zealand's climate well-known for being capricious and highly variable. The coastal areas in the west of the South Island are the wettest area, while the areas in the south-eastern region are the driest, but even the drier regions of New Zealand usually receive sufficient rainfall to sustain pastoral and crop-based farming. Precipitation is between 600 and 1600 mm and spreads throughout the year with a typical dry period during the summer. The average annual temperature ranges from 10 °C in the south to 16 °C in the north (NIWA, 2018b), with relatively small variations between summer and winter. On the other hand, sunshine hours are at least 2000 hours annually in most regions.

1.1.4.2 Climate change status and projections

The Fifth Assessment Report of the IPCC (Reisinger et al., 2014) stated that New Zealand is already experiencing climate change with projected long-term trends toward higher temperatures (Figure 1.3) and shifting rainfall patterns. New Zealand has warmed by about 0.9 °C since the 1900s and is expected to keep on rising throughout this century by about 3.5 °C above the 1986–2005 average in a high GHG emission scenario. Warming is caused by marine heatwaves (MHW), which have increased by 54% globally since the early 20th century and by 0.3–0.9 days annually for New Zealand (Oliver et al., 2018). On the other hand, an increase in extreme rainfall (up to 8% more heavy rain for every 1 °C of warming) is expected but with significant regional variations. The climate is projected to vary from year to year and decade to decade due to natural processes (Ministry for the Environment, 2016).

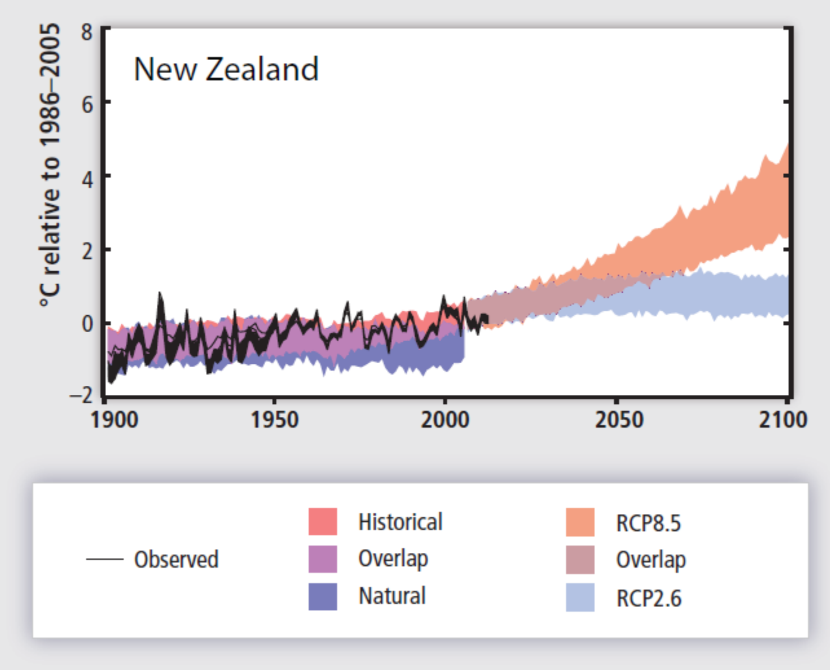


Figure 1.3 Observed and projected annual average near-surface air temperature over New Zealand Representative Concentration Pathway or RCPs: emission scenarios with RCP2.6 (with stringent mitigation) and RCP8.5 (high GHG emissions scenario) (adapted from Reisinger et al., 2014).

The IPCC data are supported by NIWA's (2018c) seven-station temperature series (measurements from seven climate stations within New Zealand), indicating that the linear trend in the annual average temperature from 1909 to 2016 is a warming of 1.02 °C (or a rate of 0.95°C per 100 years). Likewise, the five warmest years based on monthly mean temperatures occurred in the past 20 years in 2016 (+0.84 °C), 1998 (+0.80 °C), 1999 (+0.74 °C), 2013 (+0.72 °C), and 2017 (+0.54 °C). Furthermore, the forecast shows possible increases in temperature of about 0.7 °C (low emission scenario) and 1.0 °C (high emission scenario) by 2040 and about 0.7 °C (low emission scenario) and 3.0 °C (high emission scenario) by 2090 (Ministry for the Environment, 2016). The Ministry for the Environment (2020a) reported that New Zealand’s gross greenhouse gas emissions totaled 78.9 million tons of carbon dioxide in 2018, a 24% increase from the 1990 level. Two of the major contributors to New Zealand’s gross emissions are agriculture (48%) and energy (41%) sectors (Ministry for the Environment, 2020a).

The Western and Southern regions of New Zealand will receive more rain and warmer temperatures, while the eastern and northern areas will double to triple the frequency of droughts by 2040 (New Zealand Agricultural Greenhouse Gas Research Centre, 2012). Water scarcity in the Canterbury, Marlborough, Hawke's Bay, Waikato, and Northland regions is a potential problem. In an earlier study (Salinger & Porteous, 2014), four out of five spatially coherent regions in New Zealand (northern and western North Island; northern and eastern South Island; and southern New Zealand) showed a distinct trend toward higher values of drought indices (accumulated potential evapotranspiration deficit or PED) over 72 years (1941–2013), all were associated with the occurrence of distinct patterns of atmospheric circulation, especially when high-pressure systems were more common. The PED for New Zealand (1940/41 to 2019/20) showed a general increasing trend over the past 50 years (NIWA, 2020c) (Figure 1.4). Moreover, the current year, 2020, was comparable with 2013, New Zealand's worst drought on record in the past 40 or 70 years (NASA, 2013; NIWA, 2013), wherein several North Island areas recorded their driest January–April such as Whangarei, Auckland, Whitianga, Hamilton, Tauranga, Whakatane, Napier, and Taupo; and severely hot regions of Far North, Waikato, Gisborne, Hastings, and Marlborough (Figure 1.5) (NIWA, 2020b). Auckland was the hardest hit with 77 days of continuous drought (NIWA, 2020b), bringing water reservoirs down to 46.5% of the capacity compared with the average of 76% in the same time of the previous year (NZ Herald, 2020a).

According to NIWA (2020b), the 2020 drought highlights the projections of climate modeling for New Zealand's northern and eastern regions, which will become more prone to drought with the ongoing climate change over the 21st century. Water restrictions are imposed in Wellington, New Plymouth, Central Hawke's Bay, Dunedin, and South Wairarapa to counter the dry summer weather (NZ Herald, 2020b). Water flow and allocation restrictions in irrigated horticulture in some regions have been studied to determine its economic impacts. One example is in the Hawke's Bay region, where the severe economic impact was experienced in model farms when an irrigation ban was put into place during the 1998 and 2013 drought (Archer & Brookes, 2018). The 2013 drought recorded a 0.6% drop in GDP (Kamber, McDonald, & Price, 2013).

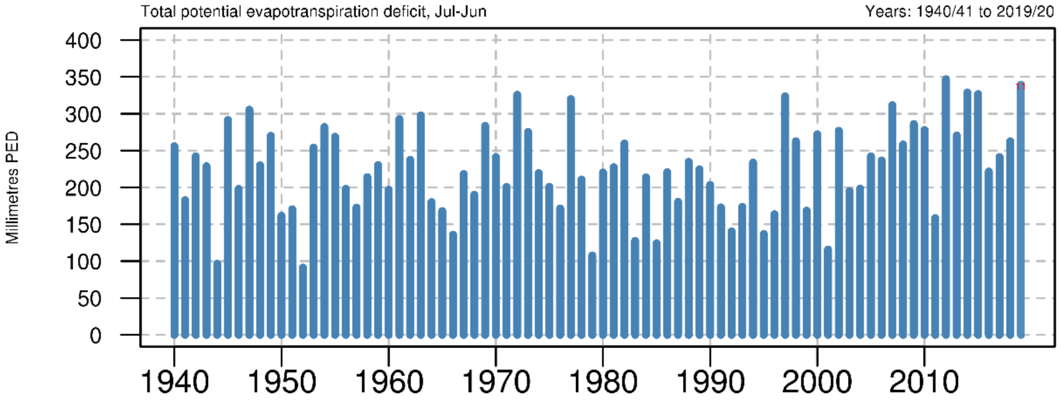


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Figure 1.4 Total potential evapotranspiration deficit (PED) from July to June for New Zealand (1940/41 to 2019/20) (adapted from NIWA, 2020c).

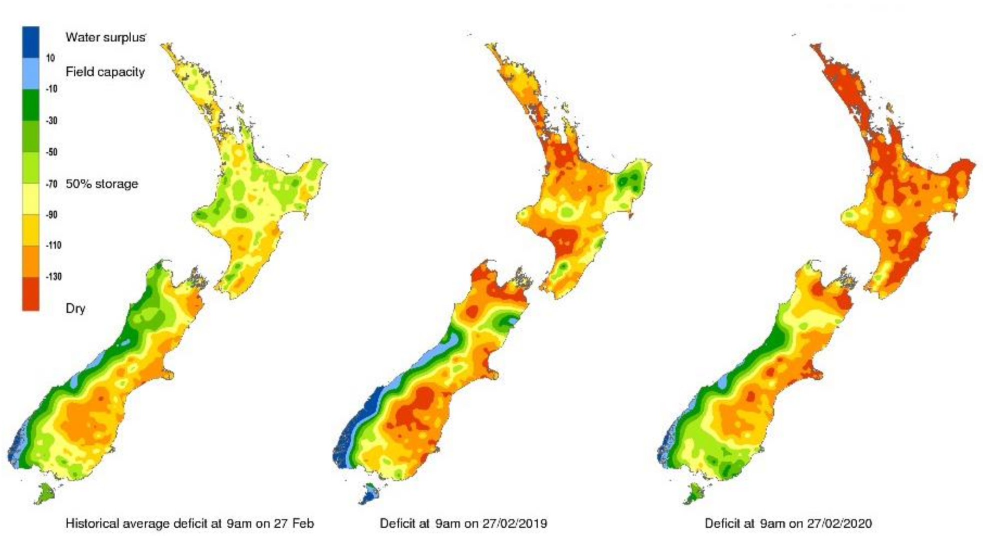

Figure 1.5 Comparison of average historical (1981-2010), and 2019 and 2020 soil moisture deficit (adapted from NIWA, 2020c).

1.1.4.3 Opportunities

The increase in atmospheric CO_2 and temperature as a consequence of climate change in New Zealand may increase the productivity of some irrigated C3 crops (e.g., wheat, rice, soybean, potato) but a decline in non-irrigated crops. This will also present some opportunities for new crop types to be grown commercially in New Zealand. C4 crops (e.g. maize, sugarcane, sorghum, millet), on the other hand, are less likely to benefit from future high CO_2 levels (Millner, Roskruge, & Dymond, 2013). Higher CO_2 levels increase radiation use efficiency, and warmer spring and autumn promote crop growth and rapid canopy development that similarly increases radiation interception (Millner et al., 2013). Warmer temperatures early in the growing season may permit early planting and early harvesting, avoiding heat and drought stress and potentially the high infestation pressure of TPP in mid-summer periods. In some temperate crops, the increased temperature may decrease the yield, but this could be compensated by higher photosynthetic activity due to increased atmospheric CO_2 levels (Gavin, 2001). As much as a 20% increase in yield in wheat and barley can be achieved given that adequate water and nutrients are available (Clark et al., 2012; Gavin, 2001). In another study on wheat crops, a 10% to 15% increase in productivity by 2050 was projected considering a range of climate scenarios (Jamieson & Cloughley, 2001).

Warmer temperatures will generally increase prospects for growing maize and similar crops in colder regions. Moreover, new broadacre commodities, such as rice and soybean, could be established in New Zealand (Clark et al., 2012) with some parts of the country, especially in the northern and eastern regions of the North Island, becoming more favourable for their cultivation. Even some fruits, such as bananas, usually grown under warm tropical environments could now be cultivated in the Northland, Bay of Plenty, and Gisborne areas (Kissun, 2019). The temperature change may also necessitate the breeding of new cultivars adapted to the new agro-climatic conditions.

1.1.4.4 Risks

Future warmer temperatures may promote crop yields because of faster emergence and rapid canopy development, where cooler temperatures inhibit crops. However, the accelerated crop growth and development inadvertently shorten the crop cycle, reducing the time for photosynthesis and ultimately negatively impacting the final yield (Clark et al., 2012).

The scarcity or surplus of water due to the extreme weather events influenced by climate change is another risk. The demand for water will likely increase due to increased evapotranspiration as affected by high temperatures combined with a reduction in average rainfall (Gavin, 2001), especially in the eastern regions of New Zealand. Rainfed farming may not be viable any longer due to variability in precipitation, often extreme events, especially drought conditions, under future climate change scenarios. Water deficit leads to reduced leaf area duration that negatively impacts yield when irrigation is unavailable (Millner et al., 2013). Supplemental irrigation could be vital in any future farming scenarios to achieve economically viable yields under new agro-climatic conditions. However, besides the already limiting irrigation water resources (e.g., rivers and aquifers), the need for irrigation may increase capital costs, thereby hindering any expansion of its use and increasing the likelihood of losses for crops under increased drought conditions (Gavin, 2001).

Conversely, excess rainfall will result in flooding events that damage crops and increase losses, especially in the western regions of New Zealand. Flooding may also affect the scheduling of farm activities, such as land preparation, planting, spraying, and harvesting, and may entail additional expense due to its negative impact on the ease of doing the activities. Moreover, increased flooding events may increase the incidence of contaminating land with fertilizer and chemical residues, the spread of antibiotic-resistant microorganisms, the spread of pathogens from animal waste to crops, and the risk of pathogen outbreak (Lake et al., 2018).

Changes in temperature and rainfall patterns may alter the global spread and distribution of existing pests and diseases and enable new ones that may create new biosecurity challenges. The drier and warmer conditions in the east of New Zealand may lower the prevalence of some cereal crop diseases, while the warm and humid conditions in the west may aggravate some diseases, such as leaf blight in maize (Gavin, 2001). The use of plant protection agents against pests and diseases will most likely intensify, exacerbating environmental contamination and associated issues with chemical residues in food products (Lake et al., 2018). The use of biocontrol agents as an integral component of integrated pest management in New Zealand to reduce reliance on synthetic pesticides and promote sustainable pest control may not be viable in the future with the changing climate. The limited genetic variability of biocontrol agents may hinder crops' ability to adjust to new agro-climatic conditions (Gerard et al., 2010).

The abovementioned risks of climate change affecting local crop productions pose immense risks to New Zealand's food security. In addition to climate change, the declining area of land for crop production, limited water resources needed for irrigation, and continuous risk of existing and new pests and diseases threaten the country's domestic production

(Horticulture New Zealand, 2017a). New Zealand is a net exporter of agricultural products (e.g., dairy, beef, lamb, fruits, and vegetables) but also heavily depends on imports of some commodities (e.g., wine, nuts, processed vegetables, coffee, bananas, and table grapes) (Fresh Facts, 2019) as well as rice and wheat from countries that may be less resilient to climate change. According to Heyes (2019), while New Zealand may not experience food shortages as a direct effect of climate change, the increasing prices and availability of essential commodities imported from other countries may be a significant issue in the future.

1.1.5 Impacts of climate change on global and New Zealand potato production

The expected impact of climate change on potato production is mainly reduced crop yields, which have significant regional differences. Several potato cropping simulation models have been used to calculate potential crop yields considering different climate change scenarios in other regions. According to Hijmans (2003), in general, global potato production is expected to decrease by 18%–32% (without adaptations) and by 9%–18% (with adaptations). The temperature rise, provided all other requirements of the potato crop are available (e.g., water), is generally expected to increase the potato yield in England and Wales (Davies et al., 1997), Scotland (Peiris et al., 1996), the Netherlands (Wolf, 2002), and Finland (Carter, Saarikko, & Niemi, 1996). This is mainly due to the extended growing season and increased suitability of arable land for potato production. By contrast, potato yields are anticipated to drop in most parts of the USA (Tubiello, Rosenzweig, Goldberg, Jagtap, & Jones, 2002) due to extreme temperatures creating suboptimal growing conditions. In tropical and sub-tropical Asia, climate change is likely to have the most significant negative impacts on potato production. Simulation models in China (Chavas, Izaurralde, Thomson, & Gao, 2009; Guoju et al., 2013) and India (Dua, Singh, Govindakrishnan, Kumar, & Lal, 2013), the top two largest potato producers in the world, show a decreasing trend in tuber yields under climate change conditions. The negative effects of climate change on potato production can be recognized from the previous occurrence of relatively recent climate-related extreme events in potato production regions. The 2011 and 2012 drought and heatwaves in the USA caused significant damages to summer crops, including potatoes, leading to a billion-dollar worth of losses (NOAA, 2012). In 2010, Russia experienced an extreme drought that caused about 30% losses in their major potato production areas (Barriopedro et al., 2011). In 2016, in the southern states of Australia, particularly Tasmania and ‘Victoria’, flood-affected potato crops resulted in difficulty in harvesting (Braithwaite, 2016) and caused a shortage in ware and processing potatoes in the market.

New Zealand has a very favourable climate for growing potatoes owing to the shorter days or photoperiod that is conducive for tuber formation. However, there is a paucity of research done on the potential effects of abiotic stresses (e.g., heat and moisture stress) brought about by extreme weather conditions often linked with climate change in potato production across growing regions. Several studies have been conducted by the Plant and Food Research in the Canterbury region of the South Island of New Zealand to investigate the potential effects of water stress on the yield and tuber quality of potatoes under rain shelters. Canterbury has the largest potato growing area in New Zealand, and it commonly requires supplemental irrigation due to insufficient rainfall during the growing months to achieve economically viable yields. One of the studies showed that induced drought stress reduced the dry biomass production in three processing potato cultivars (i.e., ‘Russet Burbank’, ‘‘Moonlight’’, and ‘Karaka’); different physiological responses (e.g., leaf area index, water use, and radiation interception) were also observed among these cultivars, suggesting different adaptation mechanisms (Michel et al., 2019). In another study, early-season drought reduced the number of tubers per plant and therefore increased the tuber size; meanwhile, drought at the latter stage decreased the size and number of tubers by up to 20% in ‘Russet Burbank’ (Martin, Jamieson, Wilson, & Francis, 1992). On the other hand, the increase in atmospheric CO_2 due to climate change is expected to enhance plant growth and carbohydrate production. However, it may limit protein synthesis and essential minerals in some crops, including potatoes (Lake et al., 2018), potentially affecting its nutritional value.

Other than the adverse effects of abiotic stress on yield and tuber quality, an expected increase in disease incidence may contribute to possible severe economic losses in potato production. Intense and frequent future drought conditions coupled with high temperatures may increase the incidence and severity of potato common scab (*Streptomyces scabies*). Dry and warm soil conditions, especially during tuber initiation, are the most susceptible stage to potato common scab infection (Agriculture ‘Victoria’, 2020; Pandey, Sinha, Mysore, & Senthil-Kumar, 2015). On the other hand, wetter conditions due to extreme precipitation events may increase the incidence and severity of potato late blight, a devastating disease caused by a fungus-like pathogen (*Phytophthora infestans*) that infects vegetative parts and tubers at any crop growth stage. Increasing worldwide risk of potato late blight was observed with reference to historical climate data (Sparks, Forbes, Hijmans, & Garrett, 2014).

Some rather unique cultural practices in New Zealand potato production systems are also affected by changing climate. As a non-chemical method, the use of mesh covering to successfully protect crops from tomato-potato psyllid (TPP) was found to increase the average temperature by 1 °C under Canterbury growing conditions (Merfield, Geary, Hale, & Hodge, 2015). Potato crops under the mesh cover senesced earlier, indicating that their growth was enhanced compared with the control plants. The common practice of ground storing in New Zealand, where ready-to-harvest potatoes are kept in the ground for weeks or months until the weather and or market conditions are suitable before harvesting (Whenua Māori, 2020), could be negatively affected by extreme weather conditions. Exposure to heat and moisture stress (i.e., drought and flooding) may dramatically affect the tuber quality and ultimately the marketable yield of potato crops stored under the ground.

The risk of the supply of potatoes being affected by local extreme weather events is rather minimal because the production is geographically spread throughout the country (Horticulture New Zealand, 2017). The effects of climate change have not been substantial in the past to significantly affect the potato industry yet. In a case study done by Kim (2013), most fruit and vegetable growers in New Zealand, including potato growers, felt that climate change is non-existent or has no significant impact on horticultural crop production. Hence, no adaptation strategies have been discussed so far. However, recent media reports suggest that climate change is already affecting potato production in New Zealand. In the 2016/17 potato production season, the term “chipocalypse” was coined from reports of a likely shortage of crisping potato supply in the country (Bezzant, 2017). Adverse weather conditions are believed to cause potato planting and harvesting problems during the season. This was corroborated by an interview with a potato grower in Opiki, one of the major potato-producing areas in the district of Horowhenua on the North Island. The grower stated that the bad weather adversely affected his potato cropping twice in the same year (Moleta, 2018). First, his ready-to-be-harvested potatoes in the middle of 2017 rotted in the ground due to the unusually heavy rain that caused flooding in his paddocks, damaging about 50% of his crop. Second, his newly planted potatoes late in the same year were severely hit by the most prolonged drought (more than 40 days) he has ever experienced in his farm. According to the same grower, the recent weather pattern was observed to be more extreme, where April and May were typically dry months in Opiki, and harvesting was typically easy. However, in 2017, the paddocks were inundated. The high rainfall and flooding not only resulted in the loss of production but also increased the harvesting cost and thus the costs of production (Moleta, 2018). This was confirmed by NIWA's data that New Zealand's annual rainfall in 2017 was above average (120%–149% of the annual normal) (NIWA, 2018c), and that the major potato production areas of Horowhenua, Matamata, and Pukekohe in the North Island were the worst hit. In a personal communication, the agronomist of A.S. Wilcox and Sons (commercial potato growers) commented that the increase in the number of days with elevated temperatures in the 2017/18 season has impeded potato tuber bulking in Ohakune (Hart, 2018).

Potato New Zealand Chief Executive Chris Claridge (2018) mentioned in a radio interview that episodic extreme weather events, for instance increase in cyclonic weather patterns, directly impacted the farmers' ability to plant and harvest, which further affected the profitability and the ability to generate export proceeds. This information was confirmed by the situation report of the Ministry for Primary Industries (2018) that the prolonged periods of wet weather in the vegetable growing districts of Pukekohe, Matamata, and Horowhenua negatively affected the planting and harvesting of crops, leading to reduced marketable yields and supply issues for crisping potatoes during the latter part of 2017. Claridge (2018) also stated, "We are seeing increasing evidence that farmers are directly being impacted by climate change. The key issue is how we make the potato and the wider vegetable sector more resilient to climate change." This prompted Potato New Zealand to highlight climate change in the organization's 2018 Industry Strategy & Business Plan to help improve the industry's resilience and to meet the target of increased domestic and export productivity (Potatoes New Zealand, 2018b). With these anecdotal reports, it is therefore important to investigate and obtain actual evidence that extreme weather conditions or abiotic stress associated with climate change are already affecting the potato production system in New Zealand and to quantify and qualify their potential effects on yield and tuber quality. This study aims to identify how resilient the current commercial potato cultivars to abiotic stress associated with climate change are, in terms of their yield and tuber quality response.

1.2 Research Questions

The specific research questions central to this study are the following:

1. Is there evidence that abiotic stress associated with climate change affects the current potato production system in New Zealand?
2. How does abiotic stress associated with climate change affect the yield and tuber quality of potatoes in New Zealand?
3. Are commercial potato cultivars differentially susceptible to abiotic stress associated with climate change impacts?

1.3 Research Objectives

General objective:

The general objective of this study is to determine the effects of abiotic stress associated with climate change on the yield and tuber quality of selected commercial potato cultivars in New Zealand.

Specifically, the study aims to:

1. Determine the potential effects of abiotic stress associated with climate change on current commercial potato cultivars from baseline farm data;
2. Investigate the effects of abiotic stress on the yield and tuber quality of selected commercial potato cultivars through multi-environment trials (MET) in the field and under controlled conditions in a glasshouse and plant growth chamber trials; and
3. Identify commercial potato cultivar(s) better adapted to wide and/or location-specific effects of climate change under New Zealand conditions.

CHAPTER 2

Literature Review

2.1. Introduction

This literature review aims to discuss the potential effects of abiotic stress commonly associated with climate change in potato production and available adaptation strategies. This will also highlight knowledge gaps in this context and will identify potential benefits to the New Zealand potato industry under changing climate. Climate change is unequivocal, and the effects of abiotic stresses commonly associated with climate change, such as heat and moisture stresses and their combination, on the growth and development of potato crops have already been well-studied. In some field trials, it has been found that the influence of the environment on yield variation of potato crops is significant. Under experimental and commercial production conditions, environmental factors significantly contributed to potato crop yield variability by 20%–60% and 40%–80%, respectively (Kalbarczyk, 2004). In another study, the influence of the environment in the variation in potato yield was recorded at 40% (Trawczyński, 2009). However, given the unique climatic conditions of New Zealand and the apparent impacts of climate change, limited local studies were conducted on the potential effects of abiotic stress on potato crops under these conditions. Thus, these knowledge gaps and research questions should be addressed to contribute to the New Zealand potato industry's resiliency to climate change.

2.2 Effects of abiotic stress on potato production

Potato was domesticated originally over 7000 years ago in South America, where it was cultivated under short day length, cool temperatures, and relatively high light intensity and humidity. Potato was then introduced in Europe in the 1570s (Brown, 1993), where it had improved yields under growing conditions of long-day length and moderate temperatures. From Europe, potato spread to most parts of the world, including tropical and sub-tropical regions, where it thrived under sub-optimal conditions. Nevertheless, these conditions were improved with appropriate farm management systems (e.g., supplementary irrigation) and cultivation in relatively high altitudes, where temperatures are more favourable for potato growth and development. This suggests that potatoes could be grown in a wide range of environments. However, the optimum yield and quality are still best achieved in temperate climates (Haverkort, 1990). With the advent of climate change and various associated abiotic stresses, these conditions are expected to be less favourable for potato production, negatively impacting tuber yield and quality. Abiotic stresses (e.g., heat, drought, high salinity, heavy metals, and ultraviolet radiation) are environmental conditions that can affect the potato crop at different growth stages (Appendix 2.1), negatively impacting yield and tuber quality.

2.2.1. Effects of heat stress

Heat stress is defined as "the rise in temperature beyond a threshold level for a period of time sufficient to cause damage to plant growth and development" (Wahid, Gelani, Ashraf, & Foolad, 2007). Heat stress is generally 10 °C–15 °C above ambient temperature (Rykaczewska, 2017). Being a temperate crop, potato grows well at ambient air temperatures around 20 °C, although it is known to have specific temperature requirements. The above-ground parts grow best within 20 °C–25 ℃, while tubers form and grow ideally between 15 °C and 20 °C (Rykaczewska, 2017). On the other hand, heat tolerance is generally defined as "the ability of the plant to grow and produce economic yield under heat stress" (Hasanuzzaman, Nahar, Alam, Roychowdhury, & Fujita, 2013). Several potato cultivars and accessions have been observed to have a certain level of heat tolerance under controlled environment and field conditions (Levy, Kastenbaum, & Itzhak, 1991; Rykaczewska 2015; Reynolds & Ewing, 1989).

2.2.1.1 Heat stress effects on morpho-agronomic characteristics and physiology of potato crops

Constant, elevated temperatures cause various morpho-anatomical, physiological, and biochemical changes in plants (Wahid et al., 2007). Heat stress affects different physiological functions, such as photosynthesis, transpiration, stomatal conductance, and water use efficiency (WUE), of potato crops. Heat stress was found to be associated with reduced photosynthetic rate (Hastilestari et al., 2018), increased transpiration rate and decreased stomatal resistance (Wolf, Olesinski, Rudich, & Marani, 1990), and decreased WUE (Guoju et al., 2013). Havaux (1993) observed that at about 38 °C, rapid and permanent loss of photosystem occurred in potato. In a study conducted by Hastilestari et al. (2018) on 'Agria' potatoes in a growth chamber, the high day and night (29 °C/27 °C) temperatures reduced photosynthesis and, correspondingly, the photosynthate production. Additionally, photosynthate partitioning to above-ground parts was enhanced due to weaker sink strength by the tubers (Hastilestari et al., 2018). However, differential susceptibility to heat stress effects on photosynthesis performance was observed in past studies (Hancock et al., 2014; Lafta & Lorenzen, 1995; Wolf, Olesinski, Rudich, & Marani, 1990). Moderately heat-resistant genotypes, such as ‘Desirée’ and ‘Norchip’, were found to be unaffected or even had increased photosynthetic activity under elevated temperatures (30 °C) (Hancock et al., 2014; Lafta & Lorenzen, 1995). Moreover, some potato clones showed an adequate capacity for photosynthesis at higher temperatures (40 °C) compared with some common cultivars (Wolf, Olesinski, Rudich, & Marani, 1990). However, a noticeable reduction in stomatal resistance and an increase in transpiration rate linked with increased air and leaf temperature differences were observed (Wolf, Olesinski, Rudich, & Marani, 1990). Hastilestari et al. (2018) suggested that heat-tolerant cultivars may not surprisingly sustain photosynthesis longer under elevated temperatures than heat-sensitive cultivars. Typically, an increase in temperature may increase the crop’s photosynthesis and WUE, but, at supra-optimal temperatures, both photosynthesis and WUE are negatively impacted (Guoju et al., 2013). At higher temperatures, the plant’s transpiration rate (Hammes & De Jager, 1990) and soil moisture evaporation are higher, resulting in more reduced crop WUE (Zhao & Yu, 2008). Stomatal conductance plays an essential role in canopy thermo-regulation under heat stress (Rizhsky, Liang, & Mittler, 2002). Schafleitner et al. (2007) observed that stomatal bahavior is somehow related to leaf area, where plants with larger canopies even under heat stress had better stomatal aperture control over plants with smaller canopies. The occurrence of heat stress is also associated with decreased leaf area (Prange, McRae, Midmore, & Deng, 1990). For this likely reason, in some heat tolerance screening and breeding programs among *Solanum* species, only accessions that showed decent shoot growth under high temperatures were further screened for tuberization (Reynolds & Ewing, 1989). The reduction in photosynthetic activity and shoot growth was attributed to chlorophyll loss, accelerated senescence, reduced CO_2 fixation rates, and reduced stomatal conductance among heat-sensitive accessions in comparison with heat-tolerant accessions (Reynolds, Ewing, & Owens, 1990). In some studies, up to 20% decrease in photosynthetic pigments like chlorophyll *a* and *b* and carotenoids was observed (Hancock et al., 2014). However, this phenomenon did not affect the carbon assimilation, which increased by 70% in this particular study due to the enhanced stomatal conductance under well-watered conditions (Hancock et al., 2014). Hancock et al. (2014) added that heat stress reduced the yield even with enhanced photosynthetic activity. This finding is probably due to limited carbohydrate production and translocation that result in reduced dry matter production in tubers under elevated temperatures (Ghosh, Asanuma, Kusutani, & Toyota, 2000). However, other environmental factors, such as photoperiod (Ewing, 1981) and light intensity (Menzel, 1985), interact with heat stress and may cause differences in the response of potato cultivars. Other than atmospheric temperature, elevated soil temperatures negatively impacted potato growth. Hammes and De Jager (1990) observed that soil temperatures above 20 °C reduced the net photosynthetic rate, particularly before tuber initiation. Although the cause of the reduction in the photosynthetic rate has not been precisely determined, it was suggested to be due to premature leaf senescence.

In potatoes, heat stress at different stages of plant growth also results in tuber physiological disorders, including deformations, gemmations, pre-harvest sprouting, and physiologically immature tubers (Rykaczewska, 2017). According to Rykaczewska (2015), the occurrence of secondary tuberization and other tuber physiological disorders must be considered as an indicator of susceptibility to the negative effects of heat stress during the growing season. Potato crops exposed to heat stress are often characterized as having thicker stolons, with more numerous and deformed tubers (Gawronska, Thornton, & Dwelle, 1992). Moreover, brief periods of heat stress cause tuber cracking attributed to the tuber's high internal turgor pressure (Lugt, Bodlaender, & Goodijk, 1964). The incidence of tuber physiological disorders is influenced by the phenological timing when the stress occurred and is often the highest at the emergence stage. Heat stress at the early growth stage under favorable soil conditions was found to promote second growth and gemmation in potatoes than under drought conditions (Rykaczewska, 2013). Potato crops subjected to heat stress are partially immature due to secondary growth (Rykaczewska, 2017). Heat stress just after tuber initiation leads to fewer and malformed tubers (Levy, 1985). Meanwhile, exposure to heat stress at the latter plant growth stage, before tuber maturity, often results in pre-harvest sprouting (Rykaczewska, 2017). Another known causative factor for pre-harvest sprouting is the high soil temperature when the soil is exposed to heat due to incomplete canopy coverage (Shock, Zalewski, Stieber, & Burnett, 1992). Moreover, differential susceptibility to tuber physiological disorders was observed among potato cultivars (Rykaczewska, 2017). These findings elucidate the presence of a wide array of negative responses operating at elevated temperatures that affect the different morpho-physiological characteristics of the potato plant and the yield and tuber quality.

2.2.1.2 Heat stress effects on yield and tuber quality

Heat stress negatively impacts yield and tuber quality. Tuber growth and development is sharply inhibited or even completely ceases at temperatures >30 °C (Acquaah, 2012; FAO, 2008e). According to Monneveux et al. (2014), tuber yield is significantly reduced at high ambient air temperature (30℃ day/23℃ night) combined with soil temperature (>18℃). Tuberization and the number of tubers formed are typically enhanced under lower temperatures and tuber-inducing short-day lengths. However, under elevated temperatures, tuberization is inhibited (Ghosh et al., 2000; Hancock et al., 2014), resulting in fewer tubers per plant. This, therefore, leads to the reduced need for the allocation of photosynthates to the tubers (Ghosh et al., 2000) but increased allocation to the above-ground-parts of haulm (Hancock et al., 2014), as observed in the increase in the dry stem weight of potato crops exposed at high temperatures (Prange et al., 1990). Long days and elevated temperatures enhance dry matter partitioning of the haulm, promoting haulm and root growth but hindering tuber growth (Lafta & Lorenzen, 1995; Levy & Veilleux, 2007). This results in increased leaf dry matter but reduced tuber fresh and dry weights, dry matter, and consequently reduced harvest index (Hancock et al., 2014; Hastilestari et al., 2018). Heat stress also promotes the development of small tubers (Hancock et al., 2014; Tang et al., 2018). Rykaczewska (2017) observed an increase in the number of tubers measuring 1–3 cm in potato crops exposed to heat stress regardless of the soil moisture level. Rykaczewska (2017) also observed that heat stress during the growing period caused negative impacts on the final yield of the tested potato cultivars, and the most substantial effect was noticed when the stress was introduced during the flowering stage. The flowering stage typically coincides with tuber initiation, as the photoperiodic pathway controlling the short-day tuber induction has the same features as the photoperiodic pathway of flowering (Brown, 2007). Although Rykaczewska (2015b) mentioned that the earlier heat stress impacts the potato plant is, the higher the adverse effect on plant growth and tuber yield will be. Heat stress at the early growth stage of potato resulted in an average of 24% decrease in yield (Rykaczewska, 2015b). This concurs with the findings of Ghosh et al. (2000), who reported that potato crops subjected to heat stress (30 °C) between the vegetative and tuber initiation stages resulted in maximum yield reduction due to the decrease in the number of tubers per plant. By contrast, Lafta and Lorenzen (1995) stated that heat stress reduced the total tuber dry weight by 24%–29%. On the other hand, heat stress between tuber bulking and maturity stages resulted in lowering of the dry tuber yield but had a relatively weaker effect than in any other growth stages (Ghosh et al., 2000). Furthermore, at all growth stages, heat stress reduced the average tuber weight. In contrast, low temperature (15 °C) between tuber initiation and initial tuber bulking stages resulted in the highest tuber yield (Ghosh et al., 2000). The high temperature at all growth stages decreased the specific gravity (as a measure of dry weight%) of the tubers, but the low temperature increased the specific gravity (Ghosh et al., 2000). In the same way, high temperatures reduced the starch content by approximately 60%, but low temperatures ameliorated starch accumulation in the tubers (Hastilestari et al., 2018).

2.2.2 Effects of moisture stress

The potato crop is well known to be sensitive to drought (van Loon, 1981) and flooding (Hincksman, 2011). This section will focus mainly on the effects of drought, being a more serious abiotic stress under future agro-climatic conditions. However, the effects of flooding will also be briefly covered in the latter part of this section.

Drought is categorized into four types, namely, meteorological, agricultural, hydrologic, and socio-economic (Wilhite & Glantz, 1985). Among these drought types, agricultural drought relates to the yield and morpho-physiological impacts of water shortages on crops. Agricultural drought arises when soil moisture is insufficient for a crop at a particular time that significantly affects yield (Panagoulia & Dimou, 1998). The potato crop requires on average 500–700 mm of water per growing season for optimum growth and yield (FAO, 2008d). Insufficient water availability will become more critical in the next decades due to climate change and the extension of potato production in drought-prone areas. Potatoes often suffer from periods of drought due to erratic rainfall and inadequate irrigation (Thiele, Theisen, Bonierbale, & Walker, 2010). Most of the potato-growing regions, especially those with rain-fed production, are already affected by the increasing drought periods.

The susceptibility of potatoes to drought is usually attributed to their shallow root system, inability to sufficiently adjust after exposure to a period of drought (Harris, 1978; van Loon, 1981), and short root length (Gregory & Simmonds, 1992). The severity of drought effects depends on the stage of potato plant growth and the duration and intensity of the stress (Schafleitner, 2009). Emergence and tuberization are usually the critical growth stages when water stress mostly affects the final tuber yield (Martinez & Moreno, 1992).

2.2.2.1 Moisture stress effects on morpho-agronomic characteristics and physiology of potato crops

Similar to heat stress, moisture stress (i.e., drought and flooding stress) affects the different morpho-agronomic characteristics and physiology of the potato crop. Drought stress was found to be linked with reduced photosynthetic activity (Li et al., 2017a; Rykaczewska, 2017a), reduced transpiration and stomatal conductance (Hirut et al., 2017; Li et al., 2017a; Schafleitner, 2009; Shahnazari, Liu, Andersen, Jacobsen, & Jensen, 2007), increased chlorophyll content (Hirut et al., 2017), and increased water use efficiency (Guoju et al., 2013). According to Li et al. (2017a), the photosynthesis rate was decreased by irradiance capture reduction, heat dissipation, and enzyme activity regulation under mild drought stress and by impairment of photosystem II and antioxidant enzymes under severe drought stress. On the other hand, the chlorophyll content increased under drought stress (Hirut et al., 2017), which can be attributed to turgor loss or decrease in leaf growth (Rolando, Ramírez, Yactayo, Monneveux, & Quiroz, 2015; Teixeiraa & Pereiraa, 2007). Under drought stress, the transpiration rate and CO_2 influx into the leaves decreased due to the closing of the stomata (Li et al., 2017a). Hence, drought-tolerant plants are usually characterized by high stomatal resistance under drought and low stomatal resistance under irrigated conditions (Araghi & Assad, 1998; Pinheiro, DaMatta, Chaves, Loureiro, & Ducatti, 2005). Inadvertently, drought stress also promotes the formation of more stomata but of smaller sizes and pores (Banik, Zeng, Tai, Bizimungu, & Tanino, 2016).

A typical morphological response of crops to drought stress is the reduction in the growth of the above-ground parts. Past drought studies on potatoes reported decreases in plant height, leaf growth, leaf area index, and canopy cover as well as shoot biomass and dry matter (Deblonde, Haverkort, & Ledent, 1999; Hirut et al., 2017; Jefferies, 1992; Mane et al., 2008; Shock, Zalewski, Stieber, & Burnett, 1992; Tourneux, Devaux, Camacho, Mamani, & Ledent, 2003b). Moreover, drought stress reduced the total number of stems by 28% in the field but not under greenhouse conditions (Lahlou, Ouattar, & Ledent, 2003). This finding could be attributed to the lower light intensity and closer planting density in the greenhouse. However, when only the number of the main stem was considered, drought had no significant effect but had substantial differences among cultivars. In other studies, the number of stems per plant was neither affected by drought (Tourneux et al., 2003b) nor occurrence of precipitation. According to researchers, the number of stems may be affected by other important factors, such as temperature changes during the growing season and storage conditions (Haverkort, Van De Waart, & Bodlaender, 1990), pre-sprouting (Harris, 2012; Haverkort et al., 1990), size (Haverkort et al., 1990; Wurr, 1974), and physiological age (Iritani, 1968) of the seed tubers. Consequently, the reduction in the growth of the above-ground parts results in decreased irradiance interception (Tourneux et al., 2003b), fresh biomass weight (Li et al., 2017a), and efficiency in dry matter production (Tourneux et al., 2003b).

In contrast to the above-ground parts, root growth is less sensitive to drought stress. Typically, root growth is enhanced under drought stress as observed in past studies where plants had increased root: shoot ratio (Turner, 1986), specific root length (Jefferies, 1993), and total root length (Shi et al., 2015). Shock et al. (1992) suggested that plants exposed to drought stress at the earlier growth stage may be tolerate it better than succeeding drought stress due to the higher root: shoot ratio. These responses support the plant to maximize water uptake during drought conditions. Cultivars were also reported to exhibit differential susceptibility to drought stress. Drought-tolerant cultivars were observed to have a robust root system, i.e., longer roots with better capacity for water absorption than drought-sensitive cultivars (Shi et al., 2015). In another study (Puértolas, Ballester, Elphinstone, & Dodd, 2014), the potato cultivar ‘Horizon’ performed better than ‘Maris Piper’ due to its higher root density in deeper soil layers (>40 cm), where it secured access to stored water, especially during the tuber bulking stage.

On the other hand, flooding can occur in the field because of heavy rainfall or from flooding from adjacent bodies of water, such as lakes, rivers, and streams. If soil remains waterlogged for extended periods, then the plant health is usually affected and yield may reduce; or if severe, then it results in total crop loss. In potatoes, waterlogging limits oxygen supply in the soil and result in the enlargement of lenticels (Hillerm & Thornton, 2008). Lenticels are inconspicuous pores on the tuber surface that are responsible for gas exchange. Prolonged waterlogging increases the severity of the enlarged lenticels, and tubers become prone to diseases, such as tuber soft rot, rendering them non-marketable. In some studies, however, overwatering did not affect potato tuber quality but was attributed to free-draining soil (Martin et al., 1992).

2.2.2.2 Moisture stress effects on yield and tuber quality

Yield and tuber quality reduction as a result of moisture stress is associated with the negative impacts on the different physiological, morphological and agronomic characteristics of the potato crop as discussed in the preceding section. Drought stress reduced the potato yield by decreasing the leaf area and photosynthesis per unit of leaf area (van Loon, 1981) and the number of stolons formed; consequently, it resulted in reduced tuber number (Eiasu, Soundy, & Hammes, 2007a; Martin et al., 1992), size (Schafleitner, 2009), fresh weight (Alichea et al., 2018), dry biomass production (Michel et al., 2019), and harvest index, with negative impacts on final tuber yield.

Moreover, similar to heat stress, these responses to drought stress often depend on phenological timing and duration of the stress in potato plants. Drought stress at stolon and tuber initiation stages hampered shoot growth and limited the number of stolons formed, resulting in reduced tuber number (Eiasu, Soundy, & Hammes, 2007b) but increased tuber size (Martin et al., 1992). Further, drought stress during the tuber bulking stage decreased the yield more than that during other growth stages (van Loon, 1981). This decrease in tuber yield under drought stress was correlated to the reduction of leaf area and photosynthesis rate per unit of leaf area (van Loon, 1981). Likewise, short water stress during tuber maturation increased malformations like dumbbell-shaped, knobby, and pointed-end tubers (MacKerron & Jefferies, 1988), which reduced the marketable yield.

On the other hand, yield reduction due to flooding usually results from the rotting of potato tubers exposed to prolonged flooded conditions. The increased severity of the enlargement of lenticels due to the anaerobic conditions of flooded soils greatly reduces tuber quality, and therefore affects the final marketable yield as well.

2.2.3 Effects of combined heat and moisture stress

Climate models predict an increased likelihood of extreme weather conditions, that is, a decrease in total annual precipitation with intense periods of drought and extreme temperatures, including more frequent heat waves (IPCC, 2014). In the field, heat stress and drought stress are two different abiotic stresses that commonly coincide or separately when supplemental irrigation is used (Rykaczewska, 2015a). Potatoes are susceptible to heat stress (Levy & Veilleux, 2007) and drought stress (Monneveux et al., 2014). When heat stress is accompanied by drought, significant yield and tuber quality loss are experienced, with considerable differential susceptibility among cultivars (Ahn & Zimmerman, 2004). This agrees with the findings of Rykaczewska (2013), who reported that continuous exposure of potato crops to combined heat and drought stress for two weeks during the flowering stage resulted in significant yield reduction among susceptible (50%) and tolerant (25%) cultivars. The lower reduction in the yield among the more tolerant cultivars can be attributed to the reduced secondary tuberization and fewer tubers with physiological disorders. In a succeeding study, Rykaczewska (2017b) also found that heat and drought stress during flowering and tuber development significantly reduced the size of individual potato tubers compared with heat stress under adequate soil moisture, and both periods of stress and type of cultivar had significant influences. The high temperature under drought conditions negatively impacted the performance index of photosystem II (ratio of variable to maximal chlorophyll *a* fluorescence) activity in the tested potato crops with variability depending on the period of stress and the type of cultivar (Rykaczewska, 2017a). Similarly, a combination of heat and drought stress under field conditions intensified tuber malformation and sprouting (Levy, 1996). In general, limited information is available on the effect of combined heat and drought stress at different stages of potato tuber growth (Levy, 1984; Levy & Veilleux, 2007).

2.3. Adaptation strategies

Adaptation strategies are essential to mitigate the negative impacts of climate change on potato production. Adaptations can provide about 10%–15% yield advantage over situations without adaptations (Lotze-Campen, 2011). These adaptation strategies could be categorized either as agronomic options, such as plant, soil, and water management; or genotypic options by breeding new cultivars for new agro-climatic conditions (George, Taylor, Dodd, & White, 2018). Combining agronomic and genetic options shows a promising prospect in climate change mitigation.

2.3.1. Agronomic options

Abiotic environmental stress is estimated to cause about 70% of yield loss in most crops (Acquaah, 2012). Several agronomic options are being implemented to mitigate the negative impacts of climate change. These options include shifting of the planting schedule and adjustments in crop rotation and water management and irrigation. Shifting of planting schedules allows farmers to make use of the longer growing season given the climate change effects on increased winter temperatures. Earlier planting could lead to increased yield potential for late-maturing cultivars, while earlier harvesting could result in avoidance of heat and drought stress in late summer (Clark et al., 2012; Lotze-Campen, 2011). Adjusting crop rotations can help mitigate the changing climate conditions by using better-adapted crops to the climate change effects (Olesen & Bindi, 2002). Using more diverse crops leads to lesser dependence on weather conditions in specific growing seasons. Hijmans (2003) suggested that at high latitudes, change in the time of planting, use of later maturing cultivars, and relocation of potato production sites could result in the reduced effect of climate change. However, at lower latitudes (tropical and sub-tropical regions like in some parts of New Zealand), shifting in planting time or location is less feasible due to the short growing seasons and limited arable areas. In some situations, such options may be inaccessible or even inappropriate due to plant–biological limitations and technological and financial restrictions. The use of more stress-tolerant cultivars could be more feasible to mitigate the effects of climate change in these regions. Hence, an alternative is to breed or select cultivars that can better resist abiotic environmental stresses while still providing economically viable crop yields.

2.3.2. Genetic options

Introduction of new crop cultivars is among the mitigation and adaptation strategies to address the potential impacts of climate change; this strategy includes breeding programs focusing on selecting new cultivars with higher heat tolerance, greater salinity tolerance, lower water requirements, higher moisture tolerance, and improved pest and disease resistance (ADB, 2014). Crop cultivars are chosen according to current market value and within the particular constraints imposed by local soil and climate (Clark et al., 2012).

Potato is often considered as a heat- and drought-sensitive crop, and its production is threatened by the increasing incidence of abiotic stresses in major production areas worldwide. Considerable research has been done to understand the physiological, biochemical, and genetic underpinnings of stress tolerance in potatoes as a foundation for improving their performance under said conditions. Genetics plays a big role in potato crop tolerance or susceptibility to different abiotic stresses. Breeding and selection of new varieties and subsequent trials determine the stability and adaptability of potato crops under different environmental conditions.

2.3.2.1. Breeding for abiotic stress

Potato breeding priorities have evolved in the past centuries. In the European Union, where the majority of new potato cultivars are bred, breeders strive to improve the economic and environmental sustainability of potato production by developing varieties with high yield, increased resistance to pests and diseases, increased water and nutrient use efficiency, high consumer acceptability, and improved nutritional and health benefits (Bradshaw, 2007). However, the response of new potato cultivars to abiotic environmental stresses is still of less priority in breeding programs. Perhaps, this is because potato was not considered as a crop of major importance in production areas with extreme conditions, e.g., drought and heat-prone areas (Li et al., 2017b). In the CIP list of Release and Adoption of Improved Potato Varieties in Southeast and South Asia, only 95 out of 457 released varieties and correspondingly 54 out of 225 adopted varieties have resistance against abiotic stresses, i.e., drought, heat, and frost (Gatto et al., 2018). Moreover, Gatto et al., (2018) observed that the release of abiotic stress-resistant potato varieties increased significantly since early in 2000 due to the strengthened adaptation measures to climate change.

The publication of the potato genome sequence is a key breakthrough in potato biology and genetics that could accelerate the breeding process. An understanding of the potato genetic blueprint would give the option to introduce desirable characteristics to existing cultivars by using advanced breeding techniques, such as marker-assisted selection (Dale, Sharma, & Bryan, 2016). Several genes involved in drought and heat tolerance in potatoes have already been identified in the past years (Monneveux et al., 2014; Mozos et al., 2018).

The adverse effects of abiotic stress can be mitigated by developing potatoes with tolerance to heat (Levy, Kastenbaum, & Itzhak, 1991; Veilleux, Paz, & Levy, 1997) and drought (Bradshaw & Bonierbale, 2010; Obidiegwu, Bryan, Jones, & Prasha, 2015). Moreover, breeding for tolerance to physiological tuber disorders associated with abiotic stresses is essential for economically viable production (van der Zaag & Horton, 1983). However, breeding for abiotic stress tolerance is a challenge because it is a genetically complex and multigenic trait requiring multiple pathways (Obidiegwu et al., 2015). Potato breeding is also even more complicated due to its autotetraploid origin (four different alleles at a locus) (Acquaah, 2012). On the other hand, researchers suggest that improvements in resistance to abiotic stress could come from wild species, adapted germplasms, and heritage crops because they have survived and evolved under extreme environmental conditions (Acquaah, 2012; Roskruge, Puketapu, & McFarlane, 2010; Sharma et al., 2013). The shoot and root biomass of potato landraces [*Solanum tuberosum* L. ssp. *andigena* (Juz & Buk) Hawkes] were negatively affected, but their yield was maintained under drought stress (Mane et al., 2008). This result agrees with the findings of Cabello et al. (2012), who reported that landraces had lower reduction in tuber yield, number, and weight under water-limited conditions in comparison with improved varieties within a breeding program.

In the review made by George et al. (2017), an ideotype with tolerance to abiotic stresses, such as drought, heat, and salinity, while maintaining an effective photosynthetic activity should be developed. George et al. (2017) further described the ideotype as follows: early maturing, achieves rapid canopy closure, water use efficient, maintains tuberization even under abiotic stress, maintains stomatal density and opening, has delayed senescence, produces more epicuticular waxes, and has increased root system size.

In New Zealand, early breeding programs focused mainly on increasing the yield of potatoes and less on other traits (Genet & Anderson, 1985). However, over the years, the breeding objectives prioritized major potato pests and diseases, including potato leafroll virus, potato cyst nematode, powdery scab, and tomato-potato psyllid. The only potato breeding program in New Zealand is being spearheaded by the government-owned Crown Research Institute, Plant and Food Research Ltd. The programme focuses on the development of potato cultivars with consumer-desired traits, including nutritional value, color, and flavor, and increasing quality and productivity for processing – size, shape, and cooking quality (Plant & Food Research, 2018). Nutrition-efficient cultivars are also sought as a need because of the increased nitrogen and phosphate leaching concerns in the potato production system (Christian, 2017). However, with the looming effects of climate change and its associated abiotic environmental stress that affects the major potato production regions in New Zealand, the need for potato cultivars with tolerance to such stress is imperative.

2.3.2.2. Multi-environment trials (MET)

Before releasing a new cultivar, promising genotypes of high potential are evaluated at different locations and over several years to determine the degree of adaptation (Acquaah, 2012). A multilocation trial is a practice used to evaluate such cultivars or strains (Piepho, 1996). This trial plays a vital role in plant breeding and agronomic studies. Data from this trials in an agricultural setting have the following primary objectives: (i) to estimate and predict yield based on limited experimental data accurately; (ii) to determine yield stability and the pattern of the response of genotypes or agronomic treatments across environments; and (iii) to provide reliable guidance for selecting the best genotypes or agronomic treatments for planting in future years and at new sites (Crossa, 1990).

The environment is per definition one of the critical factors in multilocation trials. It represents the conditions in which the plant grows and includes locations, seasons, years, and management practices adopted (Acquaah, 2012). In genotype evaluation, the environment could be categorized as predictable (e.g., soil type, planting dates, fertilizer, irrigation) and unpredictable (e.g., rainfall, temperature, relative humidity). To evaluate the effect of unpredictable environmental factors, scholars tested genotypes at different locations (genotype x location) or in different years (genotype x years) or a combination of these factors (genotype x location x years) through multi-environment trials (MET) (Acquaah, 2012). MET is necessary because trials in only one type of environment could have consequences on performance when grown in different types of environments. Hence, selection would be improved if done in the range of environments similar to those in which the cultivar is to be grown (Bradshaw, 2007b).

Genotype x environment (G x E) interaction is assessed to quantify the effects of the abovementioned unpredictable environmental factors. G x E interaction is said to occur when two or more genotypes are compared across different environments, and their relative performances are found to differ (Acquaah, 2012). From a plant breeder’s perspective, better breeding strategies could be used to develop adapted genotypes for specific locations by measuring the G x E interaction. Further, G x E could be used in the selection and recommendation of cultivars (Hongyu, Garcia-Pena, Araujo, & Dias, 2014).

The two most widely used statistical tools in the analysis of MET are the Additive Main effects and Multiplicative Interaction (AMMI) and the Genotype Main effect plus Genetics × Environment interaction (GGE). The AMMI is an essential tool used to evaluate several genotypes established in several environments; it can identify stable and adaptable genotypes (cultivars) and define the intensity of GxE interaction (Crossa, 1990). Both AMMI and GGE tools provide a comprehensive interpretation of genotype and GxE interactions to identify the best-performing genotype across environments in METs.

METs have been widely used in the evaluation of grains and cereals (Crossa, 1991, 1989; Eckhoff et al., 2017; Ram, 2007), legumes (Narh et al., 2015; Rubio, 2004; Bertagnolli et al., 2002), vegetables (Behera, 2015; Patila et al., 2016; Yang et al., 2010), fiber crops (Adugna & Labuschagne, 2003), and other crops. In potatoes, MET is used for testing and screening for improved tuber yield (Paget et al., 2015; Bai et al., 2014; Wang et al., 2017) and disease resistance (Paget, 2014). The International Potato Center (CIP) is extensively validating potato germplasms and collections for heat, drought, and salinity tolerance traits in MET settings to assess the suitability of potato clones for specific locations.

2.4. Summary and research gap

Abiotic stresses, such as heat, drought, flooding, and their combined combination, influence potato growth and development and affects yield and tuber quality. Climate change is an impending threat to the potato industry and agriculture sector in New Zealand; as such, the performance of new and existing commercial potato cultivars under adverse environmental conditions should be investigated to better equip growers with decision-making systems especially on choosing varieties to grow. Agronomic and genotypic (breeding) adaptation strategies are viable options depending on the availability of the technologies and the capacity of the end-user. Traditional potato breeding requires 12 to 20 years to develop new varieties that might be able to tolerate or resist abiotic stress; in this regard, a strategic alternative is to conduct multi-environment trials (MET) for existing potato cultivars in New Zealand to determine their stability and adaptability in major production areas.

CHAPTER 3

Baseline Data Collection on Potential Impacts of Abiotic Stress Associated with Climate Change on Commercial Potato Cultivars

3.1 Introduction

Potatoes are temperate crops with an optimum shoot and tuber production occurring at mean daily temperatures of 18 °C–20 °C (FAO, 2018b); although it is known to have specific temperature requirements, the above-ground leaf and stems grow best within 20 °C–25 °C while the ideal temperature for tuberization and tuber growth is 15 °C–20 °C (Rykaczewska, 2015b). Tuberization could be delayed by one week at temperatures below 15 °C and by three weeks at temperatures higher than 25 °C (Levy & Veilleux, 2007); at above 30 °C, tuber growth is sharply inhibited (FAO, 2018b).

Additionally, the photosynthetic rate abruptly declined at temperatures above 30 °C (Dwelle, Kleinkopf, & Pavek, 1981). The high temperature in subsequent stages of potato plant development is generally known to induce various tuber physiological disorders (Martin et al., 1992; Rykaczewska, 2017a). Besides temperature, the potato crop is well known to be sensitive to drought (van Loon, 1981) and waterlogging (Hincksman, 2011). The susceptibility of potatoes to drought is usually attributed to their shallow root system and inability to readily recover after exposure to a period of water stress (Iwama, 2008; Opena & Porter, 1998). If soil is waterlogged for extended periods, then yield reduction or total crop loss can occur through a decline in carbon assimilation and damage by plant pathogens.

With the advent of climate change and its current impact, the potential effects of associated abiotic stresses (e.g., heat and moisture stress) on the yield and tuber quality of commercial potato cultivars currently grown in New Zealand should be studied. Therefore, the goals of the baseline data collection were (i) to determine early evidence that abiotic stress associated with climate change is already affecting the current potato production system in New Zealand; (ii) to initially determine how it affects the yield and tuber quality of potatoes; and (iii) to investigate if commercial potato cultivars have differential levels of susceptibility to abiotic stress effects.

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This chapter presents the preliminary findings of the baseline data collection in February and March 2018 in three selected potato production sites in the North Island. The data collected were divided into three sections: (1) agro-climatic and farm characteristics, (2) recent and historical weather data, and (3), morpho-agronomic and physiological baseline data of representative potato cultivars from the selected trial sites.

3.2 Materials and methods

3.2.1 Sites

Three commercial farms in the North Island were identified and selected for baseline data collection (Figure 3.1). The selection of the farms was based on being a representative commercial potato production area in the region and each within a unique climate zone. Site No. 1 is in farm of the A.S. Wilcox and Sons Ltd. (-39.500, 175.459) in the town of Ohakune (Manawatu-Wanganui region) in the central North Island (Figure 3.1a). It is situated about 10 km southeast of Ohakune town and 30 km southwest of Mt. Ruapehu at 593 me above sea level (masl). Site No. 2 is in the Freshpik Farms Ltd. (-40.465, 175.481) in the town of Opiki, Horowhenua District (Manawatu-Wanganui region) in the southwest North Island (Figure 3.1b). It is located on the floodplain 3 km south of the Manawatu River and 15 km southwest of Palmerston North City at only 3 masl. Site No. 3 is in Lawson's True Earth Farm (-39.624, 176.738) in the town of Hastings (Hawke's Bay region) in the eastern North Island (Figure 3.1c). It is located about 4 km southeast of the Ngaruroro River, 8 km west of the Hastings main town, and 18 km west of the Hawke's Bay coast.

3.2.2 Data Collection

3.2.2.1 Farm characteristics

Baseline data to quantify and qualify the key production characteristics for the selected farms were collected in February 2018 through grower interviews using a standardized grower interview guide (Appendix 3.1). The data collected included total area of the farm, the area planted to potatoes, other crops planted, number of potato cropping per year, farming systems (e.g., irrigated/rainfed, crop rotation), sources of planting materials, and marketing systems used and target markets. Agronomic data recorded consisted of potato varieties planted in the farm, planting, and harvesting schedules, and cultural management practices, such as land preparation, planting depth and spacing, fertilizer and water management, pest and disease management, and harvesting practices. On postharvest quality management, postharvest practices including quality and size classification systems used were recorded. On weather and climate factors, sources of weather data of the farm as well as knowledge and perception of climate change of the farmer were recorded. Results of soil analysis were also requested from the farmers.

3.2.2.2 Weather data

Historical (60 years) and seasonal (2017/18) climate data such as maximum, average, and minimum atmospheric and soil temperatures, rainfall, sunshine hours, and growing degree days or GDD (base temperature of 4.4 °C) were retrieved (through CliFlo – New Zealand's web-based climate database) from several NIWA weather stations (where relevant data are available) within a 15 km radius to the sites (NIWA, 2020a). Soil temperature for the Hastings site was obtained from the Bridge Pa Climate Weather Station managed by the Hawke's Bay Regional Council. The mean temperature and total rainfall in the last 30 years (1988–2017) and previous 30 years (1958–1987) during potato growing seasons were compared. The number of days per month with atmospheric temperatures >25 °C and >30 °C and soil temperature >18 °C (supra-optimal temperatures for potato crops) were summarized and analyzed. The complete list of weather stations used as sources of climate and weather data retrieved through CliFlo is listed in Appendix 3.2.

3.2.2.3 Potato sample collection

One-time harvesting of tuber samples was done in March 2018 from the three sites. The main cultivars grown during the 2017/18 growing season was selected, which included table-type potatoes – 'Nadine', 'Vivaldi', and 'Victoria' in Ohakune; processing-type potatoes – 'Agria', 'Hermes', 'Taurus', 'Snowden', and 'Fianna' in Opiki; and table/processing-type potatoes – 'Agria' and 'Moonlight' in Hastings. Tubers from five plants per cultivar between 100–150 DAP (days after planting) were randomly harvested from different rows (100 cm between row spacing) in the field following the crop sampling protocol of the National Institute of Agricultural Botany (NIABCUF, 2016).

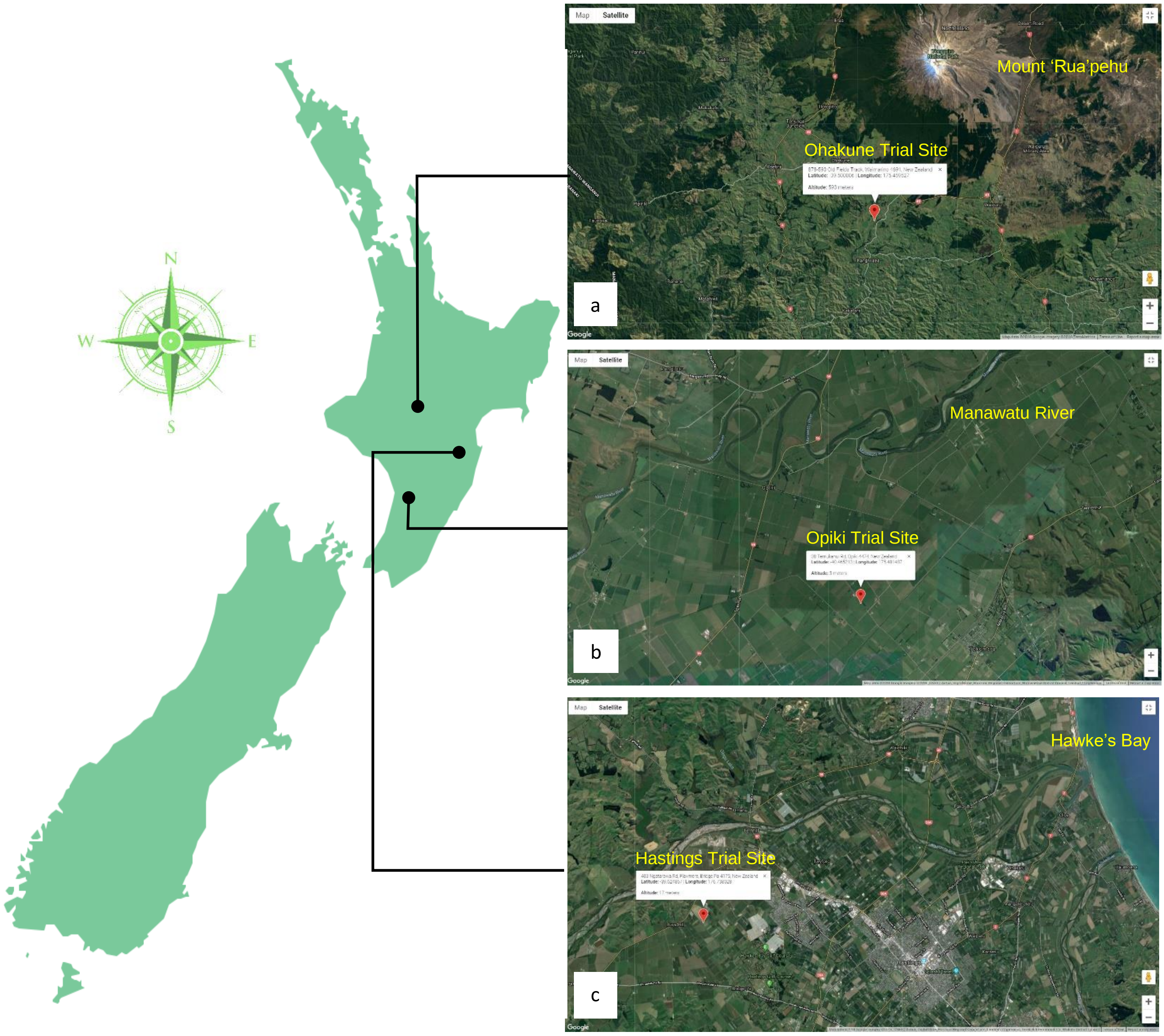


Figure 3.1 Satellite images of the location of the selected sites in (a) Ohakune – central North Island, (b) Opiki – southwest North Island, and (c) Hastings – eastern North Island (Google, 2020).

3.2.2.4 Yield and tuber quality data

At the Plant Growth Unit and Pasture & Crop Research Unit of Massey University in Palmerston North, yield and tuber quality data were measured and recorded, including estimated fresh tuber yield (t ha^{-1}), number of tubers per plant, dry matter content or DMC (%), specific gravity or SG, harvest index or HI (%), tuber size distribution, tuber physical characteristics (i.e., shape, skin color, eye depth, flesh color), and percentage of tuber physiological disorders.

Yield was estimated by weighing and averaging all the marketable tubers per cultivar per site and approximating them on a per hectare basis. Ten randomly selected marketable tubers from each cultivar were used to measure DMC and SG. SG is a measurement of the solids or starch content relative to the amount of water in the tuber. SG was determined by first weighing the tubers using a top-loading balance (weight in air) and then weighing while suspended in water (weight in water) (Haase, 2003) (Figure 3.2). SG was calculated following the equation:

$$\textbf{Specific gravity} = \frac{\text{Weight of tuber in air}}{(\text{Weight of tuber in air} - \text{Weight of tuber in water})}$$

Weight of tuber in air *Weight of tuber in water*

Figure 3.2 Set-up for specific gravity measurement: (a) weight of tuber in air measured using a digital top-loading balance and (b) weight of tuber in water using a metal mesh basket hanging under the digital top-loading balance and suspended in water.

DMC was determined by chopping and oven drying 10 potato tubers at 70 °C for five days or until the weight change was constant. The initial (fresh) and final (dry) weights after drying were measured. DMC was calculated by dividing the final dry weight by the initial fresh weight and multiplying by 100.

HI, which approximates the allocation of photosynthate between tubers and vegetative parts, was estimated using the ratio of tuber dry weight: total dry weight and multiplied by 100 (Mackerron & Heilbronn, 1985). Tubers were classified as marketable if within the marketable size standards and free or with minimal defects (mechanical or physiological disorders), while unmarketable if undersized or have severe to very severe defects. Tuber size was based on the TAG System for Potato developed by T&G Global (T&G Global, 2018), i.e., large (>90 mm), table (51–90 mm), gourmet (31–50 mm), and undersize (<30 mm). Tubers were characterized (i.e., shape, eye depth, and skin and flesh color) using the Descriptors for the Cultivated Potato developed by IBPGR-CIP (Huaman, Williams, Salhuana, & Vincent, 1977). Percent tuber physiological disorders (e.g., enlarged lenticels, netting, growth cracks, malformed tubers, sprouting, loose skin, and greening) were determined by dividing the number of tubers with defects over the total number of tubers per plant and multiplying by 100. The severity of tuber physiological defect (i.e., enlarged lenticels) was recorded and rated using the rating scale in Figure 3.3.

0 – none	5 – moderate
1 – very few	7 – severe
3 – few	9 – very severe

Figure 3.3 Rating scale for the severity of tuber physiological defect (i.e., enlarged lenticels) developed by the author.

3.2.3 Statistical analysis

All the statistical analyses were carried out in R statistical package version 3.4.0 (R Core Team, 2017). Significant difference was analyzed using Analysis of Variance (ANOVA), and mean values were compared among cultivars by using Tukey's HSD test if the overall test was significant. T-test was used for analyzing data from sites with only two representative cultivars.

3.3 Results and Discussion

3.3.1 Agro-climatic and farm characteristics

The agro-climatic and farm characteristics of each selected site are summarized in Table 3.1. Site No. 1 is A.S. Wilcox and Sons Ltd. (-39.500, 175.459) in Ohakune. Wilcox is a commercial potato farm that supplies about a quarter of the potato requirements in the domestic New Zealand market. The potato production areas of Wilcox are strategically located in different parts of New Zealand, including the Northland, Pukekohe, Matamata, Ohakune, and Canterbury, to ensure a year-round supply of table- and process-type potatoes. In Ohakune, potatoes are grown in about 150 ha of irrigated land in October and November; when they mature, all cultivars are ground-stored and harvested through winter (June–September). According to Wilcox Farm Manager Keith Watson, “Ohakune is nature's fridge because it is excellent for ground storage." Potatoes are also easily dug because of the volcanic ash soil in the area (Wilcox, 2018). Major potato cultivars planted in Ohakune are ‘Nadine’, ‘Vivaldi’, ‘Victoria’, and Inca Gold intended for the fresh market. The town of Ohakune is at 593 m above sea level (masl) around the Central Plateau of the Manawatu-Wanganui region. It is situated about 30 km southwest of Mt. Ruapehu (-39.281, 175.56). Annual rainfall is plentiful and reliable, with an average of 1500 mm (Weatherbase, 2018). In general, the warmest month is February, with an average temperature of 15.4 °C, while the coldest month is July, with an average temperature of 4.3 °C.

Site No. 2 is Freshpik Farms Ltd. (-40.465, 175.481) in the township of Opiki. The Freshpik Farm is a small-scale conventional rainfed potato farm. It caters to the crisp market, and its main client is The Griffin's Food Company in Auckland, makers of ETA and Kettle Chip brands. Major potato cultivars planted in summer and harvested through winter (for some ground-stored cultivars) are ‘Snowden’, ‘Fianna’, ‘Hermes’, ‘Taurus’, and ‘Agria’. Opiki is a small rural settlement in the Horowhenua district located on the floodplain 3 km south of the Manawatu River and 15 km southwest of Palmerston North City at only 3 masl. Being located in the lowland area of the greater Manawatu-Wanganui region, it is one of the driest areas in the North Island but rainfall is usually sufficient for agricultural needs, except during summer. Opiki has an average of 990 mm of rainfall per year or 80 mm per month (OpikiClimate, 2018). The driest weather is in February, with an average of 60 mm of rainfall, while the wettest weather is in July, with an average of 100 mm of rainfall. In general, the warmest month is February with an average temperature of 17.5 °C, while the coldest month is July, with an average temperature of 8.0 °C.

Site No. 3 is Lawson's True Earth Farm (-39.624, 176.738) located in Hastings. The Lawson's True Earth Farm is an organic farm that specializes in blueberries, onions, carrots, and potatoes. The farm is one of the major suppliers of organic fresh market potato in New Zealand. Major cultivars planted and marketed are 'Agria', 'Moonlight', and 'Draga'. Hastings is one of the two major urban areas in Hawke's Bay region. It is located about 18 km west of the Hawke's Bay coast. The region is on the east coast of the North Island and is characterized as having a highly capricious and irregular rainfall, with large and abrupt temperature variations (NIWA, 2015). Rainfall is exceptionally variable in spring and summer when westerly winds prevail over the country. Most of the time, inadequate rainfall (dry spells) results in total depletion of soil moisture to the extent that plant growth ceases. The average amount of rainfall in Hastings is about 770 mm. The wettest month on average is May with 90 mm, while the driest on average is October with 50 mm. The warmest month, on average, is January at 19.1 °C, and the coldest month is July at 8.1 °C. Additionally, the region is among the sunniest with most areas having over 2000 sunshine hours per year.

Table 3.1 Agro-climatic and farm characteristics of the three project sites in the North Island of New Zealand for the baseline data collection on potential impacts of abiotic stress associated with climate change on commercial potato cultivars.

Details	Ohakune	Opiki	Hastings
Farm name	A.S. Wilcox and Sons	Freshpik Farms	Lawson's True Earth
Region and zone	Manawatu-Wanganui – central North Island	Manawatu-Wanganui – southwest North Island	Hawke's Bay – eastern North Island
Coordinates	-39.500, 175.459	-40.465, 175.481	-39.624, 176.738
Elevation (masl)	593	3	17
Farming system	conventional-irrigated	conventional-rainfed	organic-irrigated
Area planted to potatoes	150	15	5
Market	domestic and export	Domestic	domestic
Potato products	table, processing, and specialty potatoes	chipping and crisping potatoes	organic table potatoes
Major potato cultivars cultivated	'Nadine', 'Agria', 'Red Jacket', 'Drag'', 'Fianna', 'Rua', 'Moonlight'	'Snowden', 'Fianna', 'Hermes', 'Taurus', 'Agria'	'Agria', 'Moonlight', 'Draga'
Crop history	ex-pasture	ex-pasture	ex-covercrop
Temp Av (°C)	10.2	13.2	14.0
Temp Av Max (°C)	15.0	17.7	19.1
Temp Av Min (°C)	5.5	8.6	8.1
Rainfall Av Annual (mm)	1500	990	770
Soil Classification NZ*	Orthic allophanic – volcanic ash	Humic organic – organic soils	Mottled fluvial recent soil - alluvial sand silt or gravel

*Source: Landcare Research (2020a) approximate data

3.3.2 Weather data

3.3.2.1 Atmospheric and soil temperatures

Examination of climate data, i.e., mean temperature and total rainfall in the past 60 years (1958–2018) during the potato growing months (October to March) in Ohakune, Opiki, and Hastings showed a general increasing trend for the average temperature while a decreasing trend for total rainfall (Figure 3.4 and 3.5). Comparison of the mean temperature and total rainfall in the last 30 years (1988–2017) and the previous 30 years (1958–1987) during the potato growing months, from October to March, showed varying trends across the sites. The mean temperature has an increasing trend, with Ohakune having the highest increase at 0.53 °C, agreeing with the projection of the Ministry for the Environment (2016) that warming in New Zealand will be most significant at higher elevations. The total rainfall, on the other hand, was significantly reduced in Hastings by 48.70 mm, followed by Ohakune at 24.76 mm, while slightly increased in Opiki by 4.89 mm. This finding is consistent with the IPCC report that reduced soil moisture in many parts of the eastern area but more rain in western New Zealand will be experienced (Reisinger et al., 2014).

All observations on the atmospheric temperature in the 2017/18 growing season across the trial showed an above-historical average (1981–2010) trend (Table 3.2). The increase in temperature was particularly distinct during the summer months (December, January, February). Ohakune had milder seasonal temperatures, while Opiki and Hastings had higher temperatures. About a 1 °C increase was observed in Ohakune in the 2017/18 seasonal monthly, maximum, and minimum averages compared with the historical averages, while close to a 2 °C increase was detected in the Opiki and Hastings sites. The highest monthly (18.75 °C, range 5.40 °C–31.40 °C), maximum (23.82 °C, range 5.90 °C–32.60 °C), and minimum (13.70 °C, range 5.00 °C–30.90 ℃) averages were recorded in Hastings during the 2017/18 growing season. The data are comparable with the monthly (17.73 °C, range 1.40 °C–31.50 °C), maximum (22.33 °C, range 1.90 °C–32.10 °C), and minimum (13.13 °C, range 1.00 °C–31.00 °C) averages in Opiki. The least monthly (14.60 °C, range -0.90 °C–27.70 °C), maximum (19.90 °C, range -0.30 °C–28.50 °C), and minimum (9.33 °C, range -1.40 °C– 27.30 °C) averages were recorded in Ohakune. Across sites, mid-summer (January 2018) was the hottest month with an average increase in all temperature parameters (average, maximum, and minimum temperatures) by 3 °C in Ohakune and by 4℃ in Opiki and Hastings. Hastings had the highest recorded average maximum temperature in January of 27.20 °C and a maximum temperature of 32.60 °C, followed by Opiki with an average maximum temperature of 26.50 °C and a maximum temperature of 32.10 °C, and the least was Ohakune with an average maximum temperature of 24.20 °C and a maximum temperature of 28.50 °C in January 2018. These elevated temperatures coincided with the tuber bulking stage of the potato crops in the field. Notably, elevated temperatures persisted until late summer (February) in Opiki and Hastings.

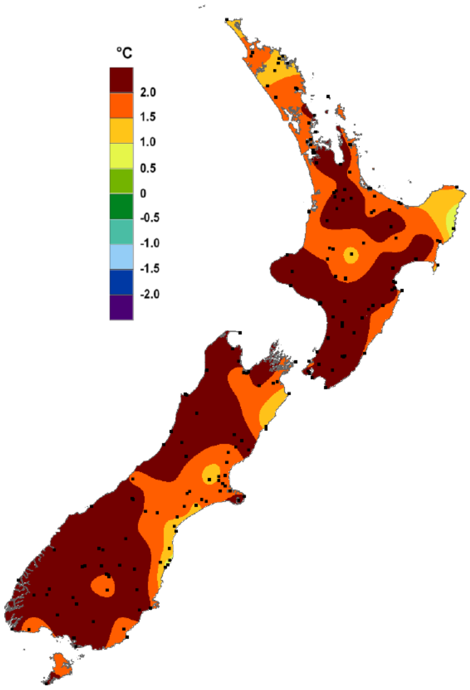
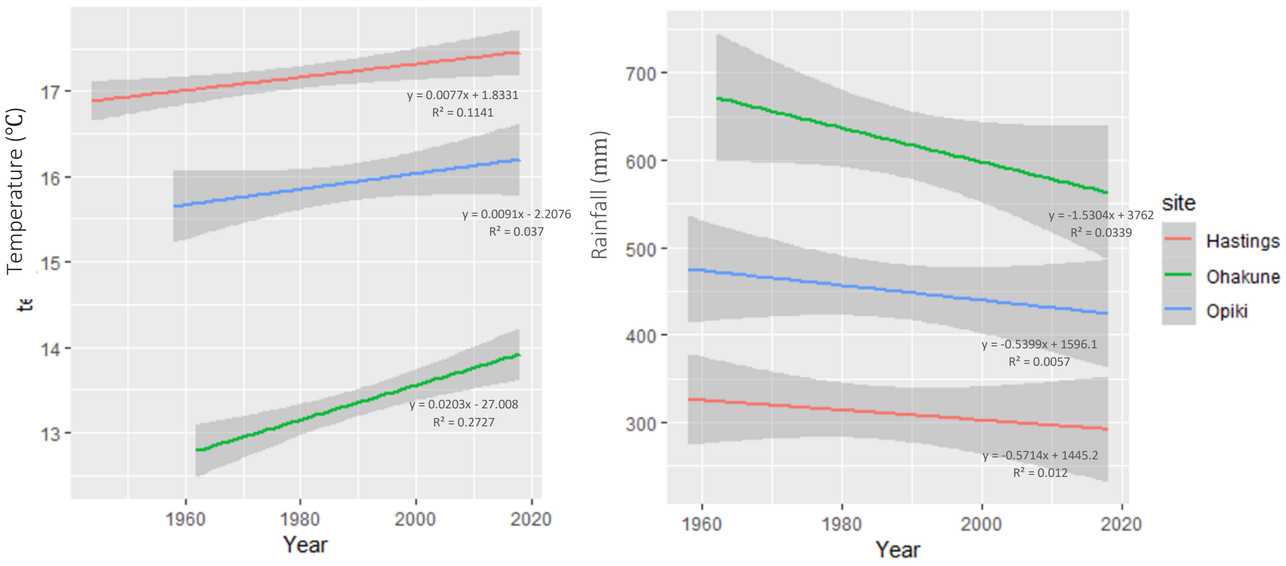


Figure 3.4 2017/18 summer temperatures in New Zealand shown as a difference in season average from the 30-year average (1981–2010) adapted from NIWA (2018d). The 2017/18 summer was New Zealand's hottest summer on record at 18.8 °C nation-wide summer temperature, which is 2.1 °C above the 1981–2010 average.

The highest number of days with supra-optimal temperatures of >25 °C believed to delay tuber growth (Levy and Veilleux, 2007; FAO, 2008c) was recorded in Hastings, with a total of 57 days with 10 days reaching >30 °C or temperatures believed to inhibit tuber growth (Levy and Veilleux, 2007; FAO, 2008c). This was followed by Opiki with a total of 56 days with only a day reaching >30 °C. The least number of days with supra-optimal temperature of >25 °C was recorded in Ohakune, with a total of 21 days without any day reaching >30 °C. Supra-optimal temperatures lasted for 2–6 hours in Ohakune, 6–11 hours in Opiki, and 7–12 hours in Hastings on any given day when extreme or elevated atmospheric temperatures occurred. According to NIWA (2018a), the 2017/18 summer was the New Zealand's hottest summer on record at 18.8 °C nation-wide summer temperature, that is, 2.1 °C above the 1981–2010 average, based on NIWA's seven-station temperature series (Figure 3.4). NIWA (2018a) explained that the high pressure over the Tasman Sea in November and early December in 2017 produced warm sea surface temperatures combined with increased frequency of warm northerly winds, resulting in unprecedented warming to the country in the 2017/18 summer. The summer started with a hot December, which has a well-above-average temperature (>1.20 °C of average) and considered the second-warmest December on record at 18.1 °C (2.4 °C above the 1981–2010 average) (NIWA, 2018d). January was the hottest month on record at 20.3 °C (3.1 °C above the 1981–2010 average), while February was above average (0.51 °C to 1.20 °C above the 1981–2010 average) to well above average temperatures across the North Island (NIWA, 2018d). According to Salinger et al. (2020), the

2017/18 heatwave could potentially represent the mean conditions at the latter part of the 21st century, and it could be the characteristic of New Zealand summer climate for 2081–2100, under the Representative Concentration Pathway or RCP 4.5 or RCP 6.0 scenario, trajectory adopted by the IPCC.



	Temperature (°C)		
	Ohakune	**Opiki**	**Hastings**
1958-1987	13.08	15.74	17.00
1988-2017	13.61	16.10	17.28
difference	0.53	0.36	0.28

	Rainfall (mm)		
	Ohakune	**Opiki**	**Hastings**
1958-1987	630.64	452.23	335.35
1988-2017	605.88	447.34	286.65
difference	-24.76	4.89	-48.70

Figure 3.5 Temperature and rainfall trend in the past 60 years (1958–2018) and comparison of average temperature and total rainfall in the last 30 years (1988–2017) and previous 30 years (1958–1987) during the potato growing months from October to March in Ohakune, Opiki, and Hastings. Data sourced from the CliFlo weather database (NIWA, 2020a).

Table 3.2 Recent (2017/18) and historical (1981-2010) atmospheric temperature data during the potato growing months (October–March) in Ohakune, Opiki, and Hastings.

Sites	Temperature (°C)								Total no. of days
	Oct	Nov	Dec	Jan	Feb	Mar	Season_{av}	Range	
Ohakune									
Mth_{av}	10.60	12.20	15.20	18.70	16.60	14.30	14.60	-0.90 - 27.70	
Hist_{av}	9.70	11.60	14.00	15.40	15.40	13.50	13.27		
Max_{av}	14.90	17.50	21.20	24.20	21.80	19.80	19.90	-0.30 - 28.50	
Hist_{av}	14.20	16.70	19.00	21.20	21.20	18.90	18.53		
Min_{av}	6.40	6.90	9.20	13.30	11.40	8.80	9.33	-1.40 - 27.30	
Hist_{av}	5.30	6.40	8.90	9.70	9.70	8.10	8.02		
No. of days >25C	0	0	5	13	2	1			21
No. of days >30C	0	0	0	0	0	0			0
Opiki									
Mth_{av}	13.60	15.50	18.40	21.80	19.60	17.50	17.73	1.40 - 31.50	
Hist_{av}	12.50	14.20	16.40	17.80	18.20	16.60	15.95		
Max_{av}	17.10	20.60	23.80	26.50	24.00	22.00	22.33	1.90 - 32.10	
Hist_{av}	16.60	18.30	20.60	22.50	22.90	21.20	20.35		
Min_{av}	10.10	10.40	13.00	17.00	15.20	13.10	13.13	1.00 - 31.00	
Hist_{av}	8.40	10.00	12.10	13.10	13.50	11.90	11.50		
No. of days >25C	0	3	12	23	11	7			56
No. of days >30C	0	0	0	1	0	0			1
Hastings									
Mth_{av}	14.40	16.50	19.20	22.70	21.10	18.60	18.75	5.40 - 31.40	
Hist_{av}	13.60	15.30	17.70	18.80	18.70	17.10	16.87		
Max_{av}	19.60	21.40	24.70	27.20	26.30	23.70	23.82	5.90 - 32.60	
Hist_{av}	18.60	20.40	22.70	23.90	23.50	22.10	21.87		
Min_{av}	9.20	11.60	13.70	18.20	16.00	13.50	13.70	5.00 - 30.90	
Hist_{av}	8.50	10.20	12.80	13.70	13.90	12.20	11.88		
No. of days >25C	0	1	11	21	16	8			57
No. of days >30C	0	0	1	2	7	0			10

Source: NIWA (2020a); Mth_{av} – Monthly Average, Max_{av} – Maximum Average, Min_{av} – Minimum Average, Hist_{av} -Historical Average, Season_{av} – Season Average

Table 3.3 Soil temperature data in Ohakune, Opiki, and Hastings during the 2017/18 potato growing season.

Sites	Soil Temp. (°C)							Total no. of days
	Oct	Nov	Dec	Jan	Feb	Mar	Season_{av}	
Ohakune								
Mth_{av}	11.38	13.46	16.71	18.75	16.91	14.12	15.22	
Max_{av}	14.70	18.70	20.70	22.20	20.70	17.20	19.03	
Min_{av}	7.70	8.50	11.50	14.70	12.30	10.90	10.93	
No. of days >18℃	0	0	21	30	15	0		66
Opiki								
Mth_{av}	14.82	19.06	22.44	23.71	21.48	19.02	20.09	
Max_{av}	24.20	29.90	32.10	31.00	26.80	27.00	28.50	
Min_{av}	7.60	12.70	15.00	16.40	15.20	14.80	13.62	
No. of days >18℃	6	29	31	31	28	31		156
Hastings								
Mth_{av}	15.64	18.57	21.97	25.07	23.07	19.53	20.65	
Max_{av}	21.90	26.70	31.30	34.00	31.60	30.00	29.25	
Min_{av}	10.30	12.10	12.60	16.40	14.00	12.10	12.92	
No. of days >18℃	18	26	31	31	28	28		162

Sources: NIWA (2020a); Soil temperature was recorded at 10cm depth; Mth_{av} – Monthly Average, Max_{av} – Maximum Average, Min_{av} – Minimum Average, Hist_{av} -Historical Average, Season_{av} – Season Average

The same as the atmospheric temperature, observations on soil temperature in the 2017/18 growing season across sites showed an above-historical average (1981–2010) trend (Table 3.3). The increase in temperature was distinct during the summer months (December, January, February). About 1.3 °C–3.3 °C increase in the average monthly soil temperature was recorded in Ohakune during the summer months compared with the historical averages, while 3.3 °C–5.6 °C and 3.3 °C–5.0 °C increases were detected in Opiki and Hastings, respectively. The highest seasonal (20.65 °C) and maximum (29.25 °C) soil temperature averages were recorded in Hastings during the 2017/18 growing season, which are comparable with the seasonal (20.09 °C) and maximum (28.50 °C) soil temperature averages in Opiki. The least seasonal (15.22 °C) and maximum (19.03 °C) soil temperature averages were recorded in Ohakune. The average minimum temperature was the highest in Opiki (13.62 °C), followed by Hastings (12.92 °C), and the least was in Ohakune (10.93 °C).

The highest number of days with supra-optimal soil temperatures of >18 °C, believed to reduce tuber yield in combination with elevated atmospheric temperature (Monneveux et al., 2014), was recorded in Hastings (162 days), followed by Opiki (156 days). The least number of days with supra-optimal temperature was recorded in Ohakune (66 days).

3.3.2.2 Rainfall

Rainfall in the sites during the 2017/18 growing season was all below the historical 30 year-averages (1981–2010) (Table 3.4). Hastings had the most significant reduction at 28.0% (from 455.40 mm to 328.00 mm), followed by Opiki at 14.7% (from 465.80 mm to 397.20 mm), and the least reduction was in Ohakune at 7.0% (from 642.10 mm to 597.40 mm). Only in Ohakune was the rainfall within the optimum range of 500-700 mm per growing season for potato production (FAO, 2008e). Across the sites, generally low rainfall occurred at the beginning of the growing season (October, November, December) especially in Opiki and Hastings with 50%–75% reduction in monthly total rainfall compared with the historical 30 year-average. This was followed by more rain in January (Ohakune and Opiki), except in Hastings, where low rainfall persisted until the end of summer (February) that also coincided with the tuber bulking stage of the potato crops in the field. These observations are consistent with the NIWA report that New Zealand received below normal (50%–79% of normal) or well below normal (<50% of normal) rainfall in December 2017 in most parts of the North Island (NIWA, 2018a). However, moisture and warm temperatures in January resulted in more rainfall in many parts of the North Island but were below normal (50%–79% of normal) or well below normal (<50% of normal) in the Hawke's Bay region. On the other hand, February 2018 had above normal rainfall (>149% of normal) due to the passage of ex-tropical cyclones Fehi and Gita, which gave substantial rainfall across the upper North Island and other parts of the mid-central North Island (NIWA, 2018a). Although all the test environments had sub-optimal rainfall, only the potato crops in Opiki experienced water deficiency because it was a non-irrigated site and received sub-optimal rain. By contrast, those in Ohakune and Hastings had supplemental irrigation.

Table 3.4 Recent (2017/18) and historical (1981-2010) rainfall data during the potato growing months (October–March) in Ohakune, Opiki, and Hastings.

Sites	**Rainfall (mm)**						
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Total (mm)**
Ohakune							
Mth$_{av}$	97.80	90.40	82.20	130.80	96.60	99.60	597.40
Hist$_{av}$	142.30	124.20	122.00	100.70	84.60	68.30	642.10
Opiki							
Mth$_{av}$	80.00	19.20	42.20	100.20	78.80	76.80	397.20
Hist$_{av}$	94.50	79.50	89.90	63.10	75.70	63.10	465.80
Hastings							
Mth$_{av}$	82.60	26.40	34.40	35.80	43.60	105.20	328.00
Hist$_{av}$	69.90	65.90	75.80	76.60	73.50	93.70	455.40

Source: NIWA (2020a); Mth$_{av}$ – Monthly Average, Max$_{av}$ – Maximum Average, Min$_{av}$ – Minimum Average, Hist$_{av}$ -Historical Average

3.3.2.3 Sunshine hours and growing degree days

Sunshine hours distinctly differed among the three sites (Table 3.5). The site in the eastern (Hastings) and northern (Ohakune) parts of the North Island received more sunshine than the western part (Opiki). Hastings had the most sunshine hours at 1,456.70 hours, followed by Ohakune at 1110.30 hours and Opiki at 1043.70 hours. The sunshine hours during the 2017/18 growing season were above the historical average by 10.0% (138.20 hours) in Hastings while below the historical averages by 11.2% (124.90 hours) in Ohakune and by 0.5% (5.30 hours) in Opiki. Reports show that sunshine hours had an increasing trend in most areas of New Zealand from 1972 to 2016 (Ministry for the Environment, 2020b). The increase in sunshine hours is due to the reduction of cloud cover (Liley, 2009) and the increasing greenhouse gas concentrations in the atmosphere (Norris et al., 2016). Correspondingly, the accumulated growing degree days (GDD) (base temperature of 4.4 °C) were the highest in Hastings at 2,498.80, followed by Opiki at 2,314.20, and the lowest in Ohakune at 1,746.60. According to the Ministry for the Environment (2020b), the increase in the average temperature in New Zealand resulted in a higher number of GDD between 1972 and 2016, wherein 16 out of 30 measured sites showed increasing trends. Faster accumulation of GDD can result in faster maturity of plants, provided that other conditions essential for plant growth and development are sufficient, such as water and nutrients. The Ministry for the Environment (2020b) further suggested that GDD is affected by climate variations (e.g., El Nino) in the short term and by the warming climate in the long term.

Table 3.5 Recent (2017/18) and historical (1981–2010) sunshine hours data and recent (2017/18) growing degree days data during the potato growing months (October–March) in Ohakune, Opiki, and Hastings.

Sites	**Sunshine Hours (hr/day)**						**Total**
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	
Ohakune	121.90	214.50	244.70	223.10	155.50	150.60	1110.30
Hist$_{Av}$	174.20	193.00	222.50	251.70	209.40	184.40	1235.20
Opiki	122.00	216.80	249.00	183.00	141.80	131.10	1043.70
Hist$_{Av}$	139.60	164.50	168.90	209.90	190.00	176.10	1049.00
Hastings	234.40	230.30	295.50	265.50	196.20	234.80	1456.70
Hist$_{Av}$	213.20	217.20	233.70	249.30	202.60	202.50	1318.50
			Growing degree days (GDD)				
Ohakune	174.60	216.70	316.10	425.50	325.00	288.70	1746.60
Opiki	266.50	314.80	414.70	519.90	408.90	389.40	2314.20
Hastings	291.90	345.80	440.40	547.40	451.80	421.50	2498.80

Source: NIWA (2020a); Hist$_{av}$-Historical Average

3.3.3 Yield and tuber quality baseline data

3.3.3.1 Yield and tuber quality

In general, the fresh tuber yield and number of tubers per plant were higher in Ohakune (Table 3.6 and Figure 3.6), where temperature and rainfall were close to the optimum levels for potato growth and development. This is despite the projection of the farm manager that production could be lower in the 2017/18 growing season due to the deviation from normal weather conditions in Ohakune, particularly the above-normal increase in temperature that hampers tuber bulking. By contrast, the tuber yield was lower in Opiki and Hastings, where drought (in Opiki) and a more significant number of days with supra-optimal atmospheric temperatures (>25 °C and >30 °C), believed to either delay or inhibit tuber growth, combined with supra-optimal soil temperatures >18 °C were recorded. The faster accumulation of GDD in Opiki and Hastings could have resulted in faster maturity of plants, therefore lesser time for tuber bulking compared with the slower GDD accumulation in Ohakune. These results are consistent with the findings of previous studies whereby drought and supra-optimal temperatures reduced the tuber yield (Ahn, Claussen, & Zimmerman, 2004; Haverkort et al., 1990; Lahlou et al., 2003; Levy, 1986; Rykaczewska, 2017a). The decline in tuber yield was primarily attributed to the reduction in the photosynthetic activity, especially under heat stress. Burton (1981) cited that for every 5 °C rise in leaf temperature above the optimum, a 25% reduction in the rate of photosynthesis was observed. Heat stress also impairs water use efficiency (Guoju et al., 2013) and enhances dry matter partitioning to the haulm, thereby promoting vegetative growth over tuber development (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018). As a consequence, fresh tuber weight, dry weight, dry matter, and harvest index decreased (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018), which eventually reduced the final yield. By contrast, plants grown under drought stress had lower stomatal conductance, which helped conserve and maintain an adequate leaf water status, thereby reducing the leaf internal CO_2 concentration and photosynthesis rate (Chaves et al., 2002). In another study, early-season drought reduced the canopy growth rate (Aliche et al., 2018) that corresponds to lower photosynthate production due to reduced leaf area for photosynthesis. Another major cause of tuber yield decline was the high volume of unmarketable tubers exhibiting an array of tuber physiological disorders that are discussed in succeeding sections.

Table 3.6 Tuber yield parameters of 10 commercial potato cultivars in Ohakune, Opiki, and Hastings during the 2017/18 growing season.

Potato Cultivars	Fresh Tuber Yield (t/ha)	Number of tubers/plant	DMC[a] (%)	SG[b]	HI[c] (%)
Ohakune					
‘Nadine’	91.9±5.5 a	26.0±2.2 a	15.1±0.2 b	1.0507	0.90±0.02 a
‘Vivaldi’	66.8±7.3 b	18.0±3.5 ab	16.4±0.6 b	1.0592	0.82±0.03 b
‘Victoria’	67.4±10.0 b	12.0±1.7 b	18.8±0.8 a	1.0712	0.80±0.01 b
Opiki					
‘Snowden’	46.7±9.6 a	6.2±0.4 b	20.8±0.2 ab	1.0770	0.83±0.01 a
‘Agria’	63.2±12.1 a	4.8±1.4 b	18.8±0.2 b	1.0707	0.68±0.04 b
‘Hermes’	55.1±8.7 a	8.2±2.2 b	20.1±0.2 ab	1.0820	0.68±0.03 b
‘Taurus’	51.4± 3.2 a	9.8±2.0 ab	21.9±0.5 a	1.0789	0.74±0.04 ab
‘Fianna’	75.7±10.6 a	17.8±3.3 a	18.9±0.3 b	1.0787	0.70±0.02 ab
Hastings					
‘Agria’	51.4±9.3 ns	9.2±1.0 ns	19.8±0.3 ***	1.0708	0.54±0.03 ns
‘Moonlight’	65.2±6.3 ns	11.6±1.5 ns	17.9±0.2	1.0660	0.59±0.02 ns

[a]Dry matter content; [b]specific gravity; [c]harvest index. Means are presented with ± standard error. Ohakune and Opiki: different letters in a column indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Hastings: statistically different on t-test (P ≤ 0.001).

Figure 3.6 Representative tubers of commercial potato cultivars collected in Ohakune: (a) ‘Nadine’, (b) ‘Vivaldi’, and (c) ‘Victoria’; in Opiki: (d) ‘Agria’, (e) ‘Fianna’, (f) ‘Taurus’, (g) ‘Hermes’, and (h) ‘Snowden’; and in Hastings (i) ‘Agria’, and (j) ‘Moonlight’.

In Ohakune, the cultivar ‘Nadine’ had the highest fresh tuber yield at 91.93 t ha^{-1} and significantly differed from the cultivars ‘Vivaldi’ and ‘Victoria’, with 66.81 and 67.40 t ha^{-1}, respectively. ‘Nadine’ is naturally a high-yielding cultivar (AHDB, 2018a; Alex McDonald, 2018) under favorable conditions, which could explain its excellent performance in Ohakune that has close to optimum environmental conditions. However, ‘Nadine’ was also reported to have low tolerance to heat and drought stress (Caithness Potatoes, 2018). The cultivars ‘Vivaldi’ and ‘Victoria’ were reported to have high yields (AHDB, 2018b; Alex McDonald, 2018); however, in the baseline data collected, ‘Vivaldi’ and ‘Victoria’ had fewer number of tubers and were more prone to tuber physiological disorders, which increased the volume of unmarketable tubers. In Opiki, ‘Fianna’ had the highest fresh tuber yield at 75.71 t ha^{-1}, but it was not significantly different from the other cultivars, while ‘Snowden’ had the least at 46.70 t ha^{-1}. ‘Fianna’ also had the greatest number of tubers per plant (17.8), while ‘Agria’ had the least number of tubers per plant (4.8). In Hastings, the fresh tuber yield and number of tubers per plant were higher in ‘Moonlight’ (65.22 t ha^{-1} and 11.6 tuber per plant) than in

‘Agria’ (51.38 t ha^{-1} and 6.2 tuber per plant), although the difference is not statistically significant.

In terms of tuber dry matter content (DMC) and specific gravity (SG), cultivars in Opiki generally had the highest values since the majority were processing-type potatoes that have inherently high DMC and SG. Higher DMC is significantly correlated with SG, which is an important quality parameter for processing of tubers (e.g., baking, chipping, frying, and mashing). DMC also influences the color of the processed chips that is important for quality standards. Among the cultivars in Opiki, ‘Taurus’ (21.9%), ‘Snowden’ (20.8%), and ‘Hermes’ (20.1%) had the highest DMC. ‘Hermes’ also had the highest SG (1.0820). In earlier studies, drought stress was found to increase the DMC of potato tubers (Lahlou et al., 2003) and decrease the SG (Hang & Miller, 1986; Shock, Feibert, & Saunders, 1998). In other studies, increase in SG was observed under irrigated systems (Waddell, Gupta, Moncrief, Rosen, & Steele, 1999; Yuan, Nishiyama, & Kang, 2003). The cultivars in Ohakune had lower DMC and SG, except for ‘Victoria’ with relatively higher SG (1.0712), which is a multipurpose cultivar (HZPC, 2018).

The harvest index (HI) was relatively higher in potato cultivars planted in Ohakune, where environmental conditions were more conducive for tuber growth and bulking, with ‘Nadine’ (90%) surpassing ‘Vivaldi’ (82%) and ‘Victoria’ (80%). By contrast, the high temperatures in Opiki and Hastings resulted in lower HI. Elevated temperatures are believed to enhance the dry matter partitioning of the haulm, thereby promoting haulm and root growth but hampering tuber growth (Lafta & Lorenzen, 1995; Levy & Veilleux, 2007).

In general, the table (51–90 mm) grade is the most common tuber size across sites (Table 3.7). Multi-purpose cultivars that naturally produce larger tubers had the greatest number of large-sized tubers (>90 mm) per plant, such as ‘Agria’ (3.2–3.4 per plant), ‘Moonlight’ (3.4 per plant), and ‘Victoria’ (5.2 per plant). No clear effects of drought or heat were observed in Opiki and Hastings on the decrease of tuber size in the 2017/18 growing season, as reported in previous studies (Martin et al., 1992; Rykaczewska, 2017a). However, high-yielding cultivars such as ‘Nadine’ in Ohakune and ‘Fianna’ in Opiki tended to have more and bigger tubers than the other cultivars. Early season water deficit may result in a reduction in tubers per plant and the formation of larger tubers (Shock, Zalewski, Stieber, & Burnett, 1992). In Opiki (Freshpik Farm pers. comm.), potatoes were exposed to stress (dry and heat) during the tuber initiation stage that resulted in fewer stolons and tubers. About 8–10 tubers are typically found per plant, but only 2–6 tubers were formed due to exposure to heat and drought stress earlier in the season. In another study conducted by Aliche et al. (2018), drought stress resulted in the downshifting of tuber sizes; the more severe the drought condition is, the lower the number of large tubers is. Drought stress was also found to reduce the tuber size (Hirut et al., 2017; Mackerron & Jefferies, 1988) or increase the number of smaller tubers (Hancock et al., 2014) by up to 20%, especially in water deficit-sensitive cultivars during the tuber expansion stage (Gandar & Tanner, 1976a).

In terms of external tuber qualities, all potato cultivars were within the standard characteristics (i.e., tuber shape, eye depth, skin, and flesh color), except for the skin color of ‘Snowden’, ‘Agria’, and ‘Hermes’ in Opiki and ‘Agria’ and ‘Moonlight’ in Hastings (Table 3.8), based on the passport data from breeder companies. The regular yellow or white skin color of the cultivars was masked by brown color due to severe skin netting. Netting is shallow fissures that give the skin a distinctive netlike appearance, which is often related to climatic conditions and physiological factors (Potatoes South Africa, 2016). Additionally, physiological disorders affected the tuber appearance, resulting in unmarketable tubers; tubers exhibited the following defects: tuber malformation (dumbbell, bottleneck, pointed-end, knobby tubers), second growth (heat sprouts, tuber chaining, secondary tuber growth), growth cracks, enlarged lenticels, and hollow heart.

Table 3.7 Tuber size distribution of 10 commercial potato cultivars in Ohakune, Opiki, and Hastings during the 2017/18 growing season.

Potato Cultivars	Tuber Size Distribution[a]							
	Large (>90 mm)		Table (51–90 mm)		Gourmet (31–50 mm)		Undersize (<30 mm)	
	Ave. No./plant	%	Ave. No. /plant	%	Ave. No. /plant	%	Ave. No. /plant	%
Ohakune								
'Nadine'	1.4±1.0 a	5.4	18.6±0.3 a	71.5	5.0±1.7 a	19.2	1.0±0.5 a	3.9
'Vivaldi'	2.8±0.4 ab	15.2	12.2±2.9 ab	66.3	2.8±1.1 a	15.2	0.6±0.4 a	3.3
'Victoria'	5.2±0.7 b	42.6	5.6±1.3 b	45.9	1.0±0.3 a	8.2	0.4±0.2 a	3.3
Opiki								
'Snowden'	1.6±1.0 a	25.8	3.6±0.8 bc	58.1	0.8±0.4 b	12.9	0.2± 0.2 a	3.2
'Agria'	3.4±0.8 a	70.8	1.2±0.6 c	25.0	0.2± 0.2 b	4.2	0.0±0.0 a	0.0
'Hermes'	1.4±0.5 a	17.1	4.8±0.9 bc	58.5	1.8±1.1 ab	22.0	0.2±0.2 a	2.4
'Taurus'	0.6±0.4 a	6.1	7.2±1.1 ab	73.5	1.6±0.9 ab	16.3	0.4± 0.4 a	4.1
'Fianna'	1.6±0.8 a	9.0	11.4±2.3 a	64.0	4.6±1.0 a	25.8	0.2± 0.2 a	1.1
Hastings								
'Agria'	3.2±1.1 ns	34.8	5.0±0.3 ns	54.1	0.6±0.4	6.5	0.4±0.2 ns	4.4
'Moonlight'	3.4±0.8 ns	29.3	4.8±0.4 ns	41.4	2.4±0.7 **	20.7	1.0±0.5 ns	8.6

[a]Based on T&G Global TAG Standards for Potatoes. Error bars indicate a ± standard error of the means. Ohakune and Opiki: different letters in a column indicate means are statistically different on Tukey's HSD (P ≤ 0.05); Hastings: statistically different on t-test (P ≤ 0.05).

Table 3.8 Observed tuber profile of 10 commercial potato cultivars in Ohakune, Opiki, and Hastings during the 2017/18 growing season.

Potato Cultivars	Tuber shape	Eye depth	Skin color	Flesh color
Ohakune				
'Nadine'	Round	Shallow	White cream	Cream
'Vivaldi'	Ovate	Shallow	Yellow	Yellow
'Victoria'	Ovate	Protruding to shallow	Yellow	Yellow
Opiki				
'Snowden'	Round	Medium	Yellow/Brown	White
'Agria'	Elliptic	Protruding	Yellow/Brown	Yellow
'Hermes'	Round	Shallow	Cream/Brown	Yellow
'Taurus'	Round	Shallow	Cream	Yellow
'Fianna'	Round	Shallow	Cream	Cream
Hastings				
'Agria'	Elliptic	Shallow	Yellow/Brown	Yellow
'Moonlight'	Elliptic	Shallow	White/Brown	White

3.3.3.2 Marketable and unmarketable tubers

Data from the three sites showed that commercial potato cultivars have varying percentage of marketable and unmarketable tubers (undersized or have severe to very severe defects) (Figure 3.7), likely in response to adverse environmental conditions. The highest percentage of marketable tubers was recorded in 'Nadine' (98%) in Ohakune and 'Taurus' (68%), and 'Snowden' (63%) in Opiki. By contrast, the highest percentage of unmarketable tubers was observed in 'Moonlight' (85%) and 'Agria' (67%) in Hastings; 'Victoria' (73%) and 'Vivaldi' (63%) in Ohakune; and 'Agria' (73%) in Opiki. The extremely high percentage of unmarketable tuber was attributed to the incidence of a wide array of tuber physiological disorders, such as enlarged lenticels, growth cracks, netting, and malformations, and pre-harvest sprouting. Moreover, significant rejection was observed among table-type potato cultivars like 'Vivaldi' and 'Victoria'. Since they are usually marketed as pre-packs, the tuber physiological disorder, i.e., enlarged lenticels negatively, affected their physical appearance and hence their potential marketability. Furthermore, multipurpose ('Agria' and 'Moonlight') and processing ('Hermes', 'Taurus', 'Snowden', and 'Fianna') potato cultivars had severe tuber physiological disorders including netting, growth cracks, and malformation (Figure 3.9), which may entail additional costs if processed.

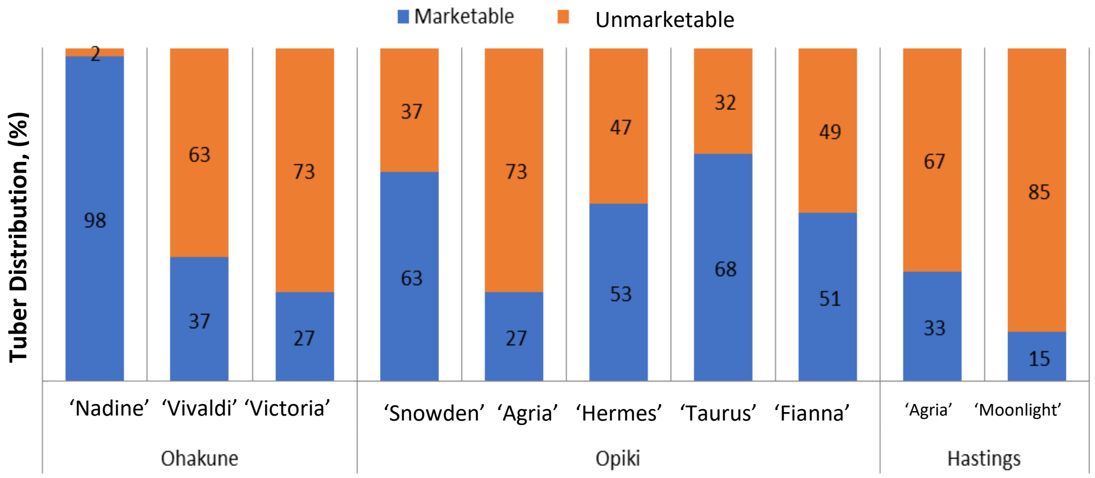


Figure 3.7 Percentage distribution of marketable and unmarketable tubers of 10 commercial potato cultivars in Ohakune, Opiki, and Hastings during the 2017/18 growing season.

3.3.3.3 Tuber physiological disorders

Initial findings showed that the high incidence and type of tuber physiological disorders in commercial potato cultivars are likely affected by the adverse environmental conditions in the 2017/18 growing season. The type and severity of tuber physiological disorders depended on the type of abiotic stress that occurred in the site during the growing season. Tuber physiological disorders were greater under heat stress (Hastings) and combined drought and heat stress (Opiki) compared with those in area with close to optimum water and temperature levels for potato growth and development (Ohakune). Commercial potato cultivars also exhibited differential susceptibility to tuber physiological defects (Figure 3.8 and 3.9). In Ohakune, ‘Nadine’ showed lower susceptibility to enlargement of lenticels, with most tubers having none to light severity; meanwhile, ‘Vivaldi’ and ‘Victoria’ had severe and medium ratings, respectively (Figure 3.10). In Opiki, ‘Snowden’ and ‘Taurus’ showed lower susceptibility to growth cracks and malformed tubers in contrast to ‘Agria’, ‘Hermes’, and ‘Fianna’. Only ‘Agria’ in Opiki exhibited a high percentage (54%) of pre-harvest sprouting among the assessed cultivars. In Hastings, ‘Agria’ and ‘Moonlight’ showed susceptibility to tuber physiological disorders, particularly to enlarged lenticels, netting, and growth cracks. The severity of tuber physiological disorders, mainly the enlargement of lenticels and formation of malformed tubers, appeared to be affected by adverse environmental conditions experienced during the season. Enlarged lenticels, which were believed to be caused by an inadequate supply of oxygen in the soil due to waterlogging (Hillerm & Thornton, 2008; Potatoes South Africa, 2016), were more severe in Ohakune (high rainfall) and Hastings (increased irrigation to manage high temperatures) than in Opiki that had dry conditions (Figure 3.10). Tubers seemed to be more prone to enlargement of lenticels when exposed to higher soil moisture toward the maturity stage. On the other hand, the formation of malformed tubers associated with moisture stress (drought) or high temperature that interrupts or stops tuber growth (Hillerm & Thornton, 2008; Potatoes South Africa, 2016) is more common in Opiki than in Ohakune and Hastings. Furthermore, growth cracks that develop from brief periods of heat stress attributed to the high internal turgor pressure within any tuber (Lugt et al., 1964) are higher and more severe in Hastings, which had more number of days with high temperatures than Ohakune and Opiki.

Across sites, a second set of tubers were formed during the long period of low water followed by rain. The new tuber initials competed with existing tubers, which resulted in reduced tuber bulking, and were often not mature (low dry matter) and unwanted because they were unmarketable. A sprout suppressant chemical was applied to suppress the second set of tubers in Ohakune and Opiki but not in Hastings, which is an organic farm.

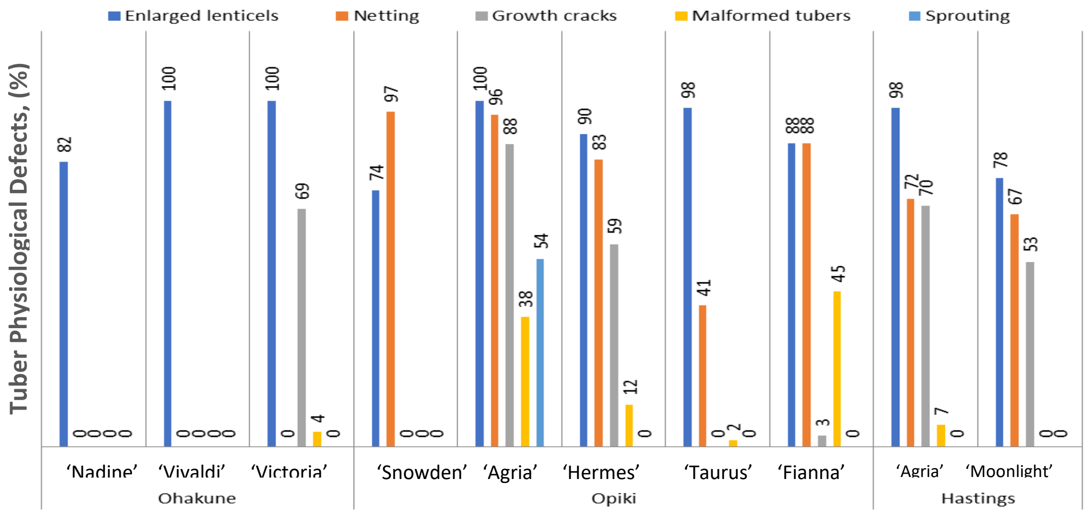


Figure 3.8 Percentage of tuber physiological defects in 10 commercial potato cultivars in Ohakune, Opiki, and Hastings during the 2017/18 growing season.

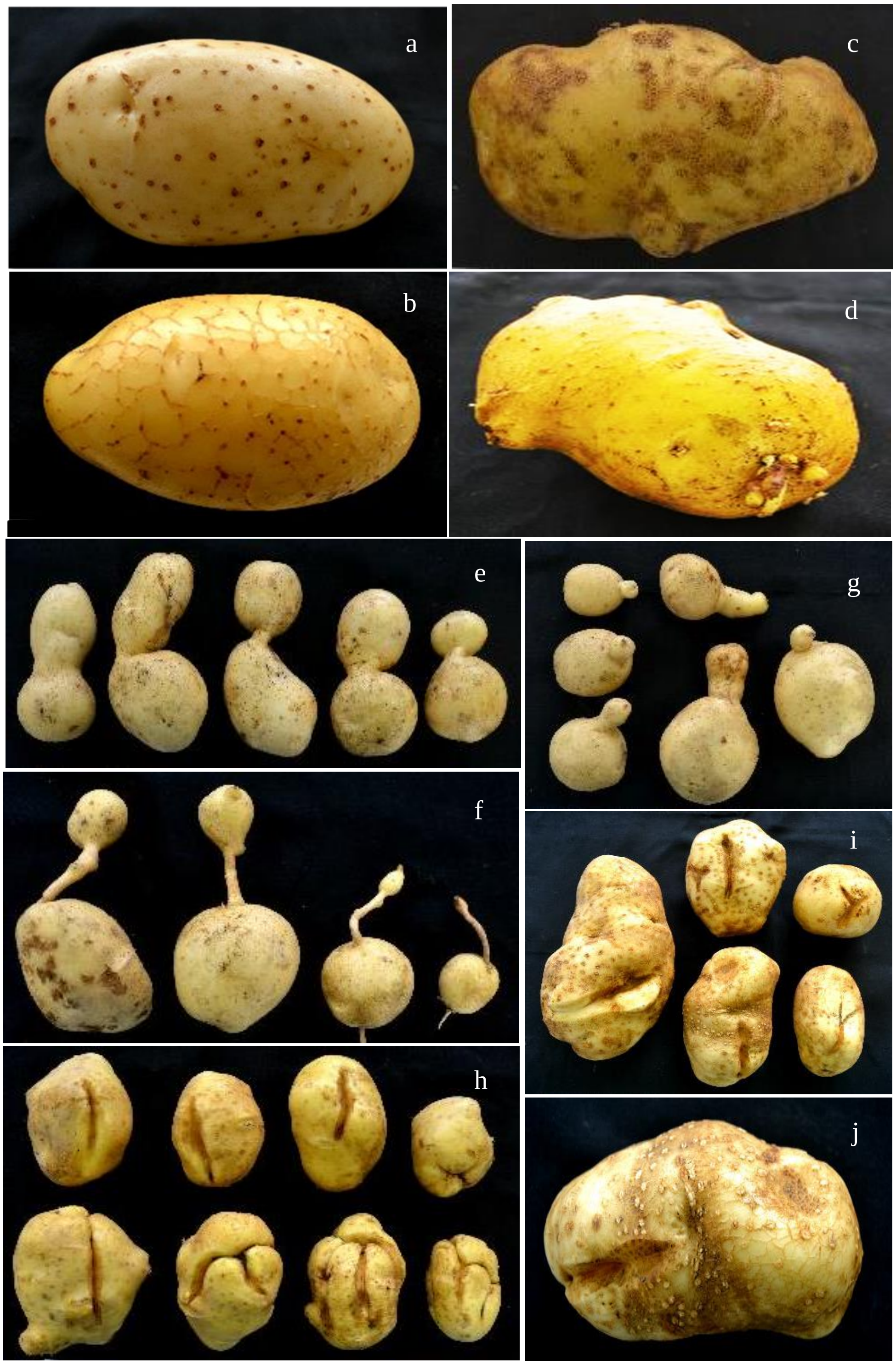


Figure 3.9 Tuber physiological disorders in Ohakune: (a) enlarged lenticels in 'Vivaldi', (b) superficial growth cracks centered on lenticels in 'Victoria'; in Opiki: (c) knobby-tuber and (d) pre-harvest sprouting in 'Agria', (e) dumbbell-tubers, (f) chained tubers, and (g) bottleneck tubers in 'Fianna'; in Hastings: (h) growth cracks in 'Agria', and (i) growth cracks, and (j) suberized and enlarged lenticels in 'Moonlight' during the 2017/18 growing season.

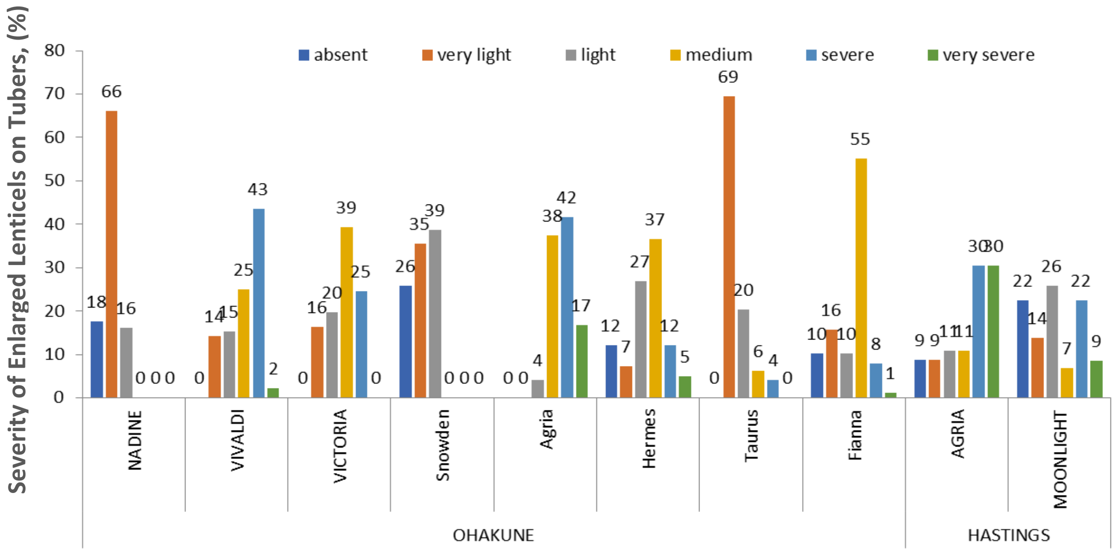


Figure 3.10 Percentage of the severity of enlarged lenticels in potato cultivars in Ohakune, Opiki, and Hastings.

3.4 Conclusion

Based on the baseline data collection, apparent and considerable changes in climate and weather patterns were observed in the identified major potato production sites on the North Island of New Zealand. In general, the average temperature had an increasing trend, whereas the total rainfall had a decreasing trend across sites specifically during the potato growing months from October until March in the past 60 years (1958-2018). Moreover, all observations on atmospheric and soil temperatures in the 2017/18 growing season across sites were all above the historical 30-year average (1981–2010). The increase in temperature was the most distinct during the summer months of December, January, and February. By contrast, rainfall at the sites during the 2017/18 growing season was all below the historical 30-year average (1981–2010). The most considerable rainfall reduction was found in the eastern (Hastings) and northern (Ohakune) regions of the North Island.

Climate change associated with abiotic stresses like heat and moisture stress affects tuber economic yield potentially in two ways. Firstly, it appears to directly alter the physiological activities of the potato crop, such as photosynthesis, transpiration, and stomatal conductance, thereby reducing fresh tuber yield, number of tubers per plant, and harvest index. Secondly, it promotes the development of a wide array of tuber physiological disorders (enlarged lenticels, growth cracks, netting, malformations, and pre-harvest sprouting), which reduce tuber quality and thus increase the percentage of rejected or unmarketable tubers. Differential susceptibility was evident among cultivars in response to abiotic stress and associated tuber physiological disorders. ‘Nadine’, ‘Snowden’, and ‘Taurus’ showed the least defects even under adverse environmental conditions, while ‘Fianna’, ‘Hermes’, ‘Agria’, ‘Vivaldi’, ‘Victoria’, and ‘Moonlight’ exhibited greater susceptibility. Further studies were performed to validate and investigate the response of selected commercial potato cultivars to abiotic stress in detail through multi-environment trial or MET (Chapter 4) and controlled-environment trial in a glasshouse and plant growth chambers (Chapter 5).

CHAPTER 4

Multi-environment Trial of Commercial Potato Cultivars during the 2018/19 Growing Season in New Zealand

4.1 Introduction

The recent losses in potato production experienced in many regions around the world are linked with extreme weather events, such as drought and heatwaves, often associated with changing climate. In general, the global potato production under climate change is estimated to decline by 18%–32% (without adaptations) and by 9%–18% (with adaptations) (Hijmans, 2003). The influence of the environment, in the genotype x environment interaction, plays a big role in the yield variation of potato crops. In a study conducted by Kalbarczyk (2004), agro-meteorological factors significantly contributed to the variability of the potato crop yield by 20%–60% in experimental conditions and 40%–80% in production conditions. In another study, Trawczyński (2009) observed about 40% of the variation in potato yield. In New Zealand, the western and southern regions are forecasted to receive more rain and experience warmer temperatures, while eastern and northern regions will experience double to triple frequency of drought episodes by 2040 (New Zealand Agricultural Greenhouse Gas Research, 2012). Therefore, the potential impacts of abiotic stress (heat and drought stress) associated with climate change on yield and tuber quality should be investigated, and superior potato cultivars with high productivity and stability that can adjust to new agro-climatic conditions should be identified. Before releasing a cultivar, genotypes of high potential are typically evaluated at different locations and over several years to determine their degree of adaptation (Acquaah, 2012). However, in most cases, a comprehensive assessment of adaptation and yield stability characteristics lacks before cultivar recommendation (FAO, 2002). As in the case of New Zealand, new potato cultivars are often tested in a limited number of sites and without an adequate focus on their tolerance to abiotic stress (e.g., drought and heat) associated with climate change before release. This trial aimed to evaluate the performance of selected commercial potato cultivars under potential adverse environmental conditions in selected potato production sites in the North Island of New Zealand through multi-environment trial (MET).

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MET is a practice used to evaluate promising potential cultivars over multiple years and multiple locations to identify superior cultivars (Acquaah, 2012). In MET, the main effects of environment *(E)*, genotype (G), and associated (if any) GxE interaction are determined using appropriate statistical systems. Through MET, yield can be estimated, and stable cultivars in different environments can be identified and are often used as a tool for selecting superior genotypes for planting at new sites (Crossa, 1990). METs are widely used in the evaluation of the performance of many crops, including grains and cereals, legumes, vegetables, and fiber crops (Adugna & Labuschagne, 2003; Behera, 2015; Bertagnolli et al., 2002; Crossa, Fox, Pfeiffer, Rajaram, & Gauch, 1991; Crossa, Westcott, & Gonzalez, 1989; Eckhoff et al., 2017; Narh et al., Patila et al., 2015; Ram, 2007; Rubio, 2004; 2016; Yang et al., 2010;). In potatoes, MET is used for testing and screening for improved tuber yield and disease resistance (Paget et al., 2014). This trial was designed to validate the findings from the baseline data collection (Chapter 3) and was conducted during the 2017/18 potato growing season in the same three sites.

4.2 Materials and methods

4.2.1 Test environments/trial sites

MET was conducted from October 2018 to March 2019 at the three commercial farms in the North Island, where the 2017/18 baseline data collection was done (Chapter 3). The trial site characteristics are summarized in Table 4.1.

4.2.2 Cultivars

This research focused on seven commercial processing (crisping and chipping) potato cultivars currently grown in New Zealand. The cultivar profiles from breeder companies, seed suppliers, and related literature are summarized in Table 4.2. The seed potatoes were provided by two major seed potato suppliers in New Zealand, namely, Eurogrow Ltd. and Alex McDonald Ltd. ‘Agria’ is one of the most commonly grown potato cultivars in New Zealand (Potatoes New Zealand, 2018b) and therefore will be used in this thesis as the reference cultivar. ‘Hermes’ is an offshore-bred cultivar well-known for maintaining its excellent growth performance under heat and drought conditions. ‘Fianna’ and ‘Taurus’ are relatively new offshore-bred cultivars that are reported to have some level of drought tolerance. ‘Snowden’ is also an offshore bred cultivar that is considered a standard for the US potato chipping industry.

Table 4.1 Trial site characteristics and 2018/19 crop management.

Details	Ohakune	Opiki	Hastings
Region and zone	Manawatu-Wanganui – central North Island	Manawatu-Wanganui – southwest North Island	Hawke's Bay – eastern North Island
Coordinates	-39.500, 175.459	-40.465, 175.481	-39.624, 176.738
Elevation (masl)	593	3	17
Farming system	conventional-irrigated	conventional-rainfed	organic-irrigated
Crop history	ex-pasture	ex-pasture	ex-covercrop
Soil Classification NZ*	Orthic allophanic – volcanic ash	Humic organic – organic soils	Mottled fluvial recent soil - alluvial sand silt or gravel
% sand/ silt/ clay	53/ 41/ 6	2/ 46/ 53	22/ 58/ 21
pH	5.9	5.6	6.4
Olsen Phosphorus (mg/L)	14	33	21
Potasium (MAF)	12	14	7
Calcium (MAF)	7	11	17
Magnesium (MAF)	15	26	26
Sodium (MAF)	4	6	7
CEC (me/100g)	17	na	18
Sulfate Sulfur (mg/kg)	na	11	6
Total Nitrogen (kg ha^{-1})	72	na	127
Date of planting	November 14, 2018	October 13, 2018	October 31, 2018
Irrigation	25 mm (01/25/19) 25 mm (05/02/19) 25 mm (18/02/19) 25 mm (06/03/19) 25 mm (12/03/19)	Rainfed	30 mm (16/11/18) 40 mm (13/12/18) 40 mm (21/12/18) 40 mm (04/01/19) 30 mm (10/01/19) 30 mm (22/01/19) 35 mm (30/01/19)
Fertilizer	dry fertilizer (1t ha^{-1}) + lime (4t ha^{-1})(14/11/18); Fe (0.05% w/w), C (15% w/w), P_2O_5 (0.04% w/w), amino acids (28% w/w), N (4.5% w/w), K_2O (2.9% w/w) (1L ha^{-1}); Nitrate-N (13.7%), Phosphorus (46.3%), Potassium K (38.4%) (2kg ha^{-1}) (07/03/19)	30% Potash (1t ha^{-1}), 8-11-20 (700kg ha^{-1}) (01/10/18); $MgSO_4$ (5kg ha^{-1})(04/01/19); $MgSO_4$ (5kg ha^{-1})(22/01/19)	Meat and bone meal (Ca & P source) (1t ha^{-1})(15/10/18); Dry blood and guano mixture (N and P source) (300 kg ha^{-1}; 200 kg blood + 100 kg guano)(31/10/18) Sulphate of potash (K source) (100 kg ha^{-1})(30/11/18)
Plant protection	Linuron (2.5L ha^{-1}) x 1 Mancozeb (2kg ha^{-1}) x7 Fluazinam (0.5L ha^{-1}) x2 Propamocarb(0.25Lha^{-1}) x1 Fenamidone (0.3L ha^{-1}) x 1 Pyraclostrobin(1.6kgha^{-1})x1 Pydiflumetofen(0.4unitsha^{-1})x1 Abamectin (0.6L ha^{-1}) x3 Paraffinic oil (1unit ha^{-1}) x3 Azoxystrobin (0.5L ha^{-1}) x3 Spinetoram (0.5L ha^{-1}) x1 Lambda-cyhalothrin(0.1Lha^{-1})x1	Mancozeb (1kg ha^{-1}) x11 Methoxyacetyl (800ml ha^{-1}) x2 Spirotetramat (560ml ha^{-1}) x2 Chlorothalonil (1.1L ha^{-1})x2 Abamectin (600ml ha^{-1})x2 Lambda-cyhalothrin (100ml ha^{-1}) x3 Copper Hydroxide (1kg ha^{-1}) x4 Spinetoram (500ml ha^{-1}) x3 Methamidophos (1L ha^{-1})x2	Installed mesh covers over potato crops to prevent pests damage i.e. potato psyllid (*Bactericera cockerelli*), tuber moth (*Phthorimaea operculella*), and aphids (*Aphis gossypii*). Used Lilliston disc within six weeks from emergence with 2-3 passes, and 3-4x manual weeding to manage weeds.
Growth Regulator		Sprout suppresant - Potassium salt of maleic hydrazide (12L ha^{-1}) (08/01/19)	
Date of Harvesting	March 24, 2019 (130 DAP)	February 20, 2019 (130 DAP)	March 10, 2019 (130 DAP)

*Source: Landcare Research (2020a) approximate data; MAF - quick test units; na – data not available; soil texture analysis in Appendix 4.1

On the other hand, 'Ilam Hardy' and 'Rua', which were bred by R G Robinson and the Plant and Food Research Institute of New Zealand, respectively, are well-known for their favourable processing characteristics. The detailed characteristics of each cultivar are presented as follows:

'Agria' originated from Germany as a cross between 'Quarta' and 'Semlo'. The plants are tall with spreading growth arising from a few thick and erect stems (Canadian Food Inspection Agency, 2020a). Initial plant development is slow but grows robust foliage during the season. The tuber numbers are usually less, but sizes are large to very large, long oval, with yellow skin and flesh. It is an early main to main crop (approx. 130 days) with a very high yield. 'Agria' is a popular multi-purpose potato cultivar in New Zealand and is suitable for fresh, chips, and crisps with high dry matter content (21.2%). The processing quality is excellent even after long-term storage at 6 °C. It has mild demand to water supply (Europlant, 2020) but is prone to common scab; hence, irrigation is required on lighter soils (Agrico, 2020). 'Agria' has medium to high drought resistance (Banik et al., 2016; Europotato, 2020a; Tekfen Agri, 2020). It has low to medium resistance to secondary growth (Agrico, 2020) and growth cracking (AHDB, 2020a).

'Hermes' is the result of a cross between DDR 5158 x SW 163 55. It is one of the standard main crop varieties from Austria for crisp production with high dry matter content (23.2%). The tubers are medium-sized, round oval to round with white to yellow skin, and light yellow to yellow flesh color, having 10–12 tubers per plant. The cultivar is high-yielding and reported to have long dormancy and very low sprouting throughout storage (Abbasi, Masud, Gulfraz, Ali, & Imran, 2011; Kyriacou, Siomos, Loannides, & Gerasopoulos, 2009). 'Hermes' has been reported to have good (de Nijs, 2020), moderate (Alsharari, Alsadon, & Alharbi, 2007), and high (Europotato, 2020b) drought tolerance. It is among the identified high-yielding cultivars with relatively higher yield stability under drought stress across different environments (Aliche et al., 2018). Drought tolerance is attributed to its ability to partition dry matter toward tuber production during periods of drought rather than canopy production, which makes it more efficient in producing yield per unit of water (Daccache et al., 2012). 'Hermes' is also reported to have good tolerance against heat (de Nijs, 2020). It has a very high resistance to secondary growth and hollow heart and medium resistance to growth cracking (Europotato, 2020b).

'Taurus' is a cross between 'Panda' and RZ –87 – 44. Tubers are medium sized and have round to round oval shapes with bright yellow flesh and yellow skin. It is a high-yielding main season crisping line from the Netherlands and is suitable for long-term storage with high dry matter content (23.3%). 'Taurus' is described to have good tolerance against drought conditions (HZPC, 2020). It has moderate resistance to splitting/cracking (AHDB, 2020c).

'Fianna' is the result of a cross between KO 62-660 and AM 64-2 from South Africa. 'Fianna' has vigorous growth with tall plants and erect stems (ANRD, 2014) and is more efficient at utilizing nitrogen than most cultivars (Craighead & Martin, 2003). Tubers are medium to large, oval-shaped, cream-skinned with creamy-white flesh. It is one of New Zealand's major crisping lines from the Netherlands and has excellent long-term storage quality. It is high yielding main to late main crop with high dry matter content (21.7%). 'Fianna' has very high yield even under drought conditions (Eurogrow, 2020) and exhibits good resistance to tuber physiological disorders like growth cracks and secondary growth (AHDB, 2020b).

'Snowden' is the result of a cross between B5141-6 and 'Wischip' of the University of Wisconsin, Madison, USA. 'Snowden' is a full-season variety with vigorous and full vine growth. Stems are green and upright with a slight pubescence on the stems and leaves (PAA, 2020). Tubers are round to oval, slightly flattened with buff skin and white flesh. 'Snowden' is a high-yielding variety with a high tuber set that responds well to nitrogen fertilization and requires a high level of moisture in the soil (Canadian Food Inspection Agency, 2020b). It has a high specific gravity, good storage quality, and short dormancy (Canadian Food Inspection Agency, 2020b).

'Ilam Hardy' is an early main variety bred from the cross of 'Arran Pilot' x 'Katahdin' by R G Robinson in New Zealand. It was previously the most widely grown potato in New Zealand but is now intended for early season fresh market and crisping (Anderson, Walker, Alspach, Jeram, & Wright, 2013). Tubers are short, oval to round with smooth yellow skin and white flesh (Sparks, 1983). The yield is moderate to high under most conditions (Alex McDonald, 2020). However, the downside of the cultivar is its deep eyes, short storage life, and low dry matter content (Genet & Anderson, 1985). The parent 'Katahdin' possesses many appropriate characteristics and is widely used for breeding purposes worldwide; it also has enhanced tolerance to drought stress (Soltys-Kalina, Plich, Strzelczyk-Żyta, Śliwka, & Marczewski, 2016b). Arran Pilot is also reported to have high drought resistance (Europotato, 2020c).

'Rua' is a late main potato crop between the cross 'Katahdin' x 'Harford' by the Crop Research Division, DSIR, New Zealand. Like 'Ilam Hardy', 'Rua' used to be among the most important cultivars that accounted for nearly 40% of the New Zealand potato crop (Genet & Anderson, 1985) but is now mainly intended as a late harvest for fresh market (Anderson, Walker, Alspach, Jeram, & Wright, 2013). The yield is moderate to high (Alex McDonald, 2020). Tubers are short-oval shapes with yellow skin and white flesh. 'Rua' often produces several uneven and very large table potatoes (McLeod, 1973).

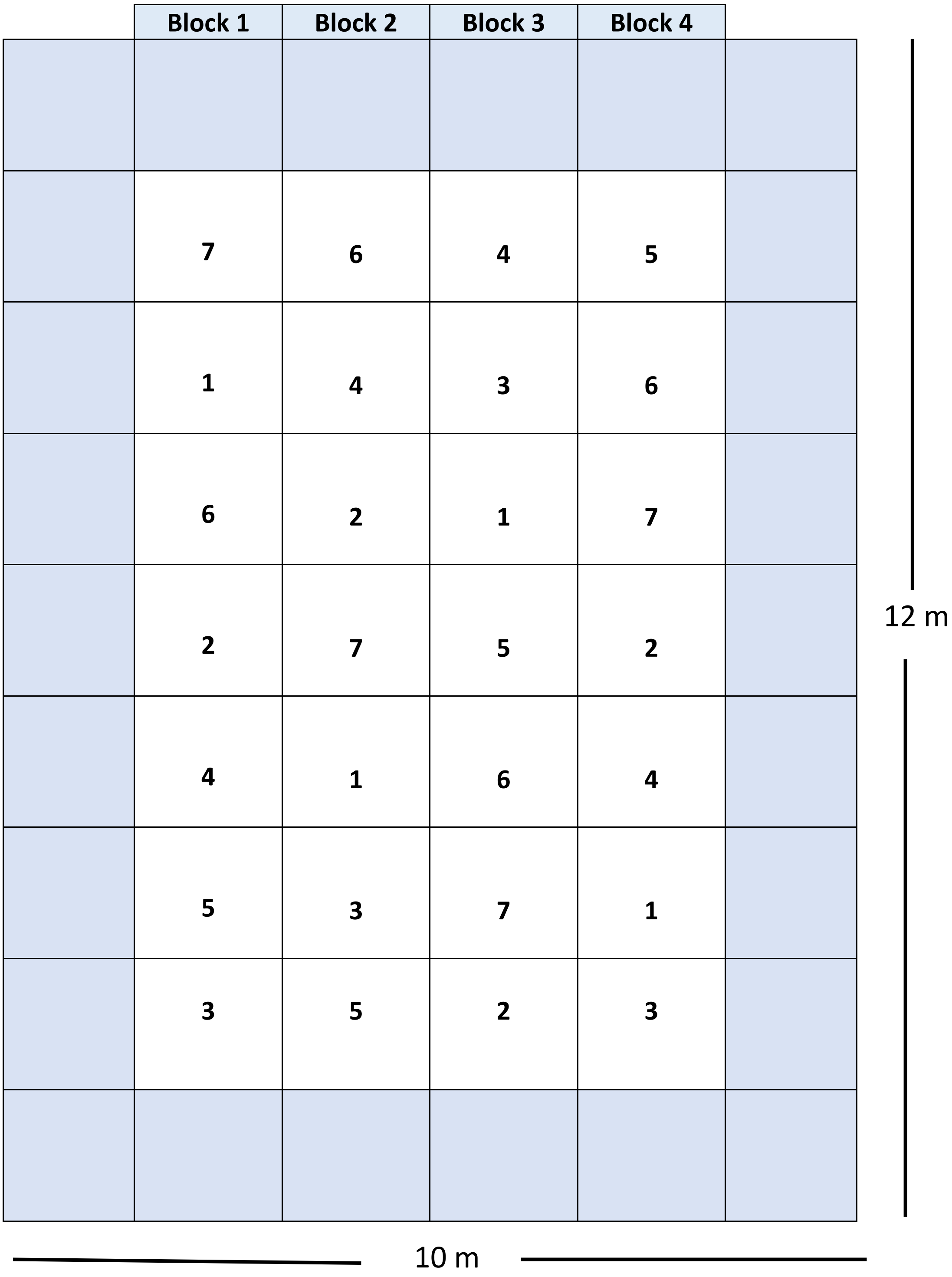
Table 4.2 Characteristics of selected cultivars based on data from breeder companies, seed suppliers, and related literature.

Details	'Agria'	'Hermes'	'Fianna'	'Taurus'	'Snowden'	'Rua'	'Ilam Hardy'
Parentage	'Quarta' x 'Semlo'	DDR5158 x SW163155	KO 62-660 x AM 64-2	'Panda' c RZ – 87 - 44	B5141-6 x 'Wischip'	'Katahdin' x 'Harford'	'Arran Pilot' x 'Katahdin'
Breeder and Country	Kartoffelzucht Böhm, GER	GB Seed Industry, UK	J.P.G. Könst, NL	HZPC, NL	University of Winconsin, USA	Crop Research Division, DSIR, NZ	R G Robinson, NZ
Market	fresh, chips, crisp, flakes	crisp	crisp	crisp	crisp	chips, boil	crisp, boil
Supplier	Eurogrow	Alex McDonald	Eurogrow	Alex McDonald	Alex McDonald	Alex McDonald	Alex McDonald
Maturity	early main/ main crop	main crop	main crop/ late main crop	main crop	medium late	late main	early main
Yield	very high	high	very high	high	high	med/ high	med/ high
Tuber characteristics	large; yellow skin; yellow flesh; shallow eyes	large round/ oval; yellow skins & flesh	medium to large oval tubers; shallow eyes	round oval; bright yellow flesh; yellow skin	round to oval, flattened buff skin, netted white flesh	short-oval shape, yellow skin, white flesh	oval to round, white skin, white flesh
DMC (%)	21.2	23.2	21.7	23.3	24.0	19.8	19.5
Storability	long	very long	very long	very long	medium	long	short
Pests & disease resistance	virus Y, A & X; blight; scab; PCN Ro 1+4	wart disease; leaf roll virus; A-virus; Yn-virus	leaf & tuber blight; common & powdery scab; PCN; virus Y&A	PVYN; foliage & tuber blight	common scab	tuber blight; foliage blight	mosaic Y
Tolerance to abiotic stress	medium to high drought resistance (Banik 2016, Europotato 2005, Tekfen Agri 2020)	good resistance against heat and drought (De Nijs, 2018)	good resistance to drought (Eurogrow. 2020)	good drought tolerance (HZPC, 2018)	na	na	na

na – data not available

4.2.3 Experimental design and crop management

The potato cultivars were planted following the local planting schedule on October 13, 2018, October 31, 2018, and November 14, 2018, in Opiki, Hastings, and Ohakune trial sites, respectively. The experiment at each trial site was set up in a Randomized Complete Block Design (RCBD) with four blocks, and each block was fully randomized. A total of 280 seed tubers (40 seed tubers per cultivar) and additional reference cultivars for border rows were planted in 12 ridged rows 12 m long with between and within row spacing of 100 and 30 cm, respectively (Figure 4.1). Seed potatoes measuring 40–60 mm in diameter were pre-sprouted (ca. 2 cm sprouts) two weeks before planting under ambient temperature and diffused lighting. The grower's cultural management practices for each trial site, including land preparation, nutrient and water management, and pest and disease management, were adopted to simulate local growing conditions and practices. A unique practice at the Hastings trial site, being an organic farm, was the use of mesh cover as a physical barrier to manage the infestation of tomato–potato psyllid or TPP (*Bactericera cockerelli*), which is the insect vector of *Candidatus Liberibacter solanacearum* that causes zebra chip. Nylon mesh cover (0.6 mm pore size) was installed over the field straight after planting and secured with sandbags at the periphery of the plots to ensure that the potato crops were physically protected from TPP (Figure 4.2c). The mesh cover also protects the potato crops from the infestation of tuber moths (*Phthorimaea operculella*) and aphids (*Aphis gossypii*) (Lawson's True Earth pers. comm.). The nets were moved three to four times during the growing season to allow manual weeding. Fertilizer application in all trial sites was based on soil nutrient analysis and followed the commercial-scale practice and was thus relatively similar for the three sites. Primary and secondary data on each trial site specified in Appendix 4.2 were obtained at specific periods and sources during the field trial.



	Block 1	Block 2	Block 3	Block 4	
	7	6	4	5	
	1	4	3	6	
	6	2	1	7	
	2	7	5	2	
	4	1	6	4	
	5	3	7	1	
	3	5	2	3	

Figure 4.1 Typical experimental layout for the multi-environment trial (MET) of selected commercial potato cultivars in the trial sites. The four inner blocks consist of two (2) rows each, and the different numbers indicate the randomization of the seven (7) potato cultivars within each block. Each number constitutes 10 seed tubers with in between and within row spacing of 100 and 30 cm, respectively. The outermost light blue rectangle represents border crops.

Figure 4.2 Standing crops at about 65 DAP in different trial sites: (a) Ohakune, (b) Opiki, and (c) Hastings.

4.2.4 Data collection

4.2.4.1 Weather data

Weather data including atmospheric and soil temperature, rainfall, soil moisture, relative humidity, vapor deficit pressure, sunshine hours, and growing degree days were obtained from primary and secondary sources. Actual atmospheric temperature data were recorded either by using onsite temperature loggers DS1921G-F5# Thermochron (Maxim Integrated, USA, www.maximintegrated.com) in Opiki and Harvest Air Temperature Sensor (Harvest Electronics NZ Ltd) in Hastings or from NIWA weather station closest to the trial site in Ohakune retrieved through CliFlo – New Zealand's web-based national climate database. The daily maximum temperature was obtained to record supra-optimal temperatures (>25 °C) for potato crops across sites, together with the daily rainfall from NIWA weather stations within a 15 km radius from the Ohakune (-39.418, 175.413), Opiki (-40.381, 175.609), and Hastings (-39.648, 176.841) trial sites.

4.2.4.2 Morpho-agronomic and physiological data

Morphological characteristics were recorded at 65 days after planting (DAP) and included plant height (mm), number of stems per plant, stem diameter (mm), and total plant leaf area (cm^2) in the subplots. Plant height was measured using a tape measure starting from the top of the soil surface to the plant shoot tip in all plants and treatments. Stem diameter was measured using a digital caliper from about 2.5 cm above the soil surface. Ten (10) fully developed leaf sub-samples per plant were randomly selected, weighed, and measured for leaf area by using a leaf area meter LI-3100C Leaf Area Meter (LI-COR Biosciences, USA, www.licor.com). The leaf area of the 10 sub-samples was then multiplied by the total plant leaf weight to obtain the total plant leaf area. The dry matter content or DMC (%) of the haulm (i.e., stem and leaves) and roots was determined by oven drying the samples at 70 °C for two to three days or until the weight change was constant. Initial (fresh) and final (dry) weights after drying were measured, and DMC was calculated by dividing the final dry weight by the initial fresh weight and multiplying by 100.

Physiological data including net photosynthesis (µmol CO_2 m^2s^1), transpiration rate (mmol H_2O m^2s^1), and stomatal conductance (mol H_2O m^2 s^1) were measured using LI-COR portable photosynthesis system IRGA LI-6400 model (LI-COR, USA, www.licor.com) on the 3rd or 4th fully expanded leaf of the main stem between 1000 and 1400 h, with eight samples measured per cultivar. Chlorophyll content or SPAD (soil plant analysis development) was recorded using a portable chlorophyll meter CCM-200plus (Opti-Sciences, Inc., USA, www.optisci.com) also on the 3rd or 4th fully expanded leaf of the main stem between 1000 and 1400 h, with eight samples measured per cultivar.

4.2.4.3 Yield and tuber quality data

Manual harvesting was done at 130 DAP on February 20, 2019, March 10, 2019, and March 24, 2019, in the Opiki, Hastings, and Ohakune trial sites, respectively. Accumulated growing degree days (GDD) at 4.4 °C base temperature (Goeser et al., 2012) were also calculated for comparison using the following formula (CIP, 2013):

$$\mathbf{GDD} = \left[\frac{(\mathbf{T}_{\mathbf{MAX}} + \mathbf{T}_{\mathbf{MIN}})}{2}\right] - \mathbf{T}_{\mathbf{BASE}}$$

where:
T_{MAX} is the maximum temperature
T_{MIN} is the minimum temperature
T_{BASE} is the threshold temperature for plant growth

Yield and tuber quality data were recorded at harvest. The data included estimated total yield (t ha^{-1}), marketable yield (t ha^{-1}), number of marketable tubers per plant, DMC (%), specific gravity or SG, harvest index or HI (%), tuber size distribution, and percentage of tuber physiological disorders.

Yield was estimated by weighing all the harvested tubers (total yield) and marketable tubers (marketable yield) from 28 plants per cultivar per site and recalculated on a per hectare basis. Yield loss was calculated using the following formula:

$$\text{Yield loss} = \frac{\text{Total Yield} - \text{Marketable Yield}}{\text{Total Yield}} \times 100$$

Ten randomly selected marketable tubers from each cultivar were used to measure SG and DMC content. SG was determined by first weighing the tubers using a top-loading balance (weight in air) and then weighing while suspended in water (weight in water) (Haase, 2003).

DMC was determined by oven drying the chopped potato tubers at 70 °C for five days or until the weight change was constant. The initial and final weights after drying were measured, and percent DMC was calculated by dividing the final tuber dry weight by the initial tuber fresh weight and multiplying by 100.

HI, which approximates the allocation of photosynthate between tubers and vegetative parts, was estimated using the ratio of tuber dry weight: total plant dry weight and multiplying by 100 (Mackerron & Heilbronn, 1985). Tubers were classified as marketable if within the marketable size standards and free or with minimal defects (mechanical damage or physiological disorders) while unmarketable if undersized or have severe to very severe defects. Tuber size was based on the TAG System for Potato developed by T&G Global (T&G Global, 2018), i.e., large (>90 mm), table (51–90 mm), gourmet (31–50 mm), and undersize (<30 mm). Percent tuber physiological disorders (e.g., enlarged lenticels, netting, growth cracks, malformed tubers, sprouting, loose skin, and greening) were determined by dividing the number of tubers with defects over the total number of tubers per plant and multiplying by 100.

4.2.5 Data analysis

4.2.5.1 Statistical analysis

All the statistical analyses were carried out in R statistical package version 3.4.0 (R Core Team, 2017). Significant difference was analyzed using Analysis of Variance (ANOVA), and mean values were compared among cultivars by using Tukey's HSD test if the overall test was significant.

4.2.5.2 Genotype x environment analysis

The additive main effect and multiplicative interaction or AMMI method was used, where an integrated ANOVA and principal component analysis (PCA) was applied to analyze the MET (Crossa et al., 1991; Zobel, Wright, & Hugh G. Gauch, 1988). ANOVA was used to determine the main effects of genotypes and environments and the PCA for the residual multiplicative interaction among genotypes and environments. After detecting a significant GxE interaction, the data were graphically analyzed by biplot technique to simultaneously classify genotypes and environments (Hongyu, Garcia-Pena, Ara´ujo, & Dias, 2014; Kempton, 1984; Zobel et al., 1988). Through this method, cultivars with high productivity and wide adaptability as well as cultivars with specific adaptability (agronomic zoning) were identified.

4.3 Results and discussion

4.3.1 Phenology and visual appearance

The phenology of the potato crop was closely monitored in the Opiki trial site owing to its proximity to the Massey University campus in Palmerston North and given the practicality of frequent visits to the trial site. However, several phenological parameters were compared and discussed below among the Ohakune, Opiki, and Hastings trial sites as appropriate.

In Opiki, emergence and root development started on November 02, 2018 (20 DAP), and stolon initiation was observed on November 15, 2018 (33 DAP). Tuber initiation and development of flower initials were observed on November 27, 2018 (45 DAP). Tuber bulking started in the middle of December 2018 (65 DAP). Stage IV or harvesting was done on February 20, 2019 (130 DAP). A distinct difference among the trial sites was the timing to maximum canopy cover. Irrigated trial sites (i.e., Ohakune and Hastings) reached the maximum canopy cover earlier than the non-irrigated (rainfed) trial site (i.e., Opiki). The maximum canopy cover was achieved fastest in Hastings at about 45 DAP, followed by Ohakune at about 50 DAP. The slowest time to the maximum ground cover was observed in Opiki at about 65 DAP. According to Genet and Anderson (1985), achieving the maximum canopy cover at the earliest possible time and maintaining this for as long as possible should be the target of potato growers to achieve high yields. The dry conditions in Opiki could have slowed down the vegetative growth of the potato crops. This observation is in line with that of Aliche et al. (2018), who reported that early-season drought could reduce the canopy growth rate; however, upon the availability of water, the canopy growth will increase until the maximum canopy cover. At maturity (~130 DAP), plants in the Opiki and Hastings trial sites already senesced, while those in Ohakune were still green. This finding could mean that potato crops in Opiki and Hastings matured faster than those in Ohakune and is correlated with the data on growing degree days (GDD) collected (Figure 4.3). The elevated temperatures during the growing season in the Hastings and Opiki trial sites accumulated the needed GDD earlier than in the cooler environment of the Ohakune trial site.

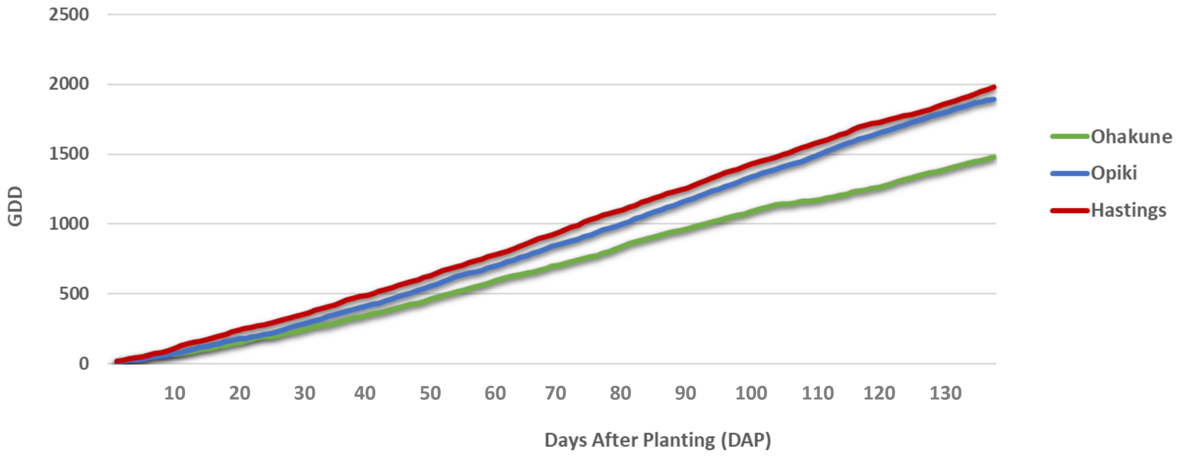


Figure 4.3 Accumulated growing degree days (GDD) in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 4.4 °C base temperature.

4.3.2 Weather data

4.3.2.1 Atmospheric and soil temperatures

Distinct variations and extreme weather patterns were observed in each of the three trial sites for the 2018/19 growing season (Table 4.3). Ohakune had the most days with temperatures close to the optimum for potato crop growth in the 2018/19 growing season as well as in the 2017/18 growing season.

For the 2018/19 season, Ohakune was the least affected trial site by extreme temperatures. Seasonal average of 13.9 °C (ranging 4.0 °C–22.4 °C), maximum of 20.0 °C (ranging 7.8 °C–31.1 °C), and minimum of 7.9 °C (ranging -2.5 °C–16.8°C) were comparable with historical averages of 13.3 °C, 18.5 °C, and 8.0 °C, respectively. The slight increase in the maximum temperature was evident throughout the summer period (December–February) when the majority of supra-optimal temperatures (>25°C) were recorded. The highest temperature recorded was 31.1 °C on January 29, 2019, which coincided with the tuber bulking of the potato crops in the Ohakune trial site.

Table 4.3 Atmospheric temperature characteristics in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	Atmospheric Temp. (°C)						Season$_{av}$	Range	Total no. of days
	Oct	Nov	Dec	Jan	Feb	Mar			
Ohakune*									
Mth$_{av}$	9.8	11.3	14.6	17.2	15.6	15.1	13.9	4.0 – 22.4	
Hist$_{av}$	9.7	11.6	14.0	15.4	15.4	13.5	13.3		
Max$_{av}$	15.1	16.9	20.4	23.4	22.4	21.8	20.0	7.8 – 31.1	
Hist$_{av}$	14.2	16.7	19.0	21.2	21.2	18.9	18.5		
Min$_{av}$	4.5	5.8	8.8	10.9	8.8	8.3	7.9	-2.5 – 16.8	
Hist$_{av}$	5.3	6.4	8.9	9.7	9.7	8.1	8.0		
No. of days >25C	0	0	2	10	7	1			20
No. of days >30C	0	0	0	1	0	0			1
Opiki**									
Mth$_{av}$	13.8	16.0	18.3	19.9	18.4	18.3	17.5	10.7 – 24.7	
Hist$_{av}$	12.5	14.2	16.4	17.8	18.2	16.6	16.0		
Max$_{av}$	18.1	24.5	26.4	27.3	25.8	24.7	25.1	14.5 – 35.0	
Hist$_{av}$	16.6	18.3	20.6	22.5	22.9	21.2	20.4		
Min$_{av}$	8.1	9.4	12.3	14.2	11.0	13.4	11.3	1.0 – 22.0	
Hist$_{av}$	8.4	10.0	12.1	13.1	13.5	11.9	11.5		
No. of days >25	1	18	24	25	19	16			103
No. of days >30C	0	3	7	9	4	1			24
Hastings*									
Mth$_{av}$	12.1	15.0	17.5	20.1	17.9	17.1	16.6	7.3 – 23.8	
Hist$_{av}$	13.6	15.3	17.7	18.8	18.7	17.1	17.5		
Max$_{av}$	18.7	20.1	22.7	25.9	24.3	23.2	22.5	11.2 – 32.1	
Hist$_{av}$	18.6	20.4	22.7	23.9	23.5	22.1	22.5		
Min$_{av}$	5.2	9.4	12.6	13.8	11.2	11.4	10.6	-0.6 – 18.3	
Hist$_{av}$	8.5	10.2	12.8	13.7	13.9	12.2	12.6		
No. of days >25C	0	1	8	19	12	9			49
No. of days >30C	0	0	0	4	4	0			8
Hastings (under mesh cover)**									
Mth$_{av}$	13.6	16.2	19.0	21.2	19.3	18.6	18.9	10.7 – 26.2	
Hist$_{av}$	13.6	15.3	17.7	18.8	18.7	17.1	17.5		
Max$_{av}$	19.7	20.9	22.4	28.2	26.6	22.6	24.1	15.2 – 36.9	
Hist$_{av}$	18.6	20.4	22.7	23.9	23.5	22.1	22.5		
Min$_{av}$	7.5	11.4	14.2	15.8	13.6	13.4	13.7	5.3 – 20.1	
Hist$_{av}$	8.5	10.2	12.8	13.7	13.9	12.2	12.6		
No. of days >25C	1	2	9	27	19	3			61
No. of days >30C	0	0	1	10	10	0			21

Sources: *NIWA (2020a), ** onsite temperature loggers; All historical averages were based on a 30-year period (1981-2010); Mth$_{av}$ – Monthly Average, Max$_{av}$ – Maximum Average, Min$_{av}$ – Minimum Average, Hist$_{av}$ -Historical Average, Season$_{av}$ – Season Ave.

On the other hand, the 2018/19 season was characterized as a hot season in Opiki. Seasonal average of 17.5°C (ranging 10.7 °C–24.7 °C) and maximum average of 25.1 °C (ranging 14.5 °C–35.0 °C) were considerably higher than the historical averages of 16.0 °C and 20.4 °C, respectively. Throughout the growing season from planting in mid-spring (October) to harvesting in late summer (February), the average daily maximum temperature increased by up to 6 °C higher than the historical average. These high temperatures coincided with critical potato growth stages, such as stolon and tuber initiation (Appendix 2.1) during late spring (November) in Opiki. Correspondingly, the duration of the supra-optimal temperatures (>25 °C) from late spring to early autumn totaled 103 days, with 24 days reaching temperatures >30 °C. The supra-optimal temperatures could last from 2 to 7 hours in any given day based on the records obtained from the onsite temperature logger installed in the Opiki trial site (data not presented). The highest temperature recorded was 35.0 °C on January 30, 2019. The extreme temperatures in Opiki could have been aggravated by the low rainfall, leading to drier conditions in the locality (data presented under monthly rainfall). The average minimum temperature of 11.3 °C (ranging 1.5 °C–19.5 °C) was very close to the historical average of 11.5 °C.

The Hastings trial site appeared to have relatively lower temperatures than Opiki. The seasonal average of 16.6 °C (ranging 7.3 °C–23.8 °C), maximum average of 22.5 °C (ranging 11.2 °C–32.1°C), and minimum average of 10.6 °C (ranging -0.6 °C–18.3 °C) were comparable with the historical averages of 17.5 °C, 22.5 °C, and 12.6 °C, respectively. Supra-optimal temperatures from early summer to early autumn were also recorded. Days with temperatures >25° C totaled 49 days, with 8 days reaching temperatures >30 °C. The supra-optimal temperatures lasted between 4 to 10 hours on any given day. However, these conditions were aggravated by mesh covers in the Hastings trial site. Mesh cover is practiced in the Hastings area especially under organic production systems as a physical barrier to protect the potato crops by using non-synthetic chemical means from the destructive tomato-potato psyllid (TPP) (*Bactericera cockerelli*), the insect vector of *Candidatus Liberibacter solanacearum* bacterium that causes zebra chip. Under the mesh, a microclimate was established that caused temperatures to rise about 2 °C higher than the ambient temperature. The seasonal average of 18.9 °C (ranging 10.7 °C–26.2°C), maximum average of 24.1 °C (ranging 15.2 °C–36.9 °C), and minimum average of 13.7 °C (ranging 5.3 °C–20.1 °C) were considerably higher than the historical averages of 17.5 °C, 22.5 °C, and

12.6 °C, respectively. The average maximum temperatures from mid- to late-summer increased by up to 4 °C higher than the historical averages. In an earlier study in New Zealand conducted by Merfield et al. (2015), the average mean daily temperature on mesh-covered potato crops was about 1 °C higher than the control plots; however, the study was conducted in the Canterbury Region in the South Island, where the average temperature is lower than that in the North Island. The average annual temperatures are 10 °C in the South Island and 16 °C in the North Island of New Zealand (NIWA, 2020d). In the study (Merfield et al., 2015), the mesh had minimal effects on relative humidity, but plants under the mesh senesced quicker than the control plants, indicating that their growth and development were accelerated. Moreover, the warming in the mesh was suspected to increase the GDD that affected the performance of the crops. This warming effect by the mesh, however, did not have a negative effect on the crop yield under the Canterbury conditions. Days with supra-optimal temperatures (>25 °C) increased from the original 49 days without mesh to 61 days under the mesh, and days with temperatures >30 °C increased from 8 days without mesh to 21 days under the mesh. The highest temperature recorded was 36.9 °C on January 28, 2019. The extremely high temperatures coincided with potato growth stages from tuber initiation to tuber bulking in the Hastings trial site.

According to NIWA (2020e), the 2018/19 summer was the third hottest summer on record (after 2017/18 and 1934/35) in New Zealand that is either above average (+0.51 °C to +1.20 °C of the summer average) or well above average (>1.20 °C of the summer average) (Figure 4.4). Moreover, the national average temperature for the 2018/19 summer was recorded at 17.9 °C, which is 1.2 °C above the 1981–2010 average, based on NIWA's seven-station temperature series that began in 1909 (NIWA, 2020e). The abnormally high temperature in 2018/19 was due to above-average sea surface temperatures (marine heatwave) around New Zealand coastlines, especially in Hawke's Bay region, where the Hastings trial site is located. According to Salinger, et al. (2020), 2018/19 austral summer was one of the three most intense marine heatwaves recorded in the New Zealand region together with 1934/35 and 2017/18 summers. Heat stress is the increase in temperature beyond a threshold that can cause damage to plant growth and development (Wahid et al., 2007); in general, the temperature is 10 °C–15 °C above the ambient temperature (Rykaczewska, 2017b). The supra-optimal temperatures (>25 °C) in Opiki and Hastings for extended periods (103 and 69 days, respectively) confirmed the presence of heat stress in the trial sites during the

2018/19 growing season. However, irrigation could have led to an evaporative cooling effect in the Ohakune and Hastings trial sites (irrigated farms), especially in Hastings, where irrigation was used to manage high temperatures in the field (J. Russel, Lawson's True Earth pers. comm.).

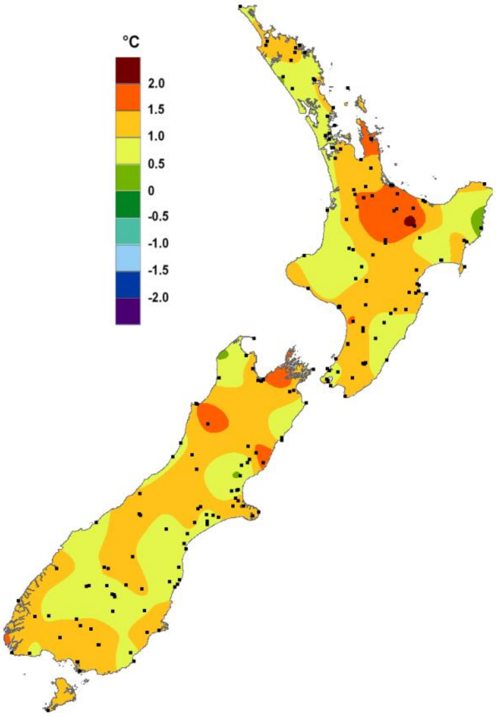


Figure 4.4 2018/19 summer temperatures in New Zealand shown as a difference of season average from the 30-year average (1981–2010) adapted from NIWA (2020e). New Zealand's temperatures were either above average (+0.51 °C to +1.20 °C of the summer average) or well above average (>1.20 °C of the summer average) (NIWA, 2020e).

Soil temperatures had the same trend as the atmospheric temperature in the Ohakune, Opiki, and Hastings trial sites. Ohakune had the mildest seasonal average of 15.7 °C (ranging 4.0 °C–27.8 °C), a maximum average of 19.8 °C, and a minimum average of 12.6 °C soil temperature. Opiki had higher seasonal average of 19.5 °C (ranging 8.4 °C–32.8 °C), a maximum average of 23.2 °C, and a minimum average of 16.5 °C soil temperature (Table 4.4). The Hastings trial site was comparable with the Opiki trial site and had a seasonal average of 19.9 °C (ranging 9.4 °C–29.4 °C), a maximum average of 23.1 °C, and a minimum average of 17.0 °C soil temperature. The soil temperature considerably increased in the summer months coinciding with tuber bulking in the Opiki and Hastings trial sites. However, irrigation in the Ohakune and Hastings trial sites could have had a cooling effect on soil temperature, while the practice of mesh covering in the Hastings trial site, in contrast, could have had an increasing effect on soil temperature the same way as its effects on atmospheric temperature. On the other hand, the Opiki trial site had the highest actual soil temperature given that it was a rainfed farm and also received sub-optimal rainfall during the 2018/19 growing season. Past studies showed that the tuber yield decreased at high ambient air temperatures (>30 °C day/>23 °C night) combined with soil temperatures higher than 18 °C (Monneveux et al., 2014).

Table 4.4 Soil temperature in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	Soil Temp. (°C)						Season$_{av}$	Range
	Oct	Nov	Dec	Jan	Feb	Mar		
Ohakune*								4.0 – 27.8
Mth$_{av}$	12.3	15.6	18.1	18.0	15.6	14.5	15.7	
Max$_{av}$	18.2	20.9	22.2	20.6	18.4	18.4	19.8	
Min$_{av}$	8.5	11.5	14.9	15.7	12.9	11.8	12.6	
Opiki*								8.4 – 32.8
Mth$_{av}$	14.5	17.1	20.3	23.1	22.0	20.4	19.5	
Max$_{av}$	17.5	19.8	23.4	27.5	26.8	24.5	23.2	
Min$_{av}$	12.1	14.8	17.6	19.6	17.9	17.0	16.5	
Hastings*								9.4 – 29.4
Mth$_{av}$	15.6	18.3	20.9	23.1	21.8	19.8	19.9	
Max$_{av}$	18.3	21.3	23.7	26.1	25.1	24.3	23.1	
Min$_{av}$	13.1	15.3	18.4	20.3	18.5	16.5	17.0	
Hastings (irrigated)**								
Mth$_{av}$			19.1	19.2	17.9	19.8	19.0	
Max$_{av}$			24.3	21.0	20.6	25.2	22.8	
Min$_{av}$			14.5	17.2	15.2	15.3	15.5	

Sources: *NIWA (2020a), ** onsite temperature loggers; Soil temperature was recorded at 10cm depth; Mth$_{av}$ – Monthly Average, Max$_{av}$ – Maximum Average, Min$_{av}$ – Minimum Average, Hist$_{av}$ -Historical Average, Season$_{av}$ – Season Average

4.3.2.2 Rainfall, soil moisture, relative humidity, and vapor pressure

With regard to the observed rainfall data in the 2018/19 growing season, all sites were below the optimum range for potato production of 500–700 mm (FAO, 2008d), especially in Ohakune with a 40% decrease in rainfall from the historical average of 642.1 mm to the 2018/19 season average of 388.0 mm (Table 4.5). Opiki had a 10% decrease in rainfall from the historical average of 465.8 mm to the 2018/19 season average of 423.0 mm. These findings coincide with the report of NIWA (2020e) that rainfall was below normal in the northern and western parts of the North Island, including the Manawatu–Wanganui region where the Opiki and Ohakune trial sites are situated. Hastings had about an 11% decrease in total rainfall from the historical average of 455.4 mm to the 2018/19 season average of 406.0 mm. Across sites, particularly low rain was experienced in mid-spring (October), and rainfall was 40%–80% lower than the historical average. This finding coincides with the crop emergence and stolon initiation stage in the Opiki trial site (Figure 4.5b). By early summer (December), a sudden and heavy downpour occurred in Opiki and Hastings, with 92% (from 89.9 mm to 172.6 mm) and 48% (from 75.8 mm to 112.2 mm) increases in rainfall, respectively. The above-normal rain level in Opiki in early summer was caused by a storm on December 24–25, 2018, while in Hastings, the above-normal rainfall (>120% of the normal) was recorded due to a wet December (NIWA, 2020e). This, however, was followed by generally drier mid-summer (January) that corresponded to tuber bulking, up to early autumn or end-of-season (March) across the sites (Figure 4.5). The dry and hot mid-summer resulted in a rapid decrease in soil moisture levels that progressed to severely dry soils in the northern and western regions of the North Island (NIWA, 2020e). Although all sites had sub-optimal rainfall, only the potato crops in Opiki potentially experienced water deficit given that was a non-irrigated site and received sub-optimal rainfall (Figure 4.5b), whereas Ohakune and Hastings had supplemental irrigation (Figure 4.5a and c).

Table 4.5 Rainfall in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	Monthly Rain (mm)						Total Rain (mm)
	Oct	Nov	Dec	Jan	Feb	Mar	
Ohakune	35.2	61.6	139.6	58.0	29.2	64.4	388.0
Hist. Ave.	142.3	124.2	122.0	100.7	84.6	68.3	642.1
Opiki	53.4	84.2	172.6	32.6	28.0	52.2	423.0
Hist. Ave.	94.5	79.5	89.9	63.1	75.7	63.1	465.8
Hastings	12.8	106.0	112.2	102.4	51.4	21.2	406.0
Hist. Ave.	69.9	65.9	75.8	76.6	73.5	93.7	455.4

Source: NIWA (2020a); All historical averages were based on 30 years (1981-2010); Hist_{av} -Historical Average

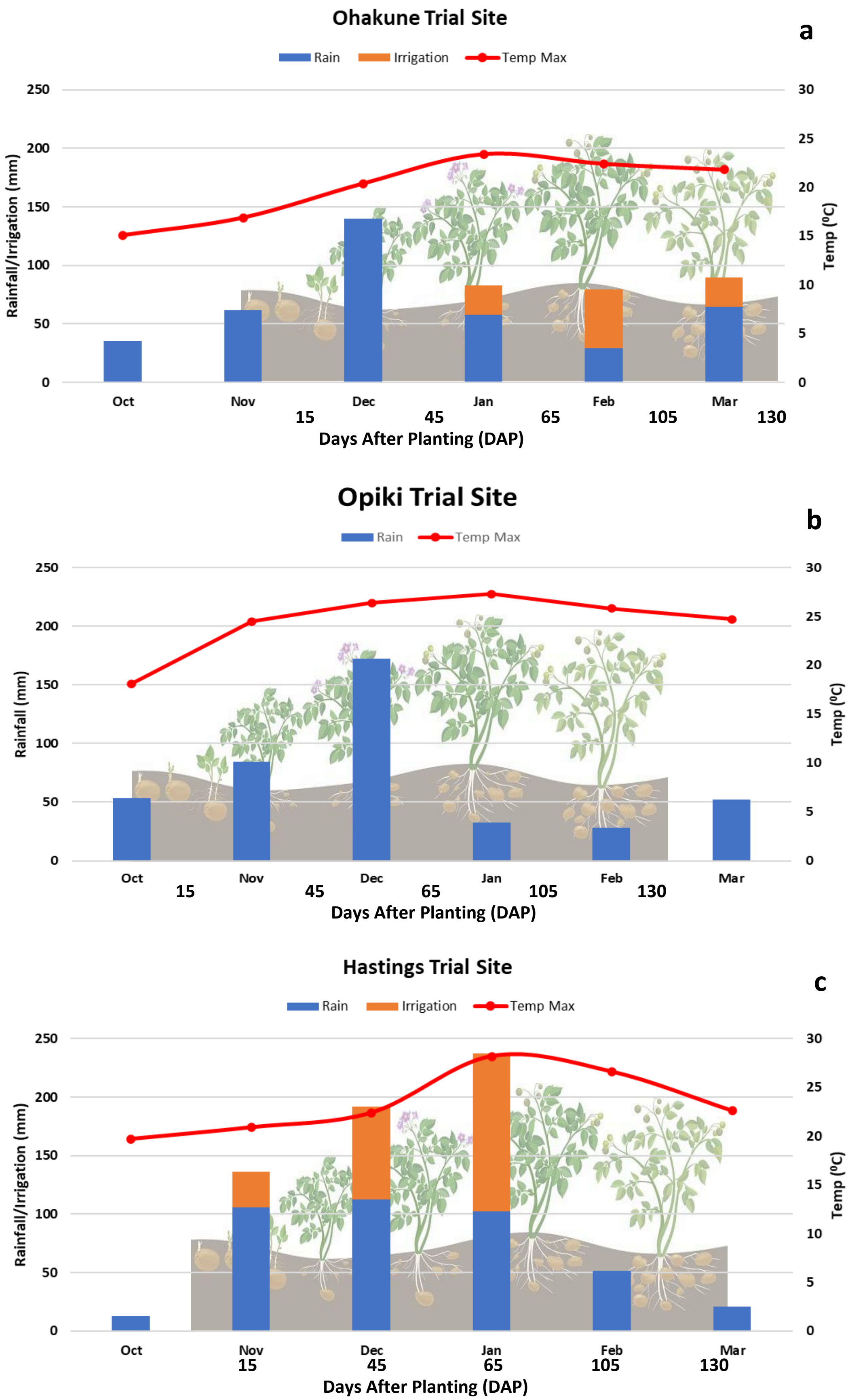


Figure 4.5 Rainfall, irrigation, and atmospheric temperature (average maximum) coinciding with the potato growth stages or days after planting during the 2018/19 growing season in (a) Ohakune, (b) Opiki, and (c) Hastings trial sites. Potato growth stage image credit: www.primalsurvivor.net.

Despite receiving low rainfall, Ohakune had the highest seasonal average soil moisture at 31.7% (Table 4.6). The porous characteristic of allophanic soils (Landcare Research, 2020b) that formed from the volcanic ash (andesitic ash) (New Zealand Soil Bureau, 1968) in the Ohakune area could have had contributed to its high-water holding capacity. Opiki had the second-highest seasonal average soil moisture of 28.4%, while Hastings had the lowest value of 23.0%. Soil had been unusually dry in late summer (February) during tuber bulking across the sites.

The mean relative humidity (RH) was the highest in Ohakune at 83.2% (ranging 24%–100%), followed by Opiki at 79.4% (ranging 24%–98%) and the lowest in Hastings at 76.7% (ranging 29%–100%) trial site (Table 4.7). Inversely, vapor pressure was the lowest in Ohakune at 12.2 hPa, while Opiki and Hastings had higher and comparable values of 14.9 and 14.5 hPa, respectively. The transpiration rate of the plant was determined by variations in vapor pressure deficit (VPD), which is affected by atmospheric temperature and RH (Kholová & Vadez, 2012). At high RH, plants transpire less. Higher VPD has a higher drying effect on plants, while lower VPD has a lower drying effect.

Table 4.6 Soil moisture in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	Soil Moisture (%)						Season$_{av}$
	Oct	Nov	Dec	Jan	Feb	Mar	
Ohakune							
Mth$_{av}$	42.6	36.7	40.4	29.6	17.8	23.0	31.7
Max$_{av}$	43.0	37.1	41.6	30.3	18.1	23.7	32.3
Min$_{av}$	42.0	36.3	39.1	28.5	17.4	22.3	30.9
Opiki							
Mth$_{av}$	35.4	34.2	35.8	29.5	16.7	18.5	28.4
Max$_{av}$	35.8	34.7	36.7	29.7	16.9	18.7	28.8
Min$_{av}$	35.0	33.6	35.0	28.9	16.5	18.2	27.9
Hastings							
Mth$_{av}$	32.0	23.8	31.9	30.3	15.3	4.8	23.0
Max$_{av}$	32.1	24.0	32.1	30.5	15.6	4.9	23.2
Min$_{av}$	31.9	23.6	31.7	30.0	15.2	4.8	22.9

Source: NIWA (2020a); Soil moisture recorded at 20cm depth; Mth$_{av}$ – Monthly Average, Max$_{av}$ – Maximum Average, Min$_{av}$ – Minimum Average, Hist$_{av}$ -Historical Average, Season$_{av}$ – Season Average

Table 4.7 Relative humidity and vapor pressure in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	Relative Humidity (%)						Season$_{Av}$ (%)	Range
	Oct	Nov	Dec	Jan	Feb	Mar		
Ohakune								
Mth$_{av}$	81.8	81.9	80.8	83.5	82.6	88.7	83.2	24 – 100
Max$_{av}$	93.4	95.6	95.1	93.0	93.9	96.1	94.5	
Min$_{av}$	58.3	60.5	57.4	53.0	49.2	53.8	55.4	
Opiki								
Mth$_{av}$	78.9	78.3	78.3	79.3	80.4	81.4	79.4	24 – 98
Max$_{av}$	94.1	93.2	93.4	91.2	90.5	92.8	92.5	
Min$_{av}$	59.7	58.9	60.4	60.6	49.8	54.6	57.3	
Hastings								
Mth$_{av}$	71.4	77.1	78.9	75.5	76.5	81.0	76.7	29 – 100
Max$_{av}$	91.2	95.5	96.4	95.7	97.7	97.7	95.7	
Min$_{av}$	54.0	57.6	58.1	55.0	51.4	57.0	55.5	
	Vapor Pressure (hpa)							
Ohakune	9.2	10.8	12.8	14.5	13.0	13.0	12.2	
Opiki	11.2	13.4	15.9	17.4	16.4	15.3	14.9	
Hastings	11.0	12.7	15.1	17.0	15.5	15.4	14.5	

Source: NIWA (2020a); *No. of hours below 50% RH: Ohakune – 235, Opiki – 84, Hastings 369*; Mth$_{av}$ – Monthly Average, Max$_{av}$ – Maximum Average, Min$_{av}$ – Minimum Average, Hist$_{av}$ -Historical Average, Season$_{av}$ – Season Average

4.3.2.3 Sunshine hours and growing degree days

Distinct differences in sunshine hours were found among the three trial sites. The eastern and northern parts of the North Island received more sunshine than the western regions (Table 4.8). Hastings had the most sunshine hours at 1,576.8 hours, followed by Ohakune at 1060.7 hours and Opiki at 985.3 hours. The sunshine hours increased in Hastings by about 20% (258 hours) but decreased in Ohakune by 14% (175 hours) and in Opiki by 6% (64 hours) during the 2018/19 season. Correspondingly, the accumulated growing degree days were the highest in Hastings at 2,096.9, followed by Opiki at 1784.2, and the lowest in Ohakune at 1473.9.

Table 4.8 Sunshine hours and growing degree days in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

Trial Sites	**Sunshine Hours (hr/day)**						**Total**
	Oct	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	
Ohakune	153.4	139.6	181.3	228.0	178.5	179.9	1060.7
Hist_{Av}	174.2	193.0	222.5	251.7	209.4	184.4	1235.2
Opiki	131.2	156.6	158.5	169.5	155.3	214.2	985.3
Hist_{Av}	139.6	164.5	168.9	209.9	190.0	176.1	1049.0
Hastings	275.7	255.7	235.6	312.5	254.7	242.6	1576.8
Hist_{Av}	213.2	217.2	233.7	249.3	202.6	202.5	1318.5
	Growing degree days (GDD)						
Ohakune	149.8	190.0	297.9	376.9	296.9	312.2	1623.7
Opiki	242.7	310.1	407.1	413.1	411.2	415.3	2199.5
Hastings	266.0	337.2	434.5	501.5	401.1	422.6	2362.9

Source: NIWA (2020a); All historical averages were based on 30 years (1981-2010); Hist_{av} -Historical Average

4.3.3. Abiotic stress effects on morpho-agronomic characteristics and physiological functions of potato crops under multi-environment trial

4.3.3.1 Abiotic stress effects on morpho-agronomic characteristics of potato crops

In the 2018/19 growing season, weather extremes were accompanied by abiotic stresses, such as drought and heat. The differences in the impacts of these stresses across trial sites were statistically significant on the different morphological characteristics of potato crops, including plant height ($p < .001$), number of stems per plant ($p < .01$), and stem diameter ($p < .001$) (Table 4.9). The heat stress due to extreme weather conditions and aggravated by mesh covering practice in the Hastings trial site resulted in increases in plant height by 43% (112.1 cm), number of stems per plant by 19% (4.4), total plant leaf area by 59% (6892 cm^2), haulm DMC by 9% (10.8%), and root DMC by 15% (17.6%), relative to the Ohakune trial site (78.5 cm, 3.7, 4340 cm^2, 9.9%, and 15.3%, respectively). However, the stem diameter was reduced by 13% (13.9 mm) in Hastings compared with that in the Ohakune (16.0 mm) trial site. By contrast, the hot and dry conditions of Opiki reduced the plant height by about 4% (75.2 cm) and the total plant leaf area by 66% (1489 cm^2) but increased the stem diameter by 6% (16.9 mm) and the root DMC by 10% (9.8%).

An increase in plant height was also recorded in past heat stress studies on potatoes (Gawronska et al., 1992; Hastilestari et al., 2018; Lafta & Lorenzen, 1995; Rykaczewska, 2015a; Tang et al., 2018). The increase in the number of stems per plant may be due to the high temperature during the growing season in the Hastings trial site. However, according to Haverkort (1990), storage conditions, differences in temperature during growth, and pre-sprouting of the seed potatoes have more influence over the number of stems developed and cannot be excluded. The increase in the whole plant leaf area could be due to the increase in the size of smaller but more leaves under supra-optimal temperatures. This result is consistent with observations from previous studies, where heat stress negatively affected leaf expansion, thereby reducing the leaf size but increasing the number of leaves produced (Gawronska et al., 1992; Lafta & Lorenzen, 1995; Tang et al., 2018). Heat stress in Hastings also increased the dry matter content of the haulm and roots, suggesting an enhanced dry matter partitioning to the haulm that promoted vegetative growth (Levy & Veilleux, 2007). Younger leaves could also compete better for limited assimilates due to their proximity to source leaves (Marinus & Bodlaender, 1975). Stem diameter, however, was the smallest in Hastings compared with those in the two other sites. This decrease in stem diameter could be attributed to the relatively rapid vegetative growth, which led to developing slenderer plants.

Table 4.9 Morphological parameters of commercial potato cultivars as affected by environments and cultivars in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 65 DAP.

	Plant height (cm)	No. of stems/ plant	Stem diameter (mm)	Total plant leaf area (cm^2)	DMC^a haulm (%)	DMC^a roots (%)
Sites	***	*	***	*		
Ohakune	78.5±0.9 b	3.7±0.1 b	16.0±0.2 b	4340±256 b	9.9	15.3
Opiki	75.2±1.0 c	3.9±0.1 b	16.9±0.2 a	1489±285 c	9.8	16.8
Hastings	112.1±0.9 a	4.4±0.1 a	13.9±0.2 c	6892±280 a	10.8	17.6
Cultivars	***	***	***	*		
‘Agria’	92.1±1.3 bc	3.0±0.2 d	15.0±0.3 c	3449±392 b	10.7	17.0
‘Hermes’	94.7±1.6 abc	5.7±0.2 a	14.8±0.4 c	5605±452 a	9.9	15.9
‘Ilam Hardy’	95.0±1.3 ab	3.8±0.2 c	15.3±0.3 bc	5506±413 a	9.9	16.6
‘Rua’	77.9±1.3 d	4.0±0.2 bc	16.2±0.3 b	3434±413 b	9.4	16.3
‘Taurus’	88.4±1.4 c	4.0±0.2 bc	14.2±0.3 c	4738±433 ab	10.9	18.3
‘Fianna’	100.5±1.9 a	2.6±0.2 d	19.1±0.4 a	3276±413 b	10.7	15.5
‘Snowden’	71.3±1.3 e	4.7±0.2 b	14.5±0.3 c	3674±413 b	9.8	15.5

^{a}DMC – dry matter content; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

In contrast, the hot and drier conditions in the Opiki trial site reduced the plant height, number of stems per plant, and whole plant leaf area. Drought stress reduced the maximum leaf area index of potato crops by as much as 29% in the field and 63% in the greenhouse (Lahlou et al., 2003). Under drought conditions, either or both the lowered leaf water potential that acts as a hydraulic signal and the hormonal signals (abscisic acid) produced in the root tips of potato crops may reduce leaf area expansion (Shahnazari et al., 2007). Drought stress reduced the stem number per plant by 28% in the field but not in the greenhouse (Lahlou et al., 2003). Stem diameter was the highest in the drier conditions at the Opiki trial site, a typical response of crops under drought stress. In soybeans, the stem diameter was enhanced in response to drought stress by accumulating assimilates and conserving water into the stem (Ohashi, Nakayama, Saneoka, Mohapatra, & Fujita, 2008). Root growth seemed to be also enhanced by drought stress, as can be seen in the slight increase in the root dry matter content of potato crops under the drier conditions in the Opiki trial site. Coincidently, drought stress increased the dry matter partitioning into the shoots and roots and increased the root: shoot ratio, resulting in a greater extent of root than shoot growth (Jefferies, 1993).

The potato cultivars had significant variation in their morphological response to abiotic stress (*p* < .001). Across sites, 'Fianna' seemed to have the most considerable vigor in terms of plant height (100.5 mm) and stem diameter (19.1 mm) but had the least number of stems per plant (2.6) (Table 4.9). On the other hand, 'Hermes' had the highest number of stems per plant (5.7) and total plant leaf area (5605 cm^2), while 'Taurus' had the highest dry matter content of haulm (10.9%) and roots (18.3%).

In the cooler environment of Ohakune, as seen in Table 4.10, 'Hermes' had the highest crop stand (91.7 mm), number of stems per plant (5.1), and total plant leaf area (6282 cm^2), while 'Taurus' had the highest dry matter content of haulm (11.7%) and roots (18.4%). Under the supra-optimal temperatures of Hastings, 'Agria' (125.3 mm) and 'Fianna' (124.8 mm) had the tallest crop stand. 'Ilam Hardy' had the highest leaf area (9202 cm^2), while 'Hermes' (5.9), 'Taurus' (5.3), and 'Snowden' (4.9) had the highest number of stems per plant, a characteristic occasionally associated with higher yield due to the increased number of tubers per plant. However, the increase in yield for potato cultivars with greater number of stems can be limited if more tubers are smaller than the average size as a result of competition. The number of stems per plant of potato crops under well-watered conditions showed a strong and positive correlation with yield (Hirut et al., 2017). On the other hand, under the hot and drier conditions of Opiki, 'Fianna' had the most significant crop stand (93.5 mm) and stem diameter (21.8 mm), while 'Hermes' had the highest number of stems per plant (6.1) and leaf area (1963 cm^2).

Table 4.10 Morphological parameters of commercial potato cultivars as affected by the interaction of site and cultivar in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 65 DAP.

Cultivars	Plant height (mm)	No. of stems/ plant	Stem diameter (mm)	Whole plant leaf area (cm^2)	DMC[a] haulm (%)	DMC[a] roots (%)
			Ohakune			
'Agria'	81.5±2.2 ab	2.4 ±0.3 c	16.0±0.5 bc	3820±678 a	10.3	15.7
'Hermes'	91.7±3.1 a	5.1±0.4 a	15.6±0.7 bc	6282±959 a	9.7	15.2
'Ilam Hardy'	86.4±2.2 ab	3.9±0.3 ab	15.5±0.5 bc	5619±678 a	9.8	15.3
'Rua'	66.4±2.3 d	3.5±0.3 bc	17.4±0.5 ab	2724±678 a	9.1	14.2
'Taurus'	76.6±2.5 c	3.3±0.3 bc	14.2±0.6 c	4920±783 a	11.7	18.4
'Fianna'	83.3±2.5 ab	2.8±0.3 bc	18.8±0.6 a	2987±678 a	9.0	13.9
'Snowden'	63.3±2.2 d	4.8±0.3 a	14.8±0.5 c	4026±783 a	10.3	14.4
			Opiki			
'Agria'	69.6±2.2 bc	3.3±0.3 bc	15.0±0.5 c	851±678 a	9.0	16.6
'Hermes'	77.2±2.2 b	6.1±0.3 a	16.3±0.5 bc	1963±678 a	9.2	15.9
'Ilam Hardy'	77.6±2.2 b	3.9±0.3 b	16.8±0.5 bc	1698±678 a	9.0	16.9
'Rua'	66.4±2.2 c	4.0±0.3 b	17.4±0.5 b	869±678 a	9.0	15.3
'Taurus'	76.5±2.2 b	3.4±0.3 bc	15.9±0.5 bc	1539±678 a	9.7	19.1
'Fianna'	93.5±4.4 a	2.0±0.6 c	21.8±1.0 a	1844±678 a	12.7	17.6
'Snowden'	65.3±2.2 c	4.3±0.3 b	14.9±0.5 c	1658±678 a	9.0	16.1
			Hastings			
'Agria'	125.3±2.2 a	3.4±0.3 bc	14.2±0.5 b	5674±678 bc	12.1	19.0
'Hermes'	115.3±3.1 ab	5.9±0.4 a	12.5±0.7 b	8569±678 ab	11.2	17.1
'Ilam Hardy'	121.0±2.2 ab	3.7±0.3 bc	13.7±0.5 b	9202±783 a	10.9	17.9
'Rua'	100.9±2.4 c	4.4±0.3 ab	14.0±0.5 b	6708±783 abc	10.0	20.2
'Taurus'	112.0±2.5 b	5.3±0.3 a	12.6±0.5 b	7755±783 abc	11.3	17.4
'Fianna'	124.8±2.7 a	2.9±0.3 c	16.6±0.6 a	4997±783 c	9.9	15.1
'Snowden'	85.2±2.2 d	4.9±0.3 a	13.8±0.5 b	5338±678 c	10.0	16.4

[a]DMC – dry matter content; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05).

4.3.3.2 Abiotic stress effects on physiological performance of potato crops

Physiological parameters measured during the field trial including net photosynthesis ($p < 0.05$), transpiration rate ($p < 0.001$), and stomatal conductance ($p < 0.001$) were significantly affected by the environment (Table 4.11) but not affected by cultivar and cultivar x environment interaction (Table 4.12). The elevated temperatures in Hastings resulted in the crop's reduced net photosynthesis by 16.5% (19.2 µmol $CO_2m^2s^1$) compared with Ohakune (23.0 µmol CO_2 m^2s^1) but were not significantly different from those under the hot and drier conditions of Opiki (21.0 µmol CO_2 m^2s^1). Opiki was also not significantly different from the cooler conditions of Ohakune. The transpiration rate increased under the hot environment of Hastings by 61.8% (5.5 mmol H_2O m^2s^1) and under the hot and dry conditions in Opiki by 55.9% (5.3 mmol H_2O m^2s^1) when compared with Ohakune (3.4 mmol H_2O m^2s^1). The stomatal conductance also increased in Hastings by 129.5% (0.342 mol H_2O m^2 s^1) and in Opiki by 52.3% (0.227 mol H_2O m^2 s^1) when compared with Ohakune (0.149 mol H_2O m^2 s^1). These findings are consistent with the results of previous studies, whereby elevated atmospheric temperatures impaired the crop's photosynthetic activity in source leaves and increased the transpiration rate and stomatal conductance (Hammes & De Jager, 1990; Hastilestari et al., 2018; Reynolds, Ewing, & Owens, 1990; Wolf et al., 1990). Burton (1981) suggested that for every 5 °C increase in the leaf temperature of European potato cultivars above the optimum (20.0 °C), the photosynthetic performance is reduced by 20%. Besides the negative impact of high temperature on photosynthesis, it also affects photosynthate allocation, shifting away from developing the tubers toward the vegetative organs (Hastilestari et al., 2018). The increased stomatal conductance at high temperatures may improve photosynthesis either through increasing CO_2 transport to the leaves and through the cooling effect on the leaves due to higher transpiration rates (Wolf, Olesinski, Rudich, & Marani, 1990). However, if temperatures surpass a certain threshold, then it may impair photosynthesis and reduce water use efficiency (Guoju et al., 2013). Past studies also showed that elevated soil temperature (>20.0 °C) resulted in decreased net photosynthetic rate, particularly before the tuberization stage (Hammes & De Jager, 1990). This could be the case in Hastings and Opiki, which experienced elevated soil temperatures and reduced net photosynthesis during the 2018/19 growing season. On the other hand, under drought stress, photosynthesis is hampered by the closure of stomata to slow down the transpiration rate, which prevents the entry of CO_2 into the leaves (Li et al., 2017). The premature closure of stomata in response to drought stress may reduce the growth rate and ultimately affect the final yield.

Table 4.11 Physiological parameters of commercial potato cultivars as affected by environments and cultivars in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 65 DAP.

	Net Photosynthesis (μmol CO_2 m^2s^1)	**Transpiration Rate (mmol H_2O m^2s^1)**	**Stomatal Conductance (mol H_2O m^2 s^1)**	**Chlorophyll Content (SPAD)**
Sites	*	***	***	*
Ohakune	23.0±0.9 a	3.4±0.3 b	0.149±0.022 c	32.7±0.6 b
Opiki	21.1±0.8 ab	5.3±0.2 a	0.227±0.020 b	36.7±0.6 a
Hastings	19.2±0.9 b	5.5±0.3 a	0.342±0.021 a	25.8±0.6 c
Cultivars	ns	Ns	ns	*
‘Agria’	22.1±1.3 a	4.9±0.4 a	0.264±0.030 a	37.1 ±0.8 a
‘Hermes’	21.1±1.4 a	4.5±0.4 a	0.240±0.035 a	29.6±1.0 cd
‘Ilam Hardy’	20.8±1.3 a	4.9±0.4 a	0.209±0.032 a	33.8±0.8 ab
‘Rua’	22.8±1.3 a	5.3 ±0.4 a	0.292±0.030 a	30.3±0.8 c
‘Taurus’	20.1±1.3 a	4.3 ±0.4 a	0.210±0.033 a	31.4±0.9 bc
‘Fianna’	20.7±1.3 a	4.8 ±0.4 a	0.253±0.033 a	27.7±1.2 cd
‘Snowden’	19.7±1.3 a	4.3±0.4 a	0.207±0.030 a	26.5±0.8 d

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns ' not significant.

Abiotic stress significantly impacted the chlorophyll content (SPAD) ($p < 0.01$) in potato crops across the trial sites. Heat stress alone in the Hastings trial site reduced the chlorophyll content by 22.4% (25.8 SPAD), while the combination of heat and drought stress in Opiki increased the content by 12.2% (36.7 SPAD) when compared with the Ohakune trial site (32.7 SPAD). In a study on the effects of high temperature (40 °C) on wild potato species, photosynthesis is primarily affected by chlorophyll loss among heat-sensitive accessions (Reynolds, Ewing, & Owens, 1990). According to the study conducted by Hancock et al. (2014), the levels of photosynthetic pigments including chlorophyll a and b and carotenoids reduced by up to 20% under heat stress. On the other hand, the increase in the chlorophyll content under the hot and dry conditions in the Opiki trial site could be explained by loss in leaf turgor pressure or reduction in leaf growth (Ramírez et al., 2014). Hirut et al. (2017) observed a 13% increase in the chlorophyll content of potato leaves under water stress. This finding is potentially caused by the effect of water stress on leaf thickness, although it was not measured in the experiment, which could have affected the SPAD values.

Across the sites, ‘Agria’ had the highest SPAD value at 37.1, followed by ‘Ilam Hardy’ at 33.8, and ‘Taurus’ at 33.8. Under the elevated temperatures of Hastings, ‘Fianna’ had the highest SPAD value at 31.2. ‘Agria’ had the highest SPAD value at 43.9 under the hot and drier conditions of Opiki and at 40.3 under the cooler condition of Ohakune.

In this field trial, cultivars (genotypes) and genotype x environment interaction (Table 4.12) did not exhibit a differential response to abiotic stress in terms of the different physiological parameters measured, except for chlorophyll content. This observation contradicts previous findings on differences in the physiological response to abiotic stress among potato cultivars (Wolf et al., 1990) and even among species (Reynolds et al., 1990). Hastilestari et al. (2018) also found out that heat-sensitive cv. ‘Agria’ had lower photosynthetic activity under elevated temperatures (29 °C); while Hancock et al. (2014) observed that moderately heat-resistant cv. Desiree and Norchip had increased or unaffected photosynthetic activity in response to heat stress (30 °C). Hastilestari et al. (2018) suggested that more heat-tolerant cultivars can maintain their photosynthetic activities under elevated temperatures than their temperature-sensitive counterparts.

The differences between cultivars and the interaction between cultivars and environment in the field trial were improved by increasing the number of sampled plants per cultivar in each site for the physiology study. The time limitation and distance of the trial sites from Massey University had a great effect on the number of samples that were measured given the limited sampling window.

Regarding observed chlorophyll content, cultivars and cultivar x environment interaction exhibited apparent differential responses to abiotic stress effects. In Ohakune, the cultivar ‘Agria’ (40.3 SPAD) had the highest chlorophyll content that was not statistically different from ‘Ilam Hardy’ (34.8 SPAD) and ‘Ilam Hardy’ was not statistically different from ‘Rua’ (33.9 SPAD), ‘Hermes’ (32.8 SPAD), and ‘Fianna’ (32.3 SPAD). In Opiki, ‘Agria’ (43.9 SPAD) also had the highest chlorophyll content that was not statistically different from ‘Taurus’ (38.9 SPAD). In Hastings, ‘Fianna’ (31.2 SPAD) had the highest chlorophyll content that was not statistically different from ‘Ilam Hardy’ (29.0 SPAD) and ‘Agria’ (26.9 SPAD). In general, ‘Agria’ was found to be the most stable cultivar in terms of chlorophyll content across environments that can be attributed to cultivar characteristics.

Table 4.12 Physiological parameters of commercial potato cultivars as affected by the interaction of site and cultivar in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 65 DAP.

Cultivars	**Net Photosynthesis (µmol CO_2 m^2s^1)** ^{ns}	**Transpiration Rate (mmol H_2O m^2s^1)** ^{ns}	**Stomatal Conductance (mol H_2O m^2 s^1)** ^{ns}	**Chlorophyll Content (SPAD)***
Ohakune				
‘Agria’	22.1±2.1 a	3.0±0.7 a	0.135±0.052 a	40.3±1.4 a
‘Hermes’	20.9±3.0 a	2.6±0.9 a	0.118±0.074 a	32.8±2.0 b
‘Ilam Hardy’	24.1±2.1 a	3.4±0.7 a	0.146±0.052 a	34.8±1.4 ab
‘Rua’	24.4±2.1 a	3.8±0.7 a	0.175±0.052 a	33.9±1.4 b
‘Taurus’	22.2±2.5 a	3.7±0.8 a	0.160±0.060 a	29.2±1.6 bc
‘Fianna’	26.2±2.5 a	4.0±0.8 a	0.168±0.060 a	32.3±1.6 b
‘Snowden’	20.9±2.1 a	3.1±0.7 a	0.141±0.052 a	25.4±1.4 c
Opiki				
‘Agria’	22.4±2.2 a	4.9±0.7 a	0.230±0.052 a	43.9±1.4 a
‘Hermes’	21.1±2.2 a	5.0±0.7 a	0.231±0.052 a	33.3±1.4 bc
‘Ilam Hardy’	21.5±2.2 a	6.1±0.7 a	0.205±0.052 a	37.7±1.4 bc
‘Rua’	23.4±2.2 a	5.3±0.7 a	0.246±0.052 a	32.5±1.4 c
‘Taurus’	21.2±2.2 a	5.3±0.7 a	0.213±0.052 a	38.9±1.4 ab
‘Fianna’	14.6±2.2 a	4.8±0.7 a	0.217±0.052 a	19.5±2.8 d
‘Snowden’	23.1±2.2 a	5.4±0.7 a	0.246±0.052 a	34.1±1.4 bc
Hastings				
‘Agria’	22.0±2.1 a	6.8±0.7 a	0.426±0.060 a	26.9±1.4 ab
‘Hermes’	21.2±2.1 a	5.8±0.7 a	0.371±0.052 a	22.9±1.7 bc
‘Ilam Hardy’	16.7±2.5 a	5.2±0.8 a	0.276±0.060 a	29.0±1.4 ab
‘Rua’	20.7±2.1 a	6.7±0.7 a	0.454±0.060 a	24.5±1.5 bc
‘Taurus’	16.8±2.5 a	4.0±0.8 a	0.258±0.052 a	26.2±1.6 abc
‘Fianna’	21.3±2.5 a	5.6±0.8 a	0.373±0.060 a	31.2±1.7 a
‘Snowden’	15.2±2.1 a	4.4±0.7 a	0.235±0.060 a	20.1±1.4 c

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns ' not significant.

4.3.4 Abiotic stress effects on final yield and tuber quality of potato crops under multi-environment trial

4.3.4.1 Abiotic stress effects on final yield and tuber quality of potato crops

Based on the results of the multi-environment trial, the environment ($p < 0.001$) and cultivar ($p < 0.001$) significantly affected yield and tuber quality parameters in potato crops (Table 4.13). In the 2018/19 growing season, the Ohakune trial site with temperature and rainfall close to optimum levels for potato growth and development had the highest total yield and number of tubers per plant, harvest index (HI), and specific gravity (SG). The different yield and tuber quality parameters were negatively impacted by the hot as well as the hot and dry environments of the Hastings and Opiki trial sites, respectively. The total yield across all cultivars was reduced by 43.4% in Opiki (41.0 ha^{-1}) and by 42.1% in Hastings (41.9 t ha^{-1}) when compared with the Ohakune (72.4 t ha^{-1}) trial site. The marketable yield was reduced by 45.2% in Hastings (31.7 ha^{-1}) and by 39.8% in Opiki (34.8 t ha^{-1}) when compared with the Ohakune (57.8 t ha^{-1}) trial site. The negative impacts of heat and drought stress on yield are multifaceted and interrelated, significantly affecting the different morpho-agronomic and physiological functions of the potato crop. Heat stress alone impairs water use efficiency (Guoju et al., 2013), photosynthesis, and photosynthate production and enhances dry matter partitioning to the haulm, thereby promoting vegetative growth over tuber development (Gawronska et al., 1992; Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018). As a consequence, the tuber fresh weight, dry weight, dry matter, harvest index decreased (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018), and the number of smaller tubers increased (Hancock et al., 2014), ultimately reducing the final tuber yield. Heat stress at the early stage of potato crop growth can completely inhibit tuber initiation (Ghosh et al., 2000; Levy et al., 1991) and reduce the dry matter partitioning to the tubers; while at the latter stage, heat stress negatively affects tuber quality by reducing specific gravity (Ghosh et al., 2000). Drought stress, on the other hand, at the early stage of potato crop growth, could reduce plant height (Shock et al., 1992), delay canopy growth rate (Aliche et al., 2018; Jefferies, 1993; Martin et al., 1992), and decrease leaf area index and number of stems per plant (Lahlou et al., 2003). At the latter stage, drought stress could hasten haulm senescence (van Loon, 1981) and crop maturity (Robins & Domingo, 1956). Aliche et al. (2018) suggested that potato crops can minimize the tuber yield loss under drought stress by balancing canopy growth with tuber growth by delaying the exponential canopy growth rate. With the reduction in the growth rate of the aboveground parts of the potato plant, assimilate production is also hampered, resulting in a reduction in total tuber weight (Shock et al., 1992) and final yield. Moreover, Hirut et al. (2017) explained that under drought stress, the extent of groundcover is the primary influencer of the final yield. Under glasshouse conditions, the combination of heat and drought stress had an even greater negative impact on potato yield (Rykaczewska, 2015b).

Table 4.13 Yield and tuber quality parameters of commercial potato cultivars as affected by environments and cultivars in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at 65 DAP.

Factors	Total Yield (t/ha)	Marketable Yield (t/ha)	Yield loss (%)	Total no. of tubers/plant	No. of marketable tubers/plant	DMC^{a} (%)	HI^{b} (%)	SG^{c}
Sites	***	***		*	*	***	***	***
Ohakune	72.4±1.3 a	57.8±1.3 a	20	24.7±0.7 a	10.7±0.4 a	19.8 ±0.2 a	70.9±0.6 a	1.078±0.001 a
Opiki	41.0±1.4 b	34.8±1.4 b	15	15.9±0.7 c	9.3±0.4 b	16.7±0.2 c	66.5±0.6 b	1.069±0.001 b
Hastings	41.9±1.3 b	31.7±1.3 b	24	20.1±0.7 b	10.0±0.4 ab	18.5±0.2 b	62.6±0.6 c	1.071±0.001 b
Cultivars	***	***		**	***	***	***	***
‘Agria’	53.3±1.9 a	37.9±1.9 bc	28.9	15.0±1.1 cd	5.9±0.6 c	17.2±0.3 de	61.9±0.9 e	1.067±0.002 c
‘Hermes’	56.2±1.1 a	43.4±2.2 ab	22.8	27.3±1.1 a	14.4±0.6 a	19.9±0.3 ab	71.1±1.1 bc	1.080±0.001 a
‘Ilam Hardy’	53.6±1.9 a	35.0±1.9 bc	34.7	24.0±1.1 a	9.0±0.6 b	16.5±0.3 e	63.1±0.9 de	1.065±0.001 c
‘Rua’	37.9±2.0 b	34.1±2.0 c	10.0	14.2±1.1 d	7.3±0.6 bc	17.0±0.2 de	52.4±1.0 f	1.070±0.001 bc
‘Taurus’	56.0±1.0 a	49.1±2.1 a	12.3	23.4±1.1 ab	13.2±0.6 a	19.1±0.3 bc	75.4±1.0 ab	1.077±0.001 ab
‘Fianna’	53.1±2.0 a	42.9±2.2 ab	19.2	18.9±1.1 bc	7.9±0.6 bc	18.0±0.3 cd	66.6±1.1 cd	1.068±0.001 c
‘Snowden’	51.9±1.8 a	47.5±1.9 a	8.5	18.7±1.1 cd	12.3±0.6 a	20.4±0.3 a	76.3±0.9 a	1.080±0.001 a

^{a}Dry matter content, ^{b}harvest index, ^{c}specific gravity; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

This result validated the 2017/18 preliminary study (Chapter 3), where the significant yield loss was due to the high incidence of physiological disorders among the harvested tubers, particularly in the Hastings and Opiki trial sites (discussed under tuber physiological disorder Section 3.3.3.3), accounting for about 24% and 15% loss (by weight), respectively, and where extreme weather conditions were also present during the 2018/19 growing season. The relatively high yield loss of about 20% in the Ohakune trial site could be attributed to the larger and heavier tuber profile harvested in the area compared with the smaller tuber profile in the Hastings and Opiki trial sites. The total number of tubers and the number of marketable tubers per plant were reduced by 35.6% and 13.1% in Opiki (15.9 and 9.3, respectively) and by 18.6% and 6.5% in Hastings (20.1 and 10.0, respectively) when compared with the Ohakune (24.7 and 10.7, respectively) trial site. Earlier planting in mid-spring (mid-October) in Opiki with low rainfall and soil moisture level (water deficit) resulted in reduced tuber initiation that translated to a lower number of tubers per plant formed. On the other hand, planting in late-spring (mid-November) in Ohakune coincided with the stolon formation and tuber initiation during higher rainfall, resulting in greater number of tubers per plant developed. The same is true for Hastings (early November planting), where tuber initiation coincided with high rainfall (above historical average), leading to enhanced tuber initiation. This finding is in line with past studies, where the number of tubers per stem relied on the amount of early-season rainfall (Haverkort et al., 1990) or irrigation (Costa, Vedove, Gianquinto, Giovanardi, & Peressotti, 1997; Lahlou et al., 2003), while water deficit caused a significant reduction in tubers (Costa et al., 1997; Deblonde & Ledent, 2001; Yuan et al., 2003). Similar to drought stress, heat stress strongly inhibits tuber formation (Levy et al., 1991), particularly in the early growth stage of the potato crop (Ghosh et al., 2000). This phenomenon is attributed to the shift in biomass distribution away from the tubers and toward the aboveground parts (Hancock et al., 2014). In a separate study, however, heat stress under favorable soil moisture conditions increased the number of tubers per plant but related this to the occurrence of secondary tuberization with physiologically younger tubers (Rykaczewska, 2015b).

Despite having the highest number of marketable tubers in Ohakune, a significant reduction (>50%) occurred from the original total number of tubers per plant (24.7). This finding can be attributed to the enhanced tuber initiation (~50% higher) at 45 DAP in Ohakune (data not presented), producing more tubers than at the two other sites. However, most of the tubers were either undersized and exhibited skin feathering (common characteristics of immature tubers) or tubers had secondary growth that increased the number of non-marketable tubers. The total yield, however, was compensated by the size and weight of the main tubers in each plant in the Ohakune trial site. These results agree with previous findings, where moisture deficits (Deblonde & Ledent, 2001; Eiasu et al., 2007a; Yuan et al., 2003) and heat stress (Ghosh et al., 2000; Levy et al., 1991) significantly decreased the number of tubers formed. These data could be related to the shift in biomass distribution away from the tubers and toward the aboveground parts of the potato crop (Hancock et al., 2014) as a typical response to heat or drought stress.

The other measured tuber quality parameters including DMC, HI, and SG were the highest in the Ohakune trial site. The DMC of tubers was reduced in Opiki by 15.7% (16.7%) and in Hastings by 6.6% (18.5%) when compared with Ohakune (19.8%). Under both drought stress (Jefferies, 1993) and heat stress (Hancock et al., 2014; Hastilestari et al., 2018), the dry matter partitioning to shoots and roots was enhanced over tuber development, leading to decreased tuber fresh weight, dry weight, and DMC (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018). However, reports indicated that drought stress could also increase the DMC of potato tubers in the field and greenhouse (Lahlou et al., 2003). Jefferies (1993) stipulated that it could be due to genotypic differences or timing of drought stress relative to tuber initiation. Moreover, the reduction in leaf area expansion due to drought stress (Shahnazari et al., 2007) could lead to reduced interception of sunlight and therefore reduced the conversion into DMC and affected the HI (Tourneux et al., 2003b).

In this field trial, the HI was reduced by 11.7% (62.6%) in Hastings and by 6.2% (66.5%) in Opiki when compared with the Ohakune (70.9%) trial site. In a past study, drought stress considerably reduced the HI in potatoes (Deblonde, Haverkort, & Ledent, 1999). Another study showed that the effect of drought stress on HI was cultivar dependent, where the HI increased in an early variety and decreased in a later one (Lahlou et al., 2003). Elevated temperatures (30 °C/20 °C day/night) also reduced the HI as a result of a shift in biomass distribution away from the tubers and toward the aboveground parts of the potato crop (Hancock et al., 2014). SG was the lowest in Opiki (1.069) but was not statistically different from Hastings (1.071), while Ohakune had the highest SG (1.078). According to Shock et al. (1992), early-season water deficit had no adverse effect on tuber SG. Elevated temperatures, on the other hand, reduced the SG of tubers in all growth stages, but the greatest impact was observed at the later growth stages (Ghosh et al., 2000).

The effect of the cultivar (Table 4.13) and cultivar x environment interaction (Table 4.14) on the different yield and tuber quality parameters in potatoes were highly significant ($p < 0.001$). 'Hermes' and 'Taurus' had the highest total yield of 56.2 and 56.0 t ha^{-1}, respectively. 'Taurus' had a higher marketable yield of 49.1 t ha^{-1}, having only a 12.3% yield loss, than 'Hermes' (43.4 t ha^{-1} yield and 22.8% yield loss). The marketable yield of 'Snowden' (47.5 t ha^{-1}) was not significantly different from 'Taurus', and the former had the least yield loss of about 8.5% only. The high marketable yield of 'Hermes', 'Taurus', and 'Snowden' can be attributed to their vigorous plant growth, i.e., greater number of stems per plant and total plant leaf area could enhance sunlight interception and dry matter accumulation, increase the number of total and marketable tubers per plant, and decrease the percentage of non-marketable tubers compared with the most tested cultivars. ‘Rua’ had the lowest total and marketable yields of 37.9 and 34.1 t ha^{-1}, respectively. These values, however, are close to the recorded total yield (32.6–43.3 t ha^{-1}) (McLeod, 1973) and marketable yield (36.7 t ha^{-1}) (Anderson, Lewthwaite, Genet, Braam, & Gallagher, 1997) of ‘Rua’. ‘Ilam Hardy’, on the other hand, had a relatively high total yield (53.6 t ha^{-1}) but also had the highest yield loss of 34.7%.

‘Agria’ also had a relatively high yield (53.3 t ha^{-1}) but also had a high yield loss of 28.9%. A common observation among varieties with higher marketable yields, such as ‘Hermes’ and ‘Taurus’, is their inherent characteristics of producing a high number of tubers. Furthermore, ‘Hermes’ had the greatest total number of tubers per plant (27.3), which was not statistically different from ‘Ilam Hardy’ (24), and ‘Ilam Hardy’ was not statistically different from ‘Taurus’ (23.4). ‘Rua’ had the least total number of tubers per plant (14.2). ‘Hermes’ also produced the greatest number of marketable tubers per plant (14.4), which was not statistically different from ‘Taurus’ (13.2) and ‘Snowden’ (12.3). ‘Agria’ had the least number of marketable tubers produced per plant (5.9), a key characteristic of the cultivar due to its fewer but larger tubers. On the other hand, DMC was the highest in ‘Snowden’ (20.4%), which was not statistically different from ‘Hermes’ (19.9%), and ‘Hermes’ was not statistically different from ‘Taurus’ (19.1%). DMC was the lowest in ‘Ilam Hardy’ (16.5%) and ‘Rua’ (17.0%), a common characteristic of both cultivars (Anderson, Lewthwaite, Genet, & Braam, 2004). SG was the highest in ‘Hermes’ and ‘Snowden’ (1.080) but was not statistically different from ‘Taurus’ (1.077). High SG seemed to be a common characteristic of ‘Hermes’ (Amjad, Randhawa, Butt, & Asghar, 2016) and ‘Snowden’ (Baritelle & Hyde, 2003; Canadian Food Inspection Agency, 2020b; PAA, 2020). However, the increase in SG affects the bruise resistance of ‘Snowden’ (Baritelle & Hyde, 2003), therefore increasing bruise-damaged tubers. In contrast, SG seems to be lower among cultivars with naturally larger tubers, such as ‘Agria’ (1.067), ‘Fianna’ (1.068), and ‘Ilam Hardy’ (1.065). HI, on the other hand, was the highest in ‘Snowden’ (76.3%), which was not significantly different from ‘Taurus’ (75.4%). HI was the lowest in ‘Agria’ (61.9%) and ‘Ilam Hardy’ (63.1%).

Table 4.14 Yield and tuber quality parameters of commercial potato cultivars as affected by the interaction of site and cultivar in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at final harvest (130 DAP).

Cultivars	**Total Yield (t/ha) *****	**Marketable Yield (t/ha)*****	**Yield loss (%)**	**Total no. of tubers/plant****	**No. of marketable tubers/plant****	**DMC^a (%)*****	**HI^b (%)*****	**SG^c***
				Ohakune				
‘Agria’	74.1±3.0 ab	59.4±3.1 ab	19.8	17.8±1.9 c	6.4±1.0 c	18.5 ±0.4 c	68.9 ± 1.6 bc	1.074±0.003 ab
‘Hermes’	74.5±4.0 ab	61.5±4.1 ab	17.4	32.1±1.9 a	14.8±1.0 a	21.9 ±0.4 a	73.5 ±2.1 ab	1.083±0.003 a
‘Ilam Hardy’	73.5±3.0 ab	42.1±3.1 c	42.7	28.8±1.9 ab	8.0±1.0 c	18.1 ±0.4 c	64.4 ±1.6 c	1.068±0.003 b
‘Rua’	58.9±3.3 c	50.6±3.3 bc	14	19.5±1.9 c	9.5±1.0 bc	18.5 ±0.4 c	52.4 ±1.7 d	1.078±0.003 ab
‘Taurus’	74.3±3.8 ab	66.1±3.9 a	11	28.0±1.9 ab	13.8±1.0 a	19.9 ±0.4 bc	80.7 ±2.0 a	1.080±0.003 ab
‘Fianna’	86.7±3.3 a	66.5±3.3 a	23.3	23.6±1.9 bc	9.5±1.0 bc	20.5 ±0.4 ab	79.4 ±1.7 a	1.078±0.003 ab
‘Snowden’	64.8±3.1 bc	58.3±3.1 ab	10	23.3±1.9 bc	13.1±1.0 ab	20.9 ±0.4 ab	77.0 ±1.6 a	1.083±0.003 a
				Opiki				
‘Agria’	44.4±3.3 ab	28.1±3.3 bc	36.7	12.4±1.9 bc	5.7±1.0 c	16.2 ±0.4 b	65.0 ±1.7 bc	1.066±0.003 dc
‘Hermes’	54.9±3.2 a	45.8±3.3 a	16.6	24.3±1.9 a	16.2±1.0 a	19.5 ±0.4 a	79.1 ±1.7 a	1.082±0.003 a
‘Ilam Hardy’	42.0±3.4 ab	33.5±3.6 abc	20.2	19.3±1.9 ab	7.3±1.0 c	14.7 ±0.4 b	63.4 ±1.8 cd	1.059±0.003 d
‘Rua’	25.9±3.5 c	25.1±3.6 c	1.6	9.8±1.9 c	6.5±1.0 c	14.8 ±0.4 b	51.1 ±1.8 e	1.061±0.003 bc
‘Taurus’	45.8±3.5 ab	41.6±3.5 ab	9.2	19.1±1.9 ab	12.1±1.0 ab	18.1 ±0.4 a	72.2 ±1.8 ab	1.074±0.003 ab
‘Fianna’	30.1±5.4 bc	29.5±4.4 bc	2.0	12.9±2.2 bc	7.9±1.2 bc	14.8 ±0.4 b	55.5 ±2.3 de	1.062±0.003 bc
‘Snowden’	42.4±3.3 ab	40.0±3.3 ab	5.7	13.3±1.9 bc	9.8±1.0 bc	18.5 ±0.4 a	79.4 ±1.7 a	1.076±0.003 ab
				Hastings				
‘Agria’	41.3±3.3 ab	26.2±3.3 bc	36.6	14.8±1.9 b	5.8±1.0 b	17.1 ±0.6 bc	51.7 ±1.7 d	1.060±0.004 b
‘Hermes’	40.2±3.0 ab	23.0±4.0 c	42.8	25.7±2.2 a	12.2±1.2 a	18.2 ±0.5 bc	60.6 ±2.0 bc	1.075±0.003 ab
‘Ilam Hardy’	45.4±3.4 a	29.2±3.4 bc	35.7	23.9±1.9 a	11.7±1.0 a	16.8 ±0.5 c	61.5 ±1.7 b	1.065±0.003 b
‘Rua’	28.8±3.5 c	26.6±3.3 bc	7.6	13.4±1.9 b	6.0±1.0 b	17.6 ±0.4 bc	53.7 ±1.7 cd	1.069±0.003 b
‘Taurus’	47.9±3.0 a	39.6±3.5 ab	17.3	23.2±2.2 a	13.7±1.2 a	19.2 ±0.5 b	73.2 ±1.8 a	1.077±0.003 ab
‘Fianna’	42.4±3.7 ab	32.8±3.8 abc	22.6	20.3±1.9 ab	6.4±1.0 b	18.6 ±0.5 bc	64.8 ±1.9 b	1.065±0.003 b
‘Snowden’	48.6±3.1 a	44.3±3.2 a	8.8	19.3±1.9 ab	14.1±1.0 a	21.9 ±0.5 a	72.4 ±1.6 a	1.084±0.003 a

^{a}Dry matter content, ^{b}harvest index, ^{c}specific gravity; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Under the cooler environment of Ohakune, 'Fianna' had the greatest total yield (86.7 t ha^{-1}) and marketable yield (66.5 t ha^{-1}). 'Agria', 'Hermes', and 'Taurus' also yielded well in Ohakune. 'Rua' had the least total yield (58.9 t ha^{-1}) and also the least marketable yield (50.6 t ha^{-1}) with a 14% yield loss. 'Snowden' had the second least total yield (86.7 t ha^{-1}) but also had among the highest marketable yield (58.3 t ha^{-1}) due to relatively lower yield loss (10%). 'Ilam Hardy', on the other hand, had the highest total yield (73.5 t ha^{-1}) but also the least marketable yield (42.1 t ha^{-1}) due to the very high yield loss (42.7%). The high yield loss in 'Ilam Hardy' was due to the incidence of secondary tuber formation potentially associated with limited adaptation of some cultivars to high temperatures during the growing season (Potatoes South Africa, 2016). Another possible reason is that 'Ilam Hardy''s early maturity could have resulted in in-field sprouting when left longer in the field as observed in the three trial sites. The number of marketable tubers per plant was the highest in 'Hermes' (14.8), which was not statistically different from 'Taurus' (13.8), and 'Taurus' was not statistically different from 'Snowden' (13.1). 'Agria', 'Ilam Hardy', 'Rua', and 'Fianna' had the least number of marketable tubers with 6.4, 8.0, 9.5, and 9.5 per plant, respectively. DMC was the highest in 'Hermes' (21.9%), which was not statistically different from 'Fianna' (20.5%) and 'Snowden' (20.9%). 'Agria', 'Ilam Hardy', and 'Rua' had the lowest DMC values of 18.5%, 18.1%, and 18.5%, respectively. SG seemed to be enhanced at the Ohakune trial site. The majority of the cultivars had improved SG, including 'Snowden' (1.083), 'Hermes' (1.083), 'Taurus' (1.080), 'Fianna' (1.078), 'Rua' (1.078), and 'Agria' (1.074). 'Ilam Hardy' had the lowest SG value (1.068). HI was the highest in 'Taurus' (80.7%), which was not statistically different from 'Fianna' (79.4%) and 'Snowden' (77.0%), while 'Snowden' was not statistically different from 'Hermes' (73.5%). 'Agria' and 'Ilam Hardy' were not statistically different from each other, with values of 68.9% and 64.4%, respectively. 'Rua' had the least HI at 52.4%.

Under the hot and dry conditions at the Opiki trial site, 'Hermes' performed best in terms of total (54.9 t ha^{-1}) and marketable yield (45.8 t ha^{-1}) with about 16.6% yield loss. This finding could be attributed to the cultivar's reported high drought (Europotato, 2020c) and good heat (de Nijs, 2020) stress resistance, and low susceptibility to common tuber physiological disorders, e.g., secondary growth and growth cracks (Europotato, 2020c). In this trial, 'Hermes' also produced the highest number of stems per plant among the cultivars tested that translated to a higher number of tuber sets. 'Taurus' and 'Snowden' also had relatively higher total yield (45.8 and 42.4 t ha^{-1}, respectively) and marketable yield (41.6 and 40.0 t ha^{-1}, respectively). 'Taurus' was also reported to have good drought tolerance (HZPC, 2020). Although 'Snowden' requires high soil moisture for optimum growth (Canadian Food Inspection Agency, 2020b), the dry conditions in Opiki were compensated by 'Snowden''s lower susceptibility to tuber physiological disorders, leading to a lower percentage of defective tubers. Hirut et al. (2017) suggested that high-yielding potatoes under drought stress can better maintain their plant vigour and tuber yield. 'Agria' had a comparable total yield (44.4 t ha^{-1}); however, it had the highest yield loss at 36.7% due to its susceptibility to tuber physiological disorders that are associated with abiotic stresses, such as drought. This finding is in line with a past study that reported the drought susceptibility of 'Agria' (Hassanpanah, 2010) but contradicts other reports revealing its medium to high drought resistance (Banik et al., 2016; Europotato, 2020a; Tekfen Agri, 2020). 'Rua' and 'Ilam Hardy', on the other hand, were among the cultivars with the lowest total and marketable yields. 'Rua' is a cross between Katahdin x Harford, while 'Ilam Hardy' is a cross between Arran Pilot x Katahdin. The cultivar Katahdin is extensively used worldwide as a parent material because it is known to have good tolerance to drought stress (Soltys-Kalina et al., 2016b). Arran Pilot has also been reported to have high drought resistance (Europotato, 2020b). The drought tolerance of Katahdin (and Arran Pilot for 'Ilam Hardy') may not be explicitly expressed in neither 'Rua' nor 'Ilam Hardy' cultivars considering that drought tolerance is a very complex trait (Anithakumari, Dolstra, Vosman, Visser, & van der Linden, 2011). Soltys-Kalina et al. (2016b) demonstrated the genetic influence of Katahdin and other parent materials on the drought tolerance of Katahdin-derived cultivars in terms of their ability to minimize the reduction in tuber yield and relative water content under drought stress.

The number of marketable tubers was the highest in 'Hermes' (16.2), which was not statistically different from 'Taurus' (12.1). The least number of marketable tubers were found in 'Agria' (5.7), 'Rua' (6.5), and 'Ilam Hardy' (7.3). DMC was the highest in 'Hermes' (19.5%), which was not statistically different from 'Taurus' (18.1%) and 'Snowden' (18.5%). High DMC content is an inherent characteristic of 'Hermes' (Abbasi et al., 2011; Amjad et al., 2016; Sincik, Turan, & Göksoy, 2008), which is a cultivar bred for industrial processing (Moschella et al., 2005). 'Hermes' can partition dry matter toward tuber production during periods of drought rather than canopy production, which makes it more efficient in producing yield per unit of water used (Daccache et al., 2012). The lowest DMC was observed in ‘Ilam Hardy’ (14.7%), ‘Rua’ (14.8%), and ‘Fianna’ (14.8%). SG was greatest in ‘Hermes’ (1.082), which was not statistically different from ‘Taurus’ (1.074) and ‘Snowden’ (1.076). The lowest SG was again recorded in cultivars with larger tubers, such as ‘Agria’ (1.066), ‘Ilam Hardy’ (1.059), ‘Rua’ (1.061), and ‘Fianna’ (1.062). HI was the highest in ‘Snowden’ (79.4%) and ‘Hermes’ (79.1%), which was not statistically different from ‘Taurus’ (72.2%), while the lowest HI was recorded in ‘Rua’ (51.1%).

On the other hand, under the hot conditions at the Hastings trial site, ‘Snowden’ performed best in terms of total (48.6 t ha^{-1}) and marketable yield (44.3 t ha^{-1}), with only about 8.8% yield loss. This cultivar was not statistically different from ‘Taurus’ in terms of total (47.9 t ha^{-1}) and marketable yield (39.6 t ha^{-1}), with about 17.3% yield loss. The performance of ‘Snowden’ was better in Hastings than in Opiki potentially due to the higher levels of soil moisture, a requirement for optimum growth of this cultivar (Canadian Food Inspection Agency, 2020b). This could also show that ‘Snowden’ is more heat tolerant than the combination of heat and drought tolerance. ‘Ilam Hardy’ had a comparable total yield (45.4 t ha^{-1}) but with reduced marketable yield (29.2 t ha^{-1}) due to high yield loss (35.7%). ‘Hermes’ had the least marketable yield (23.0 t ha^{-1}) mostly because of the highest level of yield loss (42.8%) among the tested cultivars. The very high yield loss of ‘Hermes’ in the Hastings site could be explained by the high incidence of tuber physiological disorders, primarily secondary growth (heat sprouts), which could have been induced by elevated temperatures before harvesting (Potatoes South Africa, 2016). This observation is contrary to a report that ‘Hermes’ has good heat resistance (de Nijs, 2020). ‘Snowden’ had the highest number of marketable tubers per plant (14.1), which was not statistically different from ‘Taurus’ (13.7), ‘Hermes’ (12.2), and ‘Ilam Hardy’ (11.7). The influence of genotype in terms of tuber size and number of tubers per plant was more distinct in the Hastings trial site than in the other two trial sites. Cultivars that produced relatively larger tubers, such as ‘Agria’ (5.8), ‘Rua’ (6.0), and ‘Fianna’ (6.4), produced fewer marketable tubers per plant. ‘Snowden’ had the highest DMC (21.9%). DMC was also high for ‘Taurus’ (19.2%), ‘Fianna’ (18.6%), and ‘Hermes’ (18.2%). ‘Ilam Hardy’ had the least DMC (16.8%). HI was the highest in ‘Taurus’ (73.2%) that was not statistically different from ‘Snowden’ (72.4%), while ‘Agria’ had the least HI (51.7%). SG was the highest in ‘Snowden’ (1.084) that was not statistically different from ‘Taurus’ (1.077) and ‘Hermes’ (1.075). ‘Agria’ had the least SG (1.060).

4.3.4.2 Abiotic stress effects on tuber size distribution at final harvest

In general, Ohakune produced larger tuber sizes among the trial sites (Table 4.15). The majority of the tubers per plant were table-sized 51–90 mm (11.1) and gourmet-sized 31–50 mm (7.1), while a considerable number were large >90 mm (2.7) and undersized <30 mm (3.8). Under the hot as well as the hot and dry conditions of the Hastings and Opiki trial sites, respectively, the percentage of large (up to 77.8%), table- (up to 22.5%), and gourmet-sized (up to 36.6%) tubers significantly decreased compared with the Ohakune trial site with cooler conditions and under irrigation. In another study, drought increased the number of small tubers <35 mm and reduced the number of larger tubers >55 mm (Mackerron & Jefferies, 1988). Early season water deficit may result in the formation of larger tubers that are suggested to be connected to the reduced number of tubers per plant developed (Shock et al., 1992). In a study conducted by Aliche et al. (2018), drought stress resulted in the downshifting of tuber sizes; the more severe the drought condition is, the lower the number of large tubers will be. Drought stress was also found to reduce tuber size (Hirut et al., 2017; Mackerron & Jefferies, 1988), especially in water deficit-sensitive cultivars, during the tuber expansion stage (Gandar & Tanner, 1976) by up to 20% (Martin et al., 1992). In contrast, well-watered potato crops had increased tuber size, resulting in a 20.0%–48.9% improvement in the total yield (Zarzyńska & Goliszewski, 2016). In the present study, the reduction in yield due to abiotic stress was attributed to the reduction in the total number of tubers per plant and the decrease in the tuber size. On the other hand, heat stress reduced tuber size even among potato cultivars showing heat tolerance (Rykaczewska, 2015b). This observation agrees with the present study, where the highest percentage of undersized tubers (21.2%) was under the hot conditions of the Hastings trial site. The effect of cultivar on tuber size distribution was highly significant ($p < .001$), demonstrating the strong genotypic influence on tuber size characteristics. Cultivars that have naturally large, elongated tubers produced more large tubers per plant (>90 mm) such as ‘Agria’ (4.3), ‘Rua’ (1.9), and ‘Fianna’ (2.1), while cultivars that have medium-sized circular tubers produced more table-sized tubers per plant (51–90 mm) such as ‘Ilam Hardy’ (13.1), ‘Hermes’ (12.6), ‘Taurus’ (11.2), and ‘Snowden’ (10.9). Other than having the highest number of table-sized tubers, ‘Hermes’ and ‘Taurus’ also had the highest number of undersized tubers per plant (5.8 and 5.5, respectively) which could mean that both cultivars have higher tuber set than the other cultivars tested.

Table 4.15 Tuber size distribution of commercial potato cultivars as affected by site and cultivar in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at final harvest (130 DAP).

	Tuber Size Distribution[a]							
	Large (>90 mm)		**Table (51-90 mm)**		**Gourmet (31-50 mm)**		**Undersize (<30 mm)**	
	Ave. No.	**%**	**Ave. No.**	**%**	**Ave. No.**	**%**	**Ave. No.**	**%**
Sites								
	***		***		***		**	
Ohakune	2.7±0.1 a	11.1	11.1±0.4 a	44.8	7.1±0.5 a	28 .6	3.8±0.3 a	15.5
Opiki	0.6±0.2 b	3.9	8.6±0.4 b	52.9	4.5±0.5 b	27.5	2.6±0.3 b	15.7
Hastings	0.8±0.2 b	4.2	10.4±0.4 a	51.8	4.6±0.5 b	22.8	4.3±0.3 a	21.2
Cultivars								
	***		***		***		***	
‘Agria’	4.3±0.2 a	29.1	6.1±0.6 c	41.5	3.0±0.7 d	20.5	1.3±0.5 c	8.9
‘Hermes’	0.5±0.2 c	1.7	12.6±0.7 a	46.8	8.0±0.8 a	29.9	5.8±0.5 a	21.6
‘Ilam Hardy’	0.5±0.2 c	1.9	13.1±0.6 a	54.2	6.8±0.7 abc	28.1	3.8±0.5 ab	15.8
‘Rua’	1.9±0.2 b	13.0	6.7±0.6 c	46.7	3.5±0.7 d	24.7	2.2±0.5 bc	15.6
‘Taurus’	0.4±0.2 c	1.7	11.2±0.7 ab	45.2	7.6±0.8 ab	30.8	5.5±0.5 a	22.3
‘Fianna’	2.1±0.2 b	11.2	9.6±0.7 b	51.4	3.9±0.8 cd	21.1	3.1±0.5 bc	16.4
‘Snowden’	0.2±0.2 c	1.0	10.9±0.6 ab	57.9	4.6±0.7 bcd	24.8	3.1±0.5 bc	16.3

[a] Based on T&G Global TAG Standards for Potatoes; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

The effect of cultivar x environment (Table 4.16) interaction was significant on tuber size distribution specifically for large and table-sized tubers. In the cooler environment of the Ohakune trial site, the same trend was observed, where cultivars that have naturally large elongated tubers produced more large-sized tubers per plant (>90 mm), such as ‘Agria’ (6.3), ‘Fianna’ (5.1), and ‘Rua’ (4.1); meanwhile, cultivars that have medium-sized circular tubers produced more table-sized tubers per plant (51–90 mm), such as ‘Ilam Hardy’ (14.3), ‘Snowden’ (13.3), ‘Hermes’ (12.9), and ‘Taurus’ (12.8). The combination of large and table-sized tubers (70.6% of the total number of tubers) in ‘Fianna’ conferred the cultivar with the highest total yield among the tested cultivars. In the hot and dry environment of the Opiki trial site, only ‘Agria’ produced the highest number of large tubers per plant (3.6) but had the lowest table-sized tubers per plant (6.3). ‘Hermes’ had the highest number of table-sized tubers per plant (14.0), which accounts for about 60% of the total number of tubers formed, while ‘Rua’ had the least (5.8) but already accounts for about 60.0% of the total number of tubers formed. In the hot environment of Hastings, only 'Agria' produced the highest number of large tubers (3.0) but had the lowest table-sized tubers per plant (7.2). 'Ilam Hardy' had the highest number of table-sized tubers per plant (14.4), which was not statistically different from 'Taurus' (12.0) and 'Snowden' (11.8). 'Rua' had the least number of table-sized tubers per plant (6.5), which accounts for about 46.7% of the total number of tubers formed.

4.3.4.3 Abiotic stress effects on tuber physiological disorders of potato crops

Physical deformations of tubers, such as presence of mechanical harvest damage, pest and disease damage, and tuber physiological disorders, significantly affect the saleability of potato crops. The literature strongly suggests that many tuber physiological disorders are influenced by unfavorable environmental factors, including suboptimal atmospheric and soil temperatures, rainfall, and humidity (Hiller, Koller, & Thornton, 1985; Lugt et al., 1964; Rykaczewska, 2015b, 2017b). The changing weather pattern and increasing incidence of extreme weather events as a consequence of climate change promote the incidence of tuber physiological disorders in the potato field. In the present field trial, tuber physiological disorders among harvested sample tubers manifested as early as 65 DAP, coinciding with Stage III or tuber filling stage. The Hastings trial site had the most observed tuber physiological disorders, such as second growth, enlargement of lenticels, and stained tubers, compared with the Ohakune and Opiki trial sites (data not presented). Across all the three trial sites, 'Ilam Hardy' and 'Rua' had the most recorded incidence of tuber physiological disorders, including tuber malformation and second growth.

Table 4.16 Tuber size distribution of commercial potato cultivars as affected by the interaction of sites and cultivars in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at final harvest (130 DAP).

Cultivars	Tuber Size Distribution[a]							
	Large (>90 mm)***		Table (51–90 mm)**		Gourmet (31–50 mm)^{ns}		Undersize (<30 mm) ^{ns}	
	Ave. No./plant	%	Ave. No. /plant	%	Ave. No. /plant	%	Ave. No. /plant	%
Ohakune								
‘Agria’	6.3±0.4 a	35.7	4.9±1.1 c	27.7	4.6±1.2 b	25.8	1.9±0.9 c	10.8
‘Hermes’	1.3±0.4 c	3.9	12.9±1.1 a	40.3	11.4±1.2 a	35.6	6.5±0.9 a	20.3
‘Ilam Hardy’	0.9±0.4 c	3.2	14.3±1.1 a	49.8	8.8±1.2 ab	30.4	4.8±0.9 abc	16.5
‘Rua’	4.1±0.4 b	20.9	7.8±1.1 bc	39.7	5.0±1.2 b	25.6	2.7±0.9 bc	13.7
‘Taurus’	1.1±0.4 c	3.9	12.8±1.1 a	45.7	7.9±1.2 ab	28.2	6.3±0.9 ab	22.2
‘Fianna’	5.1±0.4 bc	21.5	11.6±1.1 ab	49.1	5.3±1.2 b	22.3	1.7±0.9 c	7.1
‘Snowden’	0.4±0.4 c	1.8	13.3±1.1 a	56.8	6.7±1.2 ab	28.6	3.0±0.9 abc	12.9
Opiki								
‘Agria’	3.6±0.00 a	28.5	6.3±1.1 b	50.3	1.5±1.2 b	11.9	1.2±0.9 a	9.3
‘Hermes’	0.0±0.0 b	0.0	14.0±1.1 a	60.9	5.7±1.2 ab	24.7	3.3±0.9 a	14.5
‘Ilam Hardy’	0.0±0.0 b	0.0	10.5±1.1 ab	54.3	5.7±1.2 ab	29.3	3.2±0.9 a	16.4
‘Rua’	0.2±0.4 b	1.9	5.8±1.1 b	61.0	2.3±1.3 b	23.8	1.3±0.9 a	13.3
‘Taurus’	0.2±0.4 b	0.7	8.8±1.1 b	37.1	10.5±1.3 a	43.9	4.3±0.9 a	18.2
‘Fianna’	0.4±0.4 b	3.6	7.4±1.3 b	60.4	2.4±1.4 b	19.8	2.0±1.0 a	16.2
‘Snowden’	0.0±0.0 b	0.0	7.6±1.1 b	55.8	3.3±1.2 b	24.5	2.7±0.9 a	19.7
Hastings								
‘Agria’	3.0±0.4 a	21.3	7.2±1.1 bc	50.9	3.0±1.2 a	21.3	0.9±0.9 c	6.5
‘Hermes’	0.1±0.4 b	0.4	10.9±1.3 abc	42.6	7.0±1.4 a	27.4	7.6±1.0 a	29.6
‘Ilam Hardy’	0.4±0.4 b	1.7	14.4±1.1 a	59.4	5.9±1.2 a	24.4	3.5±0.9 bc	14.4
‘Rua’	1.3±0.0 b	9.6	6.5±1.1 c	46.7	3.3±1.2 a	23.9	2.6±0.9 bc	19.8
‘Taurus’	0.0±0.0 b	0.0	12.0±1.3 ab	53.2	4.6±1.4 a	20.2	6.0±1.0 ab	26.6
‘Fianna’	0.6±0.4 b	3.8	9.4±1.1 abc	47.4	4.2±1.2 a	21.1	5.5±0.9 ab	27.8
‘Snowden’	0.2±0.4 b	0.9	11.8±1.1 ab	60.8	3.9±1.2 a	20.3	3.5±0.9 bc	18.1

[a] Based on T&G Global TAG Standards for Potatoes; Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

As observed in the 2017/18 season, the environment at the three trial sites significantly ($p <$ .001) affected the occurrence of tuber physiological disorders at final harvest (130 DAP) during the 2018/19 growing season (Table 4.17). The occurrence of a particular type of tuber physiological disorder depends on the environment and types of abiotic stress present during the growing season (Figure 4.5). In the cooler environment of the Ohakune trial site, feathering was the most common physiological disorder (28.1%). Feathering is characterized by having a thin skin that can easily be torn at harvest and during handling (Hillerm & Thornton, 2008) and is a common characteristic of immature tubers. The common causes of feathering are harvesting prematurely when the tuber skin has not been matured completely (Hillerm & Thornton, 2008). Excessive nitrogen and wet soil late in the season will exaggerate this phenomenon (Potatoes South Africa, 2016). In this field trial, the probable cause of the feathering of tubers at the Ohakune trial site is likely the slower GDD (growing degree days) accumulation rate due to the relatively cooler environment throughout the growing season. Considerable percentages of tuber malformation (19.1%) and growth cracks (19.1%) were observed among the harvested tubers at the Ohakune trial site. The supra-optimal atmospheric (>25 °C) and soil (>18 °C) temperatures experienced early- to mid-summer (December 2018 to January 2019) induced significant tuber malformation in Ohakune. On the other hand, the heavy downpour experienced early-summer (December 2018) could have induced the rapid water uptake into the tubers, thereby increasing tuber turgidity and promoting growth crack formation.

Table 4.17 Tuber physiological disorders of commercial potato cultivars as affected by environments and cultivars in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at final harvest (130 DAP).

Factors	Malformation	%	Second Growth	%	Growth Cracks	%	Enlarged lenticels	%	Feathering	%	Vascular browning	%
Sites	***		**		***		***		***		***	
Ohakune	3.4±0.3 a	19.9	2.4±0.3 b	14.0	3.4±0.4 b	19.9	3.1±0.3 b	18.1	4.8±0.2 a	28.1	0.0±0.0 c	0.0
Opiki	0.8±0.3 b	6.3	2.7±0.3 b	21.1	6.6±0.4 a	51.6	1.2±0.3 c	9.4	0.1±0.2 b	0.8	1.4±0.2 a	10.9
Hastings	2.6±0.3 a	18.7	3.9±0.3 a	28.1	1.4±0.5 c	10.1	4.6±0.4 a	33.1	0.7±0.3 b	5.0	0.7±0.2 b	5.0
Cultivars	***		***		***		***		***		ns	
'Agria'	2.7±0.4 abc	18.0	4.9±0.4 b	32.7	4.9±0.7 b	32.7	3.5±0.5 b	23.3	3.1±0.4 a	20.7	0.4±0.3 a	2.7
'Hermes'	1.2±0.5 cd	4.4	2.5±0.4 cd	9.3	10.1±0.7 a	37.4	4.3±0.5 ab	15.9	1.4±0.4 bc	5.2	0.4±0.3 a	1.5
'Ilam Hardy'	3.2±0.4 ab	13.3	8.8±0.4 a	36.7	2.1±0.7 c	8.8	0.6±0.5 d	2.5	2.9±0.4 ab	12.1	1.3±0.3 a	5.4
'Rua'	3.5±0.4 a	24.6	0.6±0.4 e	4.2	1.2±0.7 c	8.5	2.3±0.5 bcd	16.2	1.1±0.4 c	7.7	0.6±0.3 a	4.2
'Taurus'	1.6±0.5 bcd	6.8	1.1±0.4 de	4.7	3.5±0.7 bc	15.0	2.8±0.5 bc	12.0	1.4±0.4 bc	6.0	0.9±0.3 a	3.8
'Fianna'	3.7±0.5 a	19.6	3.1±0.4 c	16.4	1.1±0.7 c	5.8	6.5±0.5 a	34.4	1.5±0.4 bc	7.9	1.1±0.3 a	5.8
'Snowden'	0.1±0.4 d	0.5	0.2±0.4 e	1.1	5.7±0.7 b	30.5	1.1±0.5 cd	5.9	1.3±0.4 c	7.0	0.3±0.2 a	1.6

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

In the Opiki trial site, growth cracks (51.6%) and second growth (21.1%) were the greatest tuber physiological disorders recorded. The arid spring (October–November 2018) followed by a very wet early summer (December 2018) that was almost 100% above the historical average rainfall may have encouraged the growth crack formation of tubers in the Opiki trial site. This moisture stress combined with supra-optimal temperatures (>25 °C) that was 3 °C–6 °C higher than the historical average during the summer months (December 2018–February 2019) may have caused the premature breaking of tuber dormancy (and or enhanced tuber maturity), resulting in second-growth formation, e.g., heat sprouts, chain tubers, and secondary tuber formation. According to Levy (1986), heat stress and drought stress may enhance tuber preharvest sprouting, but the effects could vary among the cultivars depending on the physiological status of the seed tubers. Preharvest tuber sprouting was suggested to be an indirect effect of incomplete canopy coverage due to drought stress and high temperature (Shock et al., 1992). Incomplete canopy coverage exposes the soil to a very high temperature, which then increases its temperature and induces heat sprouting.

Figure 4.6 Tuber physiological disorders at the final harvest (130DAP) in the different trial sites: in Ohakune, (a) feathering in ‘Agria’, (b) tuber cracking (superficial cracks) in ‘Hermes’, (c) second-growth (secondary tubers), and (d) tuber malformation in ‘Ilam Hardy’; in Opiki, (e) secondary tubers and (f) vascular browning in ‘Ilam Hardy’, (g) second-growth (heat sprouts) in ‘Agria’, (h) superficial cracks in ‘Hermes’, (i) second-growth (chain tubers) in ‘Ilam Hardy’; in Hastings (j) heat sprouts in ‘Ilam Hardy’, (k) enlarged lenticels in ‘Hermes’, (l) chain tubers in ‘Fianna’, (m) secondary tubers and (n) hollow heart in ‘Agria’, and (o) heat sprouts in ‘Hermes’.

A tuber physiological disorder that occurred only in the Opiki and Hastings trial sites was the vascular browning, characterized by a discoloration of the vascular ring usually at the stem end but may extend all over the vascular ring in severe cases (Potatoes South Africa, 2016). Known causes of vascular browning are soil moisture deficit, elevated temperatures during foliage die-off, and infection by *Verticillium*, *Fusarium,* and leaf roll virus (Potatoes South Africa, 2016).

In the Hastings trial site, the most common tuber physiological disorder observed was the enlargement of lenticels and second-growth, accounting for 33.1% and 28.1% of the total tubers harvested, respectively. The extremely high atmospheric temperatures (>25 °C) aggravated by the mesh covering practice and the use of irrigation to manage the temperature extremes were the likely cause of the high tuber physiological disorder rate in the Hastings trial site. Frequent and heavy irrigation possibly resulted in waterlogging and heavy soils that promoted the enlargement of lenticels on the tuber surface. Similar to the Opiki and Hastings trial sites, the moisture stress combined with elevated temperatures caused the pre-mature breaking of tuber dormancy (or enhanced tuber maturity) and resulted in the second-growth formation, e.g., heat sprouts, chain tubers, and secondary tuber formation. In a study conducted by Rykaczewska (2013), favorable soil moisture combined with heat stress in the early growth stage promoted second growth and gemmation than under drought. Another physiological disorder observed only in the Hastings trial site though it occurred only in a small number of tubers was hollow heart. It is a longitudinal or transverse cavity in the flesh of the potato tuber. According to Hillerm and Thornton (2008), severe stress ceases the growth of potato plants but induces them to absorb water and nutrients from the young cells in the tubers, leading to their deterioration; when growth resumes, the rapid expansion of tubers results in the separation of the injured cells and the formation of a cavity.

The effect of the cultivar (genotype) on the incidence of tuber physiological disorders was highly significant (*p* < .001), indicative of either strong differential susceptibility or tolerance to abiotic stresses that are the major contributory factor of the disorders. Cultivars that have naturally large elongated tubers such as ‘Agria’, ‘Rua’, ‘Fianna’, and ‘Ilam Hardy’ (round–oval-shaped cultivar, to some extent) were more susceptible to tuber malformation. In contrast, cultivars that have medium-sized circular tubers such as ‘Hermes’ and

‘Snowden’ were more susceptible to growth cracks. The medium rough and slightly netted skin characteristics of ‘Hermes’ and ‘Snowden’, respectively, appeared to be enhanced by abiotic stress, which were then developed into growth cracks, specifically superficial growth cracks and netting. ‘Taurus’, on the other hand, with relatively smooth skin was less susceptible to growth crack formation. ‘Agria’ was also susceptible to growth cracks (32.7%) and second growth (32.7%). ‘Ilam Hardy’ appeared to be particularly susceptible to second-growth formation such as heat sprouts and secondary tubers across the trial sites. This can be attributed to the delayed harvesting of ‘Ilam Hardy’, which is an early maturing cultivar (Anderson, Lewthwaite, Genet, & Braam, 2004; Lewis, Lancaster, Meredith, & Walker, 1994) that is usually harvested 80-90 DAP. Retaining the ‘Ilam Hardy’ crops in the field longer than necessary will expose the tubers to high atmospheric and soil temperatures, which are precursor to tuber dormancy break, thereby increasing the incidence of pre-mature sprouting and secondary tuber formation. Furthermore, ‘Ilam Hardy’ has a very short dormancy period, i.e., sprouts early, and thus has short storage life (Genet & Anderson, 1985). Among the tested cultivars that showed relative tolerance or susceptibility to tuber physiological disorders, the following is the order of tolerance: ‘Taurus’ > ‘Snowden’ > ‘Hermes’, while the following is the order of susceptibility: ‘Agria’ > ‘Ilam Hardy’ > ‘Rua’ > ‘Fianna’. The effect of cultivar x environment interaction on the incidence of tuber physiological disorders was significant (Table 4.18). In the cooler environment of the Ohakune trial site, tuber malformation was the most common tuber physiological disorder especially among the cultivars that have naturally large, elongated tubers such as ‘Agria’, ‘Fianna’, ‘Rua’, and ‘Ilam Hardy’. ‘Agria’ was the most susceptible to feathering that accounted for 40.4% of the total tubers. ‘Ilam Hardy’ was susceptible to second-growth with 31.6% of the total tubers, while ‘Fianna’ was susceptible to enlarged lenticels with 41.1% of the total tubers. Among the tested cultivars that showed relative tolerance or susceptibility to tuber physiological disorders in the Ohakune trial site, the following is the order of tolerance: ‘Taurus’ > ‘Snowden’ > ‘Hermes’, and the following is the order of susceptibility: ‘Agria’ > ‘Ilam Hardy’ > ‘Rua’ > ‘Fianna’.

Under the hot and dry conditions of the Opiki trial site, growth cracks were the most common tuber physiological disorder especially in ‘Agria’ (83.1%), ‘Hermes’ (70.0%), ‘Taurus’ (40.3%), and ‘Snowden’ (33.1%). ‘Agria’ was also susceptible to second growth (40.3%) and enlarged lenticels (33.9%). ‘Ilam Hardy’ was the most susceptible to second growth, with 47.7% of the total tubers. Vascular browning was a common tuber disorder among the cultivars 'Fianna' (23.3%), 'Rua' (15.3%), 'Ilam Hardy' (14.0%), and 'Taurus' (11.5%) in the Opiki trial site. Among the tested cultivars that showed relative tolerance or susceptibility to tuber physiological disorders in the Opiki trial site, the following is the order of tolerance: 'Snowden' > 'Taurus' > 'Hermes', while the following is the order of susceptibility: 'Agria' > 'Ilam Hardy' > 'Rua' > 'Fianna'.

Table 4.18 Tuber physiological disorders of commercial potato cultivars as affected by the interaction of site and cultivar in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season at final harvest (130 DAP).

Factors	Malformation ***	%	Second Growth **	%	Growth Cracks ***	%	Enlarged lenticels ***	%	Feathering *	%	Vascular browning **	%
Ohakune												
'Agria'	4.8±0.8 ab	27.0	3.4±0.7 b	19.1	3.8±1.1 b	21.3	2.8±0.9 bc	15.7	7.2±0.6 a	40.4	0.0±0.0 a	0
'Hermes'	0.0±0.8 c	0	0.3±0.7 c	0.9	8.7±1.1 a	27.1	4.4±0.9 b	13.7	3.7±0.6 b	11.5	0.0±0.0 a	0
'Ilam Hardy'	6.4±0.8 a	22.2	9.1±0.7 a	31.6	0.2±1.1 b	0.7	0.3±0.9 c	1.0	7.2±0.6 a	25.0	0.0±0.0 a	0
'Rua'	4.7±0.8 ab	24.1	0.5±0.7 bc	2.6	0.7±1.1 b	3.6	1.6±0.9 bc	8.2	3.4±0.6 b	17.4	0.0±0.0 a	0
'Taurus'	2.8±0.8 bc	10.0	0.5±0.7 bc	1.8	2.5±1.1 b	8.9	2.3±0.9 bc	8.2	4.1±0.6 b	14.6	0.0±0.0 a	0
'Fianna'	5.3±0.8 ab	22.5	2.6±0.7 bc	11.0	3.3±1.1 b	14.0	9.7±0.9 a	41.1	4.3±0.6 b	18.2	0.0±0.0 a	0
'Snowden'	0.2±0.8 c	0.9	0.2±0.7 c	0.9	4.5±1.1 ab	19.3	0.3±0.9 c	1.3	3.8±0.6 b	16.3	0.0±0.0 a	0
Opiki												
'Agria'	1.7±0.8 a	13.7	5.0±0.7 b	40.3	10.3±1.1 b	83.1	4.2±0.9 a	33.9	0.0±0.0 a	0	0.0±0.0 b	0
'Hermes'	0.3±0.8 a	1.2	1.8±0.7 c	7.4	17.0±1.1 a	70.0	0.8±0.9 ab	3.3	0.0±0.0 a	0	0.0±0.0 b	0
'Ilam Hardy'	0.8±0.8 a	4.1	9.2±0.7 a	47.7	5.9±1.1 bc	30.6	0.0±0.9 b	0	0.0±0.0 a	0	2.7±0.5 a	14.0
'Rua'	1.0±0.8 a	10.2	0.4±0.7 d	4.1	2.9±1.1 cd	29.6	0.0±0.9 b	0	0.0±0.0 a	0	1.5±0.5 ab	15.3
'Taurus'	1.0±0.8 a	5.2	0.4±0.7 c	2.1	7.7±1.1 bc	40.3	0.4±0.9 b	2.1	0.3±0.0 a	1.6	2.2±0.5 ab	11.5
'Fianna'	0.8±0.9 a	6.2	2.1±0.8 bc	16.3	0.0±1.1 d	0	2.8±1.0 ab	21.7	0.0±0.0 a	0	3.0±0.6 a	23.3
'Snowden'	0.0±0.8 a	0	0.3±0.7 c	2.3	4.4±1.1 cd	33.1	0.0±0.9 b	0	0.0±0.0 a	0	0.5±0.3 b	3.8
Hastings												
'Agria'	1.7±0.8 b	11.5	6.4±0.7 ab	43.2	0.6±1.1 b	4.1	3.4±0.9 bcd	23.0	2.1±0.6 a	14.2	1.2±0.5 a	8.1
'Hermes'	3.3±0.9 ab	12.8	5.2±0.8 abc	20.2	4.6±1.1 ab	17.9	7.8±1.0 a	30.4	0.6±0.0 a	2.3	1.1±0.6 a	4.3
'Ilam Hardy'	2.5±0.8 ab	10.5	8.2±0.7 a	34.3	0.3±1.1 b	1.3	1.3±0.9 d	5.4	1.7±0.0 a	7.1	1.3±0.5 a	5.4
'Rua'	4.8±0.8 a	35.8	0.8±0.7 d	6.0	0.0±1.1 b	0	5.4±0.9 abc	40.3	0.0±0.0 a	0	0.3±0.3 a	2.2
'Taurus'	1.0±0.9 b	4.3	2.3±0.8 cd	9.9	0.2±1.1 b	0.9	5.8±1.0 abc	25.0	0.0±0.0 a	0	0.7±0.6 a	3.0
'Fianna'	5.1±0.8 a	25.1	4.5±0.7 bc	22.2	0.0±1.1 b	0	7.1±0.9 ab	35.0	0.1±0.0 a	0.5	0.1±0.5 a	0.5
'Snowden'	0.2±0.8 b	1.0	0.3±0.7 d	1.6	8.3±1.1 a	43.0	3.2±0.9 cd	16.1	0.2±0.0 a	1.0	0.4±0.4 a	2.1

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Under the hot conditions in the Hastings trial site, tuber physiological disorders such as tuber malformation, second growth, and enlarged lenticels were the most common. ‘Rua’ and ‘Fianna’ were the most susceptible cultivars to tuber malformation, accounting for 35.8% and 25.1% of their total tubers, respectively. ‘Agria’ and ‘Ilam Hardy’ were the most susceptible cultivars to second growth, accounting for 43.2% and 34.3% of their total tubers, respectively, while ‘Snowden’ was the most prone to growth cracks (43.0%). ‘Fianna’ and ‘Hermes’ were the most susceptible to enlarged lenticels, accounting for 35.0% and 30.4% of their total tubers, respectively. Vascular browning was also a common tuber disorder among the tested cultivars in the Hastings trial sites. Among the tested cultivars that showed relative tolerance or susceptibility to tuber physiological disorders in the Hastings trial site, the following is the order of tolerance: ‘Snowden’ > ‘Taurus’ > ‘Hermes’, while the following is the order of susceptibility: ‘Agria’ > ‘Ilam Hardy’ > ‘Rua’ > ‘Fianna’.

4.3.5 Genotype x environment interaction under multi-environment trial of potato crops

Based on the ANOVA on the genotype x environment analysis, the individual effects of the environment (trial sites), genotype (cultivars), and genotype x environment (GxE) interaction were found to be highly significant (Appendix 4.3). The ANOVA of average marketable yields across the seven cultivars and the three environments showed that 77.2 % of the total SS (sum of squares) was attributed to environmental effects, 13.8% to genotypic effects, and 9.0 % to G×E interaction effects. A large environment's SS showed that the environments were diverse, causing most of the variation in the average marketable yield. The significant effect of the G×E interaction also showed that the genotypes had differential performance in the trial sites or test environments, requiring a more refined analysis to increase the efficiency of the selection of the cultivars. Hence, the data were graphically analyzed using the additive main effect and multiplicative interaction or AMMI to interpret adaptability and stability (Hongyu, García-Peña, Araújo, & Dias, 2014) and summarize relationships of genotypes and environments (Gauch & Zobel, 1988). The AMMI1 (interaction principal component analysis - IPCA1 or Factor 1 vs. means) (Figure 4.6a) and the effect of GxE interaction, namely, the AMMI2 (IPCA2 or Factor 2 vs. IPCA1 or Factor 1) biplots, demonstrate the effect of each genotype and environment (Figure 4.6b). The x-axis represents the main effects (average marketable yield), and the y-axis represents the effects of IPCA1 that accounted for 54.0% in this particular trial.

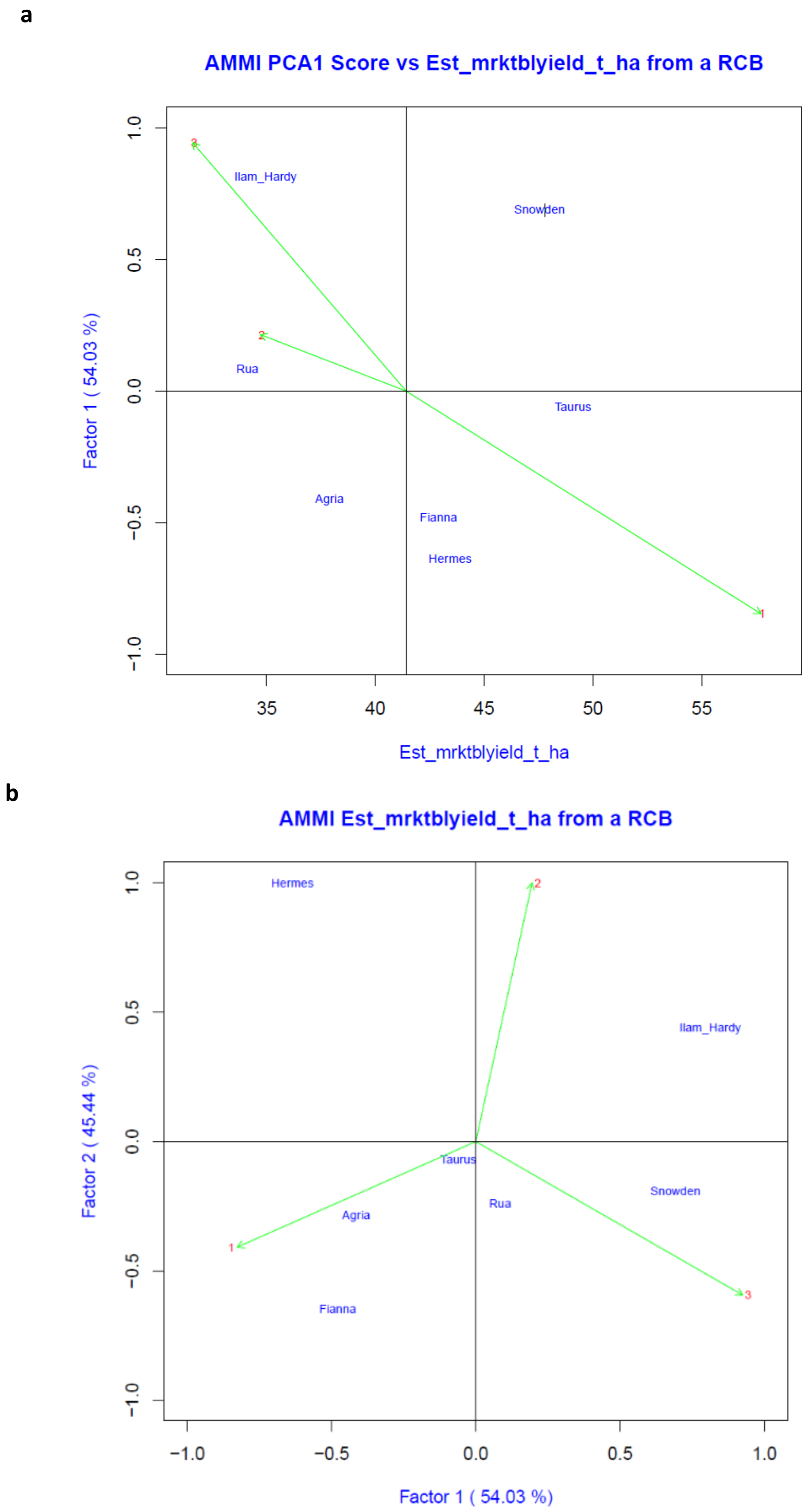


Figure 4.7 Additive Main Effect and Multiplicative Interaction (AMMI1) biplot showing the (a) Interaction Principal Component Analysis (IPCA1) (Factor1) vs. estimated marketable yield and (b) AMMI2 biplot showing the first two principal axes of interaction (IPCA2 vs. IPCA1) of 7 genotypes evaluated in three environments in the North Island during the 2018/19 growing season.

In the generated biplot, tested cultivars that showed high average marketable yield is in the following decreasing average marketable yield order: ‘Taurus’ > ‘Snowden’ > ‘Hermes’ > ‘Fianna’ > ‘Agria’ > ‘Ilam Hardy’ > ‘Rua’ (Figure 4.6a). The marketable yields of ‘Taurus’ (49.1 t ha-1) and ‘Snowden’ (47.5 t ha-1) were well-above the mean (41.4 t ha-1) (intersect in the biplot); those of ‘Hermes’ (43.4 t ha-1) and ‘Fianna’ (42.9 t ha-1) were close to the mean; while those of ‘Agria’ (37.9 t ha-1), ‘Ilam Hardy’ (35.0 t ha-1), and ‘Rua’ (34.1 t ha-1) were below the mean.

The lower the IPCA1 value is, the lower its influence on the G×E interaction and the more stable the genotype will be. In terms of the average marketable yield, ‘Taurus’ and ‘Rua’ were found to be the most stable cultivars (positioned near the origin of the biplot). However, ‘Rua’ had the lowest average marketable yield (Figure 4.6a). The cultivar ‘Taurus’ could be highlighted and identified as an ideal genotype because it had the highest average marketable yield and stability compared with the reference cultivar ‘Agria’ and the other tested cultivars. In contrast, ‘Ilam Hardy’ was identified as an undesirable genotype owing to its low productivity and low stability (IPCA1 values farthest from zero) (Gauch & Zobel, 1988; Kempton, 1984). On the other hand, ‘Agria’ showed intermediate stability only and average marketable yield below the overall average. ‘Ilam Hardy’, ‘Snowden’, ‘Hermes’, and ‘Fianna’ were the most unstable cultivars (positioned away from the biplot origin), with the last two cultivars having averages close to the overall average. The unstable cultivars meant that they perform well under specific environments only. Genotypes and environments located close to each other in the biplot have positive relations; thus, these enable the creation of a group of genotypes within an agronomic zone (Figure 4.6b). For example, the cultivar ‘Hermes’ performed better in the Opiki trial site, while ‘Snowden’ in the Hastings trial site and ‘Fianna’ in the Ohakune trial site (Figure 4.6b). Variability in the relative performances of the same cultivars tested in different environments or years can be attributed to the effect of GxE interactions (Falconer & Mackay, 1996).

The Ohakune and Hastings environments stood out with a high contribution to the interaction, while the Opiki environment had the lowest contribution. All the environments had some cultivars with marketable yield averages above the overall average of 41.4 t ha^{-1}; only Ohakune had cultivars with above the overall average, indicating that this was the most favorable environment to obtain high yield. The possible reason for the high marketable yields are the mild atmospheric and soil temperature, good precipitation and water distribution that occurred during the growing season, and the relatively higher natural fertility and soil properties compared with the two other environments. The soil in the Ohakune trial site is predominantly allophanic, which is common in North Island volcanic ash; this soil type is easy to dig and characterized as porous with low bulk density structure and hence has small resistance to root growth (Landcare Research, 2020b). In general, cultivars are often selected with wide geographic adaptation and high productivity. However, considering that this is not often achieved, Silveira et al. (2013) suggested identifying genotypes with location-specific adaptations to improve their regional productivity.

4.4 Conclusion

Numerous simulation models show considerable potential losses in potato production worldwide due to extreme weather conditions, such as drought and heatwaves, which are often associated with changing climate. Recent weather anomalies in New Zealand, particularly the summer heatwaves of 2017/18 (hottest on record) and 2018/19 (third hottest on record after 1934/35 summer) during the growing season have impacted potato production. It is therefore imperative to ascertain the presence of abiotic stresses associated with observed climate change affecting potato crops in major producing areas in New Zealand, determine how it affects yield and tuber quality, and investigate if differential susceptibility exists among the available commercial potato cultivars. Weather extremes were evident during the 2018/19 growing season, including the occurrence of supra-optimal atmospheric (>25 °C) and soil (>18 °C) temperatures and sub-optimal seasonal rainfall and soil moisture for potato crop growth and development. Weather extremes are coupled with abiotic stresses (i.e., heat and drought stress) in the potato field. Moreover, elevated temperatures in the eastern (Hastings) and western (Opiki) regions of the North Island combined with prolonged sunshine hours (Hastings) accelerated the accumulation rate of growing degree days or GDD, thereby accelerating the early maturity and senescence of potato crops in the field.

Abiotic stress affects the different morpho-agronomic characteristics and physiological functions of the potato crop. Heat stress alone or in combination with drought stress reduces the harvest index, total yield, marketable yield, dry matter content, total number of tubers per plant, and percentage of large- and medium-sized tubers. Heat stress increases the plant height, leaf area, transpiration rate, and stomatal conductance. Drought stress, on the other hand, suppresses vegetative growth and stomatal conductance, leading to a decrease in net photosynthesis. This study confirms that abiotic stress increases the incidence of tuber physiological disorders, resulting in reduced total yield and marketable yield by up to 43.3% and 45.1%, respectively. The incidence of tuber physiological disorders inversely correlates with the marketable yield, that is, the higher the incidence of tuber physiological disorder is, the lower the marketable yield will be. As observed in the 2017/18 growing season, tuber physiological disorders due to heat and drought stress were also present during the 2018/19 growing season. The occurrence of a particular type of tuber physiological disorder depends on the environment and type, duration and the timing of abiotic stress present during the growing season. Feathering is more common in cooler environments (Ohakune), growth cracks and second growth are common in hot and dry environments (Opiki), and enlargement of lenticels and second growth are common in hot environments (Hastings). Cultivars that have naturally large and elongated tubers such as 'Agria', 'Rua', 'Fianna', and 'Ilam Hardy' (to some extent) are more susceptible to tuber malformation. In contrast, cultivars that have medium-sized circular tubers such as 'Hermes' and 'Snowden' are less susceptible to tuber malformation but more susceptible to growth cracks. Abiotic stress intensifies the naturally netted skin characteristics of 'Hermes' and 'Snowden' to the point that they develop into superficial growth cracks and netting.

Genotype x environment analysis shows location-specific adaptations (agronomic zoning) among the tested commercial potato cultivars during the 2018/19 growing season. The cultivar 'Hermes' is tolerant to a combination of heat and drought stress (Opiki) but less tolerant to heat stress alone (Hastings), while 'Snowden' is tolerant to heat stress (Hastings). 'Taurus', on the other hand, is the most stable and adaptable cultivar across the trial sites/test environments during the 2018/19 growing season.

Cultural practices that are unique in New Zealand potato production systems, such as the use of mesh covering as a physical barrier to protect crops by non-chemical means from the tomato-potato psyllid or TPP, aggravates the increase in summer temperatures. The practice of ground storing could also expose the potato tubers to extreme weather conditions (e.g., heat stress and flooding), which dramatically affect the tuber quality. These circumstances will affect more the table-type cultivars where the skin finish is vital for the saleability of pre-packs; thus, the future focus in potato production could be more towards the processing market. Moreover, rainfed farming could be less feasible in the coming years with the changing rainfall patterns and frequent incidence of drought during the growing season. The increasingly stringent water restriction policies in the different regions of New Zealand may aggravate the conditions and hamper potato production (e.g., Hawke’s Bay). Besides the application of appropriate cultural management (e.g., irrigation at critical stages, planting, and harvesting timing), identifying the right commercial cultivars with tolerance to abiotic stress (i.e., heat and drought stress) that would perform well either in a wide array of environments (high stability and productivity) or specific locations (agronomic zones) should be conducted to increase productivity and tuber quality.

Despite the observed negative impacts of abiotic stress in the past two growing seasons on the yield and tuber quality of potatoes, the New Zealand potato industry still registered about 7% increase in the production volume compared with the data in 2013 (493,872 MT) and 2019 (533,030 MT) seasons (Potatoes New Zealand, 2020). Several factors that could have contributed to this finding include the slight increase in production area from 10,328 ha (2013) to 10,417 ha (2019) (Potatoes New Zealand, 2020). Another is the improved crop management practices of potato growers to mitigate the unfavorable weather conditions. In the Lawson’s True Earth Farm in Hastings, irrigation was applied to somehow mitigate the extreme temperatures in the field especially during the summer months that usually coincide with tuber bulking. Lastly, the strategic positioning of potato production areas in New Zealand could have provided an advantage for the industry to ensure the year-round supply of potatoes and potentially reduce the impact of unfavorable weather conditions that affect specific growing regions only. A. S. Wilcox & Sons Limited has strategically positioned their potato production in the different parts of New Zealand, including in Northland, Pukekohe, Matamata, Ohakune, and Canterbury. The flooding of 2017 greatly affected the Matamata and Pukekohe production areas only. These and other factors could have contributed to the reduction in the impact of unfavorable weather conditions on potato production and made the potato industry resilient. However, with the increasing threat of climate change, better strategies are needed to improve climate change resilience.

CHAPTER 5

Yield, Morpho-agronomic, and Physiological Effects of Abiotic Stress on Commercial Potato Cultivars Under Controlled Environment Conditions

5.1 Introduction

The manifestations of climate change are expected to vary from year to year and decade to decade due to natural processes (Ministry for the Environment, 2016). Hence, natural variability in weather and climate pattern and their potential impact on crops will vary as well. To validate the results and analyses of the 2017/18 season baseline data collection (Chapter 3) and the multi-environment trial (MET) of the 2018/19 season (Chapter 4), different abiotic stresses, i.e., drought, heat, and drought and heat combination, commonly associated with climate change were applied in a controlled-environment trial under glasshouse and plant growth chamber conditions. The yield, morpho-agronomic, and physiological responses of two selected commercial potato cultivars i.e., susceptible and tolerant (based on the MET findings), to abiotic stresses, particularly drought, heat, and their combination, were determined. The morpho-agronomic characteristics and physiological functions of the two cultivars that contribute to either susceptibility or tolerance to abiotic stress and their influence on the final tuber yield and other plant performance characteristics were closely examined.

5.2 Materials and methods

5.2.1 Experimental site

The experiment was carried out from October 2019 to January 2020 in a glasshouse (6 m x 6 m) and the plant growth chamber (Contherm Biosyn Series 6000) at the Plant Growth Unit and Pasture & Crop Research Unit (40.381; 175.606) of Massey University, Palmerston North.

5.2.2 Cultivar selection, experimental design, and crop management

Commercial potato cultivars ‘Agria’ and ‘Taurus’ were used in the glasshouse trial as reference cultivar and the most stable and adaptable cultivar, i.e., with potential abiotic stress tolerance based on the 2018/19 multi-environment trial or MET, respectively (Figure 5.1). The cultivar ‘Agria’ was bred in Germany from a cross between its parents Quarta and Semlo. ‘Agria’ plants are tall and have spreading growth with few thick and erect stems

(Canadian Food Inspection Agency, 2020a). Initial plant development is slow, but it grows robust foliage during the season. The number of tubers is usually less, but their sizes are large to very large and they have long oval shape with yellow skin and flesh. It is a main crop harvested in about 130 DAP with a very high yield. ‘Agria’, a popular multi-purpose potato cultivar in New Zealand, is suitable for fresh, chips, and crisps and has high dry matter content (ca. 21.2%). The processing quality is excellent even after long-term storage at 6 °C. It has mild demand for water supply (Europlant, 2020) but is prone to common scab; hence irrigation is required on lighter soils (Agrico, 2020). ‘Agria’ has medium to high drought resistance (Banik et al., 2016; Europotato, 2020a; Tekfen Agri, 2020). It has low to medium resistance to secondary growth (Agrico, 2020) and growth cracking (AHDB, 2020a). The cultivar ‘Taurus’ is a cross between Panda and RZ –87 – 44. Tubers are medium-sized, round to round oval shapes with bright yellow flesh and yellow skin. It is a high-yielding main season crisping line from the Netherlands, is suitable for long-term storage, and has high dry matter content (ca. 23.3%). ‘Taurus’ is described to have good tolerance against drought conditions (HZPC, 2020). It has moderate resistance to splitting/cracking (AHDB, 2020c). ‘Taurus’ is the most stable and adaptable cultivar across trial sites/test environments during the MET 2018/19 growing season (Chapter 4).

Figure 5.1 Potato cultivars (a) ‘Agria’ and (b) ‘Taurus’ used in the controlled-environment trial as reference cultivar and cultivar with potential abiotic stress tolerance, respectively.

Certified potato seed tubers were obtained from local seed suppliers Eurogrow and Alex McDonald. The seed tubers (80–100 g) were pre-sprouted for two weeks by exposing them to diffuse natural lighting under ambient temperature.

The seed potatoes were planted on October 20, 2019. An improvised PVC pipe was used to dig a hole 10 cm deep in each 10 L pots with six holes at the bottom, filled with 8 L of 2:1 (by volume) potting mix of sand and peat moss (Yates Hauraki Gold Peat), and wetted at 80% pot capacity (PC). The potting mix was supplemented with 1.5 g L^{-1} Osmoform (22-5-11+2MgO+TE, ICL, Israel) and 4 g L^{-1} Osmocote (19-9-10+2MgO+TE, ICL, Israel). The pH of the potting mix was measured as 5.4 by using a portable pH meter (Bluelab Combo Meter, New Zealand). The seed tubers with 8–10 mm long sprouts were planted with the side with the most sprouts oriented upward then covered with potting mix. The density of the pots in the glasshouse was four pots per square meter. Throughout the experiment, the plants were watered regularly close to PC (80%–90%) for control plants. Drought-treated plants were watered regularly close to PC from planting until the start of the drought treatment and from the end of drought treatment until harvesting.

The PC of the substrate (2:1 v/v sand: peat mixture) was determined by the following procedure:

- Pre-weigh a sample pot (pot weight) that will be used in the trial
- Weigh the needed amount of potting mix per pot and dry in an oven for at least two days (dry weight or DW)
- In a bucket of water, partially submerge (water level just up to the pot rim) the pot with the potting mixture and soak overnight
- Let the pot drip until no more excess water can be seen dripping; weigh the pot with the mixture (saturated weight or SW)
- Determine the PC by using the equation: [(SW – DW) x %] + DW
- Add the weight of the seed tuber and the weight of the plant (extra sample plants) to the weight of water to estimate PC

When the shoots were about 5 cm above the pot rim, multiple stems were reduced to a single main stem and an additional substrate mix was added to fill the pots up to 2.5 cm below the pot rim. Regular thinning of new stems that grew from the base of the plant was done to maintain a single main stem per pot. The pruning shears were sterilized with SteriGENE® (Ethical Agents Veterinary Marketing, Auckland), an antibacterial solution, every after a plant pruned to prevent cross-contamination of potential disease.

The glasshouse had 30% shading with lighting within the range of 600–900 µmol $m^{-2}s^{-1}$ at the canopy level. Light intensity was measured using the light meter LI-250 (LICOR Quantum/ Radiometer/ Photometer, USA). Actual temperature and humidity data were recorded throughout the growing season by using the temperature logger DS1921G-F5# Thermochron (Maxim Integrated, USA, www.maximintegrated.com), which was hanged about 2 m off the glasshouse floor in a rectangular wooden casing with an opening at each end and with a small blower. The glasshouse had vents that automatically opens when the temperature inside reaches 22 °C to allow warm air to flow out and cooler air to flow into the glasshouse. Wetting of the glasshouse floor was done at mid-day to manage the decline in humidity.

The glasshouse was fitted with fine steel mesh covering on its vents to prevent the entry of pests. However, this did not completely prevent the entry of pests and diseases. Fungicide Manzate Evolution® (Mancozeb) at 7.5g 5 L^{-1} was applied every fortnight as preventive management to potato blight. Insecticides Chess® (Pymetrozine) at 3.0 g 10 L^{-1} (31/12/2019) and Verdex® (Abamectin) at 2.0 mL 5 L^{-1} (10/1/2020) were applied to manage aphids and psyllids, respectively.

The experiment was laid out as a 2 x 2 x 4 factorial experimental design (two varieties, two growth stages, and four abiotic stress treatments) with five replicates, each plant represented a biological repetition (experimental unit). The treatments/pots were laid out in completely randomized design (Figure 5.2). The pots were rearranged randomly every few days during the trial period to avoid position effects, i.e., to even out the plants by exposing them to a range of potential microclimates within the glasshouse. Daily monitoring of the crops in the glasshouse was done to ensure proper cultural management (Figure 5.3).

Extra potted plants or border crops of ‘Agria’ and ‘Taurus’ cultivars were used for destructive sampling to monitor the growth stage below ground i.e., stolon, tuber initial formation, tuber bulking, and maturity.

J	T12	T28	A36	T23	T7	T19	A19	T20
I	A27	T13	T37	T2	A31	A25	A9	T26
H	T27	A7	A14	A13	T35	A30	T1	T15
G	A2	T33	A38	A8	T10	T14	T8	T3
F	A6	A26	T16	A40	A20	A15	T11	T29
E	A22	A21	A1	A16	A28	A32	T36	A24
D	T21	A4	T30	T25	T17	A29	T9	A12
C	A11	T31	A23	A33	T18	A17	A10	A35
B	T4	T38	A37	T32	T5	T34	T6	A34
A	A3	T24	T22	A18	A39	T40	T39	A5
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**

ENTRANCE OF GLASSHOUSE

Note:

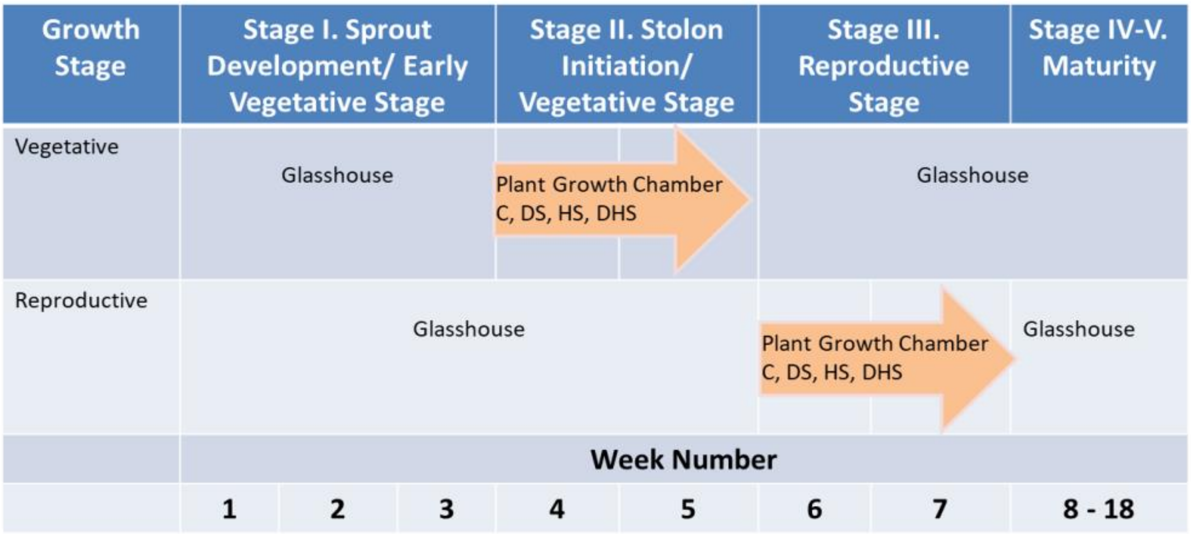
- A is the cultivar ‘Agria’
- T is the cultivar ‘Taurus’
- The different numbers represent the biological repetitions (single pot) randomly designated/positioned, each exposed to different abiotic stress and combination (control, drought, heat, and drought + heat combination) at two growth stages (vegetative and reproductive stages)

Figure 5.2 Layout of potted potato plants in the glasshouse.

Figure 5.3 Monitoring of potato crops in the glasshouse at about 90 DAP.

5.2.3 Heat and drought treatments

Treatments of heat and drought stresses and their combination were applied at two different growth stages i.e., vegetative and reproductive stages of the potato crops separately (Figure 5.4 and Appendix 2.1). Control plants (C) (non-stressed, 80%–90% PC) and drought stress (DS) (40% PC) were transferred to the plant growth chamber (Contherm Biosyn Series 6000, New Zealand) under 15 h photoperiod at 0800–1000 µmol $m^{-2}s^{-1}$ light intensity (from 06:00 until 21:00) with 22 °C day temperature (from 09:00) and 18 °C night temperature (from 16:00). Plants for heat treatment were transferred to the plant growth chamber at each specified growth stage for 14 days and grown under the same photoperiod and light intensity with 38 °C day temperature (from 09:00) and 25 °C night temperature (from 16:00) at a ramp rate of 4 min $℃^{-1}$. Half of the plants were kept at 80%–90% PC (HS) by watering two to three times a week, while the other half was maintained at 40% PC (DHS) as determined by weighing pots individually on an electronic balance (1.0 g precision). The DHS started with pots at PC, and the watering interval and volume were reduced progressively until the pots reached 40% PC (about 1 week) in the glasshouse before the start of the treatment in the growth chamber. Drought treatment was maintained for 14 days by calculating the water requirement based on the saturated soil weight and current weight of the pot with the soil mixture. After the end of each stress regimen, the plants were returned to the glasshouse for further growth and development under conditions close to optimum. Temperature (maximum, minimum, average) and relative humidity (%) were monitored using a data logger installed in the glasshouse.



Growth Stage	Stage I. Sprout Development/ Early Vegetative Stage	Stage II. Stolon Initiation/ Vegetative Stage	Stage III. Reproductive Stage	Stage IV-V. Maturity
Vegetative	Glasshouse	Plant Growth Chamber C, DS, HS, DHS	Glasshouse	
Reproductive	Glasshouse		Plant Growth Chamber C, DS, HS, DHS	Glasshouse
	Week Number			
	1 **2** **3**	**4** **5**	**6** **7**	**8 - 18**

Figure 5.4 Timing of abiotic stress treatments – Control/non-stress (C); DS – drought stress; HS – heat stress; and DHS – drought + heat stress on the potted plants of potato cultivars ‘Agria’ and ‘Taurus’ in the plant growth chamber.

5.2.4 Phenotyping and data collection

The phenology of the potato crop in the glasshouse was closely monitored throughout the trial, particularly at the vegetative and reproductive stages, when the plants were transferred to the growth chamber for heat and drought stress treatments. Days to 50% and 100% emergence were determined to compare the growth performance of the two potato cultivars.

Before (baseline) and after (treatment effect) each stress regimen, different morpho-physiological data were gathered including plant height (mm), stem diameter (mm), number of leaves (compound leaves) per plant, chlorophyll content (SPAD value), canopy cover (%), stomatal (density and size, number of open, partially open and closed stoma) and trichome (density) characteristics, leaf relative water content or RWC (%), leaf water potential or ψ_L (bars), net photosynthesis or P_N (µmol CO_2 $m^{-2}s^{-1}$), transpiration rate or E (mmol H_2O $m^{-2}s^{-1}$), and stomatal conductance or g_S (mol H_2O $m^{-2}s^{-1x}$), and leaf dry matter content or DMC (%).

Plant height (mm) was measured using a tape measure starting from the top of the soil surface to the plant shoot tip in all plants and treatments. Stem diameter (mm) was measured using a digital caliper at about 2.5 cm above the soil surface. The number of leaves was counted per plant. Chlorophyll content was measured through an SPAD meter, which measures the greenness of plants or chlorophyll concentration; transmittance was measured using a portable chlorophyll meter CCM-200plus (Opti-Sciences, Inc., USA, www.optisci.com) on the 3rd or 4th fully expanded leaf of the main stem. Four readings per leaflet were taken on each plant. Canopy cover (%) was measured using the mobile application Canopeo® (Canopeo, USA, www.canopeoapp.com). Canopeo® measures the canopy cover (%) of the green vegetation by obtaining downward-facing photos using a mobile device (Canopeo, 2020). Canopeo® selects pixels according to the ratios of red to green (R/G) and blue to green (B/G) and an excess green index (2G–R–B) (Patrignani & Ochsner, 2015). The result is a binary image, where white pixels correspond to the satisfied selection criteria (green canopy) and black pixels correspond to those outside the selection criteria (not green canopy) (Figure 5.5). The fractional green canopy cover ranges from 0 (no green canopy cover) to 1 (100% green canopy cover).

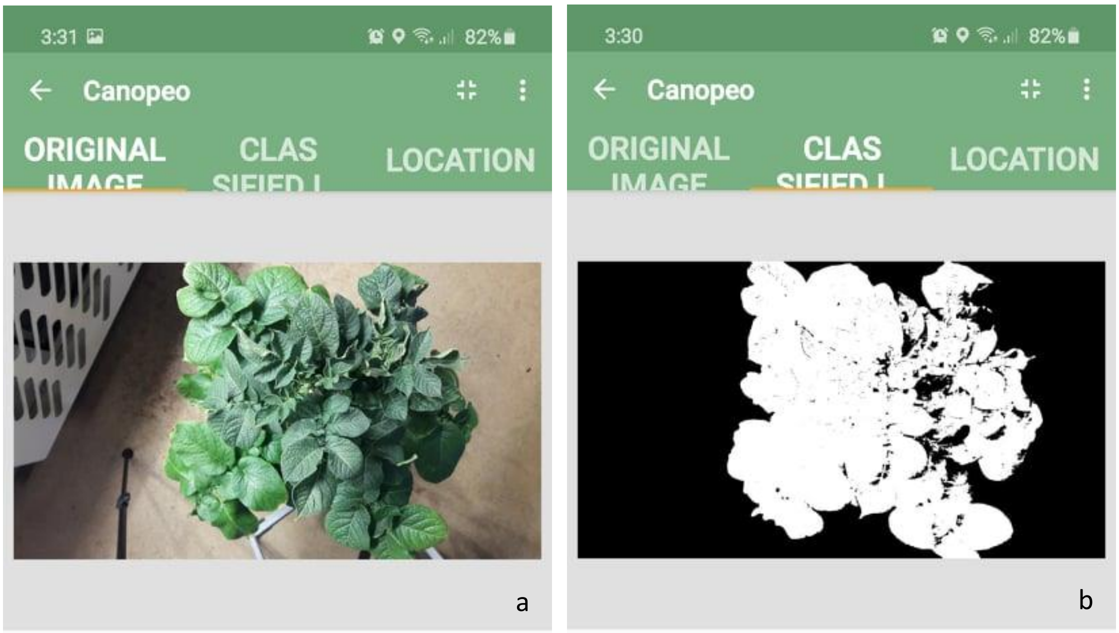


Figure 5.5 Sample measurement of canopy cover (%) in Canopeo® showing (a) original image of the crop and (b) classified or processed image, where the white pixels correspond to the satisfied selection criteria (green canopy) and the black pixels correspond to those outside of the selection criteria (not green canopy).

With the use of a cork borer (No. 7), three-leaf discs (0.5 cm diameter) from three different sample plants were collected at random from one lateral leaflet of the youngest fully expanded leaf in each treatment (C, DS, HS, DHS) for ‘Agria’ and ‘Taurus’ during their stressed period at about 11:00. The characteristics of stomata including density (count mm^{-2}), area (µm^2), length (µm), width (µm), and number of open, partially open, and closed stomata were observed from the prepared/fixed leaf disc samples and recorded under a scanning electron microscope or SEM. A total of four images, one representative image per quadrant, were captured for each leaf disks. Additionally, the density of glandular and non-glandular trichomes (count mm^{-2}) or leaf hairs was recorded.

The following modified sample preparation method of the Manawatu Microscopy and Imaging Centre or MMIC of Massey University for SEM was adopted in the study:

- To maintain the morphological state of the leaf and stomata, the leaf disks samples were immediately fixed in modified Karnovsky's fixative (3% glutaraldehyde, 2% formaldehyde in phosphate buffer, pH 7.2, 0.1M) for at least 8 hours
- After rinsing three times in phosphate buffer (pH 7.2, 0.1M), the samples were dehydrated in a graded series of ethanol (25%, 50%, 75%, 95%, and 100%) for 15 minutes each and a final 100% for 1 hour
- The samples were dried at the critical point by using liquid CO_2 as the CP fluid and 100% ethanol as the intermediary (Polaron E3000 series II critical point drying apparatus)
- Once dried, the samples were mounted on an aluminum stub, abaxial side (lower surface) on top, sputter coated with approximately 100 nm gold (BAL-TEC SCD 005 sputter coater), and viewed in an FEI Quanta 200 scanning electron microscope at an accelerating voltage of 20 kV

Stomatal density (count mm^{-2}), area (μm^2), length (μm), width (μm), number of closed and open stoma, and glandular and non-glandular trichomes density (count mm^{-2}) were observed and recorded from each image using ImageJ (ImageJ, USA) (Schneider, Rasband, & Eliceiri, 2012). ImageJ is a Java-based image processing program developed at the National Institutes of Health and the Laboratory for Optical and Computational Instrumentation (LOCI), University of Wisconsin, USA. Stomatal density was counted from images at 100× magnification, while the area, length, and width were measured from images at 400× magnification. Stomatal length is the distance between the ends of the guard cells, and the width is the distance across the guard cells.

Leaf relative water content (RWC) and leaf water potential (ψ_L) were measured just before the end of the abiotic stress treatment at the vegetative and reproductive stages, respectively, following the modified protocol of Tourneux, Devaux, Camacho, Mamani, and Ledent (2003a). Six leaf discs (0.5 cm diameter) were collected at random with a cork borer (No. 7) from each cultivar from all treatments between 11:00 and 13:00. The leaf discs were immediately weighed (fresh weight) and allowed to float (underside of the leaf on top) on distilled water in a Petri dish for 24 hours at 5 °C in darkness. The leaf disks were lightly pat dried using paper towels to remove excess moisture and then weighed (turgid weight). After weighing, the leaf disks were placed in vials and oven-dried at 70 °C for 24 hours and then weighed again (dry weight). RWC was calculated using the following equation:

$$RWC = (\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}) \times 100$$

Ψ_L was simultaneously measured with gas exchange measurement, where an adjacent leaf was excised and inserted in a pressure chamber to determine water potential. The pressure chamber was set up by connecting the hose to the nitrogen tank, and the inner wall of the chamber was lined with a damp paper towel to ensure that the air entering the chamber was humidified to prevent water loss in the pressure chamber itself. A clean single cut on the petiole was made and inserted in the hole of the pressure chamber cap. The cap was tightened by twisting and pushing down until locked. The pressure valve was gradually opened until the first instance of sap became visible on the tip of the petiole. The pressure valve was then closed, and the reading was recorded. The pressure valve was released to remove the pressure in the chamber. The chamber was opened, and the process was repeated for the succeeding samples.

Other physiological data including P_N (µmol CO2 m^2s^1), E (mmol H_2O m^2s^1), and g_S (mol H_2O m^2s^1) were measured using LI-COR portable photosynthesis system IRGA LI-6400 model (LI-COR, USA, www.licor.com) on the third or fourth fully expanded leaf of the main stem between 10:00 and 14:00 (Figure 5.6).

Figure 5.6 Measurement of net photosynthesis (P_N), transpiration rate (E), and stomatal conductance (g_S) using LI-COR portable photosynthesis system in the plant growth chamber.

At the final harvest on January 28, 2020 (100 DAP), the following yield parameters were gathered:

- average tuber fresh and dry weights
- average marketable tuber fresh weight
- average number of tubers per plant
- average number of marketable tubers per plant
- tuber size distribution
- tuber physiological defects
- dry matter content
- harvest index

Tuber classification (i.e., based on tuber size) was based on the TAG System for Potato developed by T&G Global (see Section 4.2.4.3) (T&G Global, 2018).

DMC was determined by oven drying the chopped potato tubers at 70 °C for five days or until the weight change became constant. The initial and final weights after drying were measured, and percent DMC was calculated by dividing the final dry weight by the initial fresh weight and multiplying by 100. On the other hand, harvest index (HI) was estimated using the ratio of tuber dry weight: total tuber dry weight (Mackerron & Heilbronn, 1985; Pereira, Nova, Ramos, & Pereira, 2008). Tubers were classified as non-marketable if undersized (e.g., <30 mm diameter) or have severe physiological disorders (e.g., enlarged lenticels, netting, growth cracks, malformed tubers, sprouting, loose skin, and greening).

Volumetric soil moisture content (%) was recorded before the stress treatment and at the end of weeks 1 and 2 of the stress treatment by using the Time-domain Reflectometer (Trase TDR Soil Moisture Meters Mini, Soilmoisture Equipment Corp., Santa Barbara, CA, USA).

5.2.5 Statistical analysis

Statistical analyses were carried out in R statistical package version 3.4.0 (R Core Team, 2017). The significant differences were analyzed using Analysis of Variance (ANOVA) and significantly different means were separated using Tukey's HSD test.

5.3 Results and discussion

5.3.1 Phenology and visual appearance

The phenology of the potato crop in the glasshouse was closely monitored throughout the growing season (Figure 5.7). ‘Taurus’ had faster initial growth and emergence than ‘Agria’. At 10 DAP, ‘Taurus’ already had more than 50% emergence, while ‘Agria’ had none. At 15 DAP, ‘Taurus’ and ‘Agria’ reached 100% emergence. At the same time, ‘Taurus’ had taller plants and formed numerous shoots. From 10 randomly selected plants, the average plant height (from base to tip of the plant) was 69 mm in ‘Taurus’ and only 24 mm in ‘Agria’, while the average shoot number per plant was five shoots in ‘Taurus’ and only three shoots in ‘Agria’. Stolon initiation “hook” stage, where tiny leaves at the rhizome or stolon end had a hook-like appearance, was observed at 20 DAP in both ‘Taurus’ and ‘Agria’; however, more stolon initials were observed in ‘Taurus’ compared with ‘Agria’ (Figure 5.7 c and d). Tuber initiation stage, where the tiny leaves at stolon-end were no longer evident and stolon tip became swollen with a spherical shape, was observed at 30 DAP. Earlier harvesting was done at 100 DAP on January 28, 2020 to avoid the exposure of the crops to extreme summer temperatures and potential pests and diseases in the glasshouse.

5.3.2 Glasshouse and plant growth chamber conditions

5.3.2.1 Glasshouse temperature and relative humidity

Atmospheric temperature for the 2019/20 growing season in the glasshouse had been generally mild in terms of the recorded average and minimum temperatures (Figure 5.8a). However, in terms of maximum temperatures, prolonged supra-optimal temperatures (>25 °C) were recorded from late spring (November 2019) to mid-summer (January 2020). Fifty-two days had temperatures >25 °C, wherein 3 days had >30 °C. The supra-optimal temperatures usually lasted for 6 hours a day, but the range was from 1 to 9 hours on any given day (data not presented). Supra-optimal temperatures were recorded as early as 10:30 and as late as 19:40 during mid-summer. An even extremely high temperature (>40 °C) close to the latter part of summer (February 2020) was recorded in the glasshouse. This extremely high temperature was recorded after the harvesting of the potato crops on January 28, 2020 (100 DAP). This event could have occurred due to the high seasonal temperature and aggravated by the greenhouse effect in the glasshouse, which did not have a full thermo-control capability.

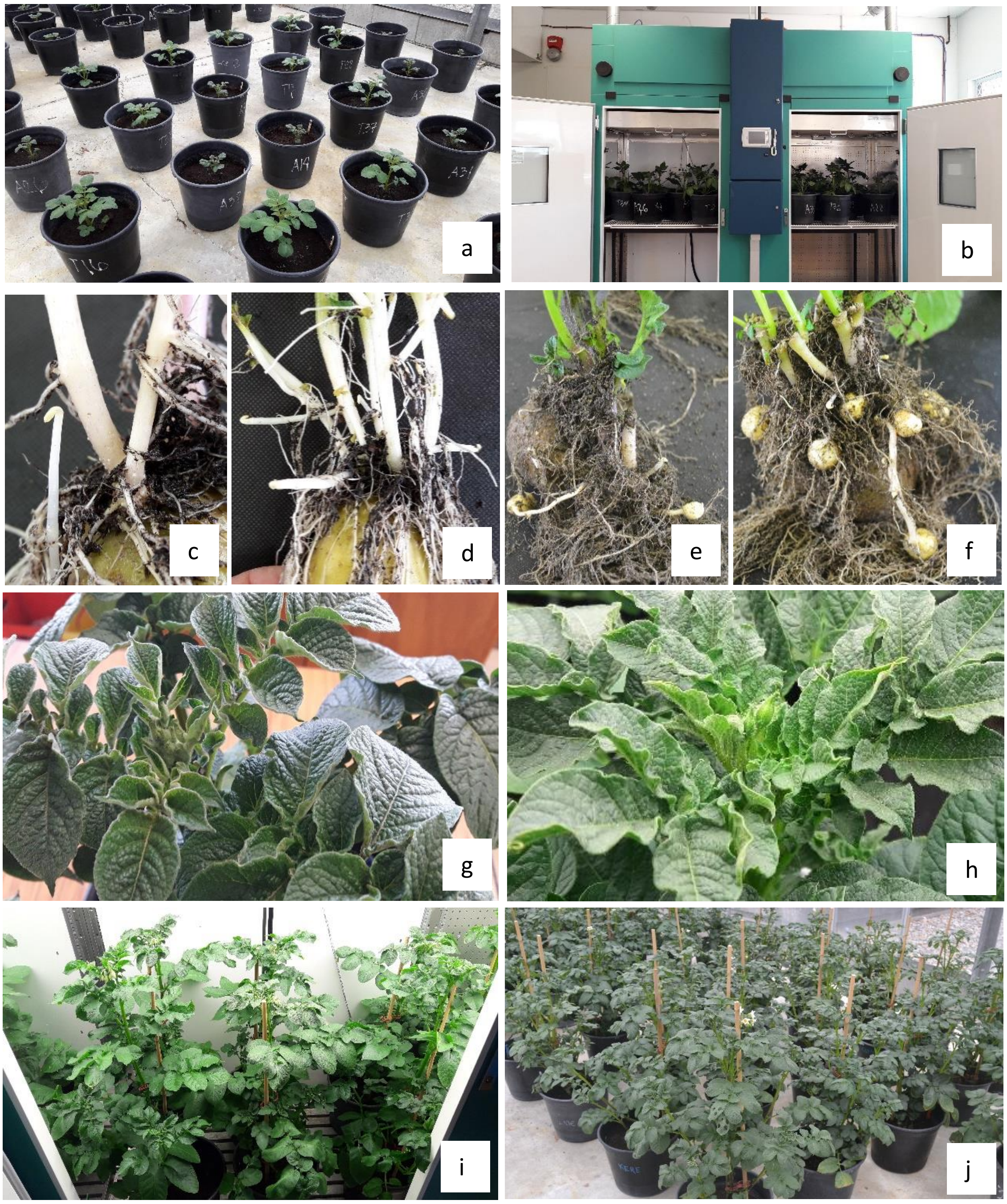


Figure 5.7 Experimental potato crops (a) at the vegetative stage in the glasshouse at 15 DAP, (b) in the growth chamber at 20 DAP; stolon initiation in potato cultivars (c) 'Agria' and (d) 'Taurus' at 20 DAP; tuber initiation in (e) 'Agria' and (f) 'Taurus' at 30 DAP; flower initial development in (g) 'Agria' and (h) 'Taurus' at 30 DAP; (i) potato crops at reproductive stage in the growth chamber at 35 DAP; and (h) standing potato crops in the glasshouse at 50 DAP after exposure to heat and drought stress treatments in the plant growth chamber.

According to Grange and Hand (1987), relative humidity or RH between 55% and 90% at 20 °C had a small influence on the physiology of horticultural crops. However, values below this range may lead to plant stress and cause reduced growth, while values above this range may promote diseases as well as growth and development disorders. In the 2019/20 season, the average and maximum RH were within the optimum range. However, the condition in the glasshouse was particularly dry, as seen in the recorded minimum RH (Figure 5.8b). About 90 out of the 100 days of growth in the glasshouse had RH below 55% between midday to late afternoon. This is despite the practice of wetting the glasshouse floor to increase humidity.

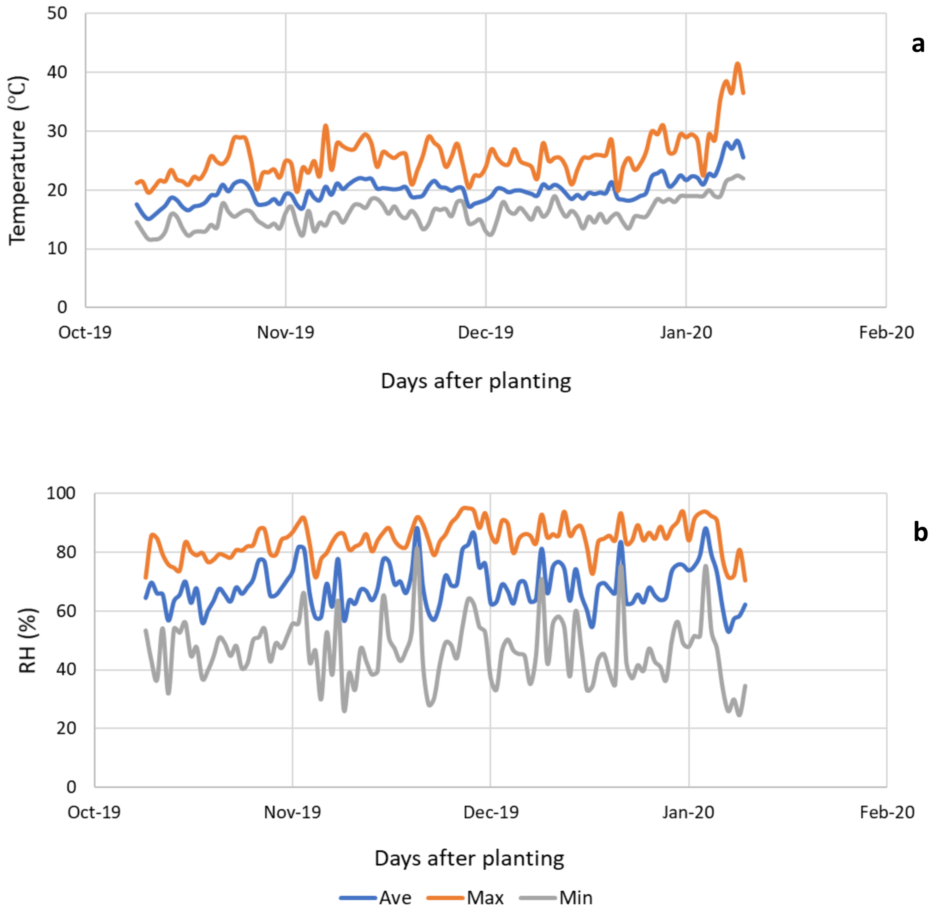
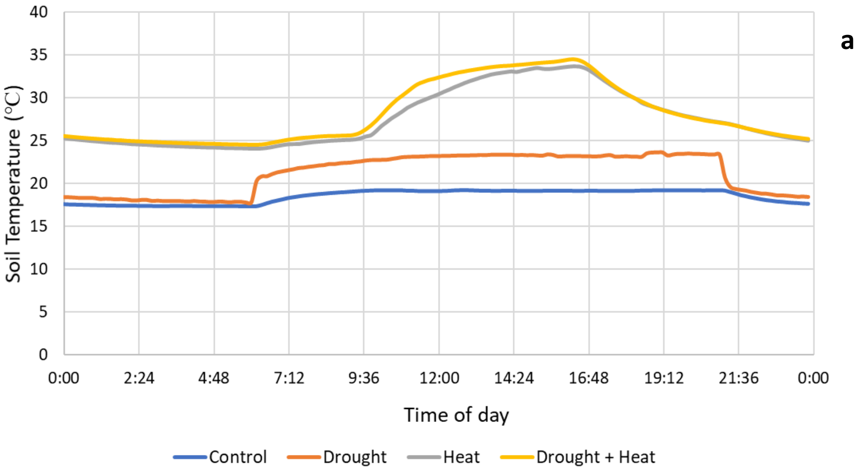


Figure 5.8 Environmental conditions in the glasshouse including (a) atmospheric temperature and (b) relative humidity in the 2019/20 growing season.

5.3.2.2 Soil temperature in the plant growth chamber

The effects of atmospheric temperature on soil temperature in the individual pots were substantial during the two weeks under non-stressed condition (C) and stressed conditions (DS, HS, and DHS) in the plant growth chamber at two different growth stages, i.e., vegetative and reproductive stages (Figure 5.9a and 5.9b). Soil temperature in C (22 °C/18 °C day/night atmospheric temperature, day from 09:00–night from 16:00, 80%–90% PC) both in vegetative and reproductive stages had mild increases starting from about 06:00 and begun to drop at about 21:00. DS (22℃/18℃ day-night atmospheric temperature, day from 09:00–night from 16:00, 40%–50% PC) had stronger effect on the increase in soil temperature than in the C. On the other hand, HS (38 ℃/25 °C day–night atmospheric temperature, day from 09:00–night from 16:00, 80%–90% PC) drastically increased the soil temperature about an hour after exposure to heat stress (10:00) and started to decline but still at supra-optimal temperature levels (>25 °C) about an hour after the stress treatment (17:00). Furthermore, the same with the individual effects of DS, DHS (38 °C/25 °C day-night atmospheric temperature, day from 09:00–night from 16:00, 40%–50% PC) resulted in an even greater increase in soil temperature at the vegetative and reproductive stages.

Soil temperatures at the reproductive stage were generally higher than those at the vegetative stage. The highest average (28.8 °C), maximum (36.9 °C), and minimum (25.1 °C) soil temperatures recorded were in the DHS at the reproductive stage (Appendix 5.1). The more advanced crop growth at the reproductive stage had greater transpiration rate that dried out the soil faster and could have contributed to the increase in the soil temperature. This finding is true for all treatments, except for DS, where the maximum and average temperatures were higher at the vegetative stage (21.2 °C and 23.6 °C, respectively) than at the reproductive stage (20.1 °C and 21.7 °C, respectively). Compared with the reproductive stage, the vegetative stage still had smaller canopy cover due to the drought stress-reducing effect on canopy development; hence, greater soil area in this pot experiment was exposed to evaporation, resulting in further drying of the soil that contributed to the increase in the soil temperature.



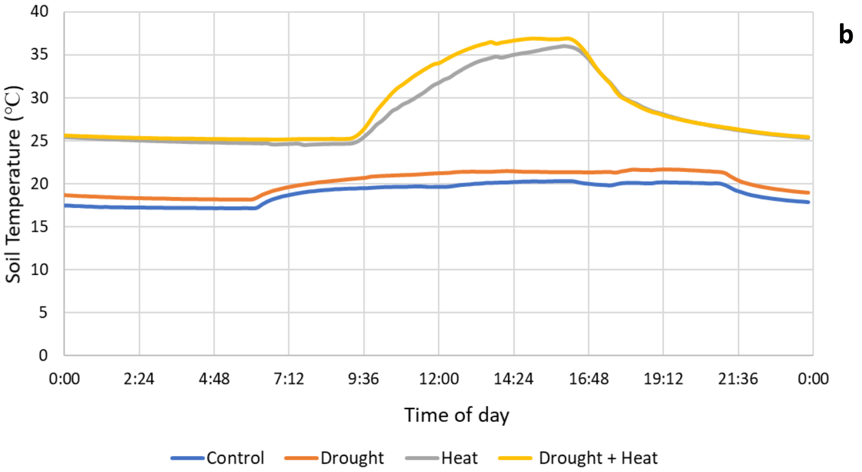


Figure 5.9 Daily average soil temperature for the two weeks at two different growth stages (a) vegetative and (b) reproductive stage under the optimum temperature (22 °C/18 °C Day–night atmospheric temperature, control), drought, heat (38 °C/25 °C day–night atmospheric temperature), and heat and drought stress combination in potted plants in the plant growth chamber.

5.3.3 Abiotic stress effects on morpho-agronomic characteristics and physiological functions of potato crops under controlled environment conditions

5.3.3.1 Abiotic stress effects on morpho-agronomic characteristics of potato crops

The effects of abiotic stress, i.e., drought stress (DS), heat stress (HS), and their combination (DHS) manifested in various ways in both cultivars that were exposed to the stresses at the two different growth stages. At the vegetative and reproductive stages, the most evident visual index of DS and DHS was moderate to severe wilting from mid-day to few hours after the stress treatment, especially under DHS (Figure 5.10a). This finding is supported by the reduced leaf relative water content or RWC of plants under DS and DHS discussed in the succeeding sections. Leaf curling was also visible under DS in 'Agria' but not in 'Taurus' (Figure 5.10b). Leaf curling can also be a form of wilting due to the declined leaf water potential and leaf turgor potential (Jensen, 1981). This finding may illustrate 'Agria''s susceptibility and 'Taurus'' relative tolerance to water deficit. Slight to moderate scorching at the tip, margins, and to some extent on the leaf lamina were commonly observed in 'Taurus' and 'Agria' subjected to HS and DHS treatments at both growth stages (Figure 5.10c). In the control or non-stressed plants (C) of 'Agria' and 'Taurus', beginning in week 1, at the vegetative and reproductive stages, small nodule-like structures developed on the leaves (Figure 5.10d and e). The condition is known as edema (oedema), a non-infectious, physiological disorder, where the plant roots absorb water faster than can be used by the plant through the transpiration of the leaves (Missouri Botanical Garden, 2020; University of Illinois Extension, 2020). Cool temperatures and high moisture levels in the air and soil, where uptake of water is faster than transpiration, confer the plant cells with high water content, which results in edema (Royal Horticultural Society, 2020; University of Illinois Extension, 2020). Initial symptoms appear as green, white, or tan-colored bumps or blister-like structures on the leaf surface, petiole, or stem. The excess water ruptures the cells that form into water-soaked patches with white, tan, or brown raised wart-like corky growths (Missouri Botanical Garden, 2020). Eventually, the leaves may turn chlorotic and necrotic, wilt, and fall-off, while the whole plant may become spindly if the condition is not improved. According to Eisa and Dobrenz (1971), the chloroplasts in the palisade cells are reduced due to chlorosis- and necrosis-affected leaves and may hamper plant growth, ultimately reducing the tuber yield. Edema is a temporary response; once the conditions improve, new growths will not show symptoms (University of Massachusetts Amherst, 2020).

Figure 5.10 Visual appearance of potato crops as affected by abiotic stress: (a) wilting of shoots and (b) leaf scorching under heat stress (HS) and combination of drought and heat stress (DHS); (c) curling of leaves under drought stress (DS); edema or abnormal water retention in the control plants (C) on the (d) surface and (e) underside of the leaves; potato plants formed side shoots with numerous but smaller leaves after exposure to (f) heat stress treatment compared with plants grown under (g) control or optimum conditions.

The high humidity that accumulated in the plant growth chamber due to regular watering of plants and limited movement of air in the small confinement exacerbated the incidence and severity of edema during the trial. Relative humidity was not monitored in the plant growth chamber due to the limited number of data loggers. The control plants recovered from edema after few days from opening an extra vent to allow air movement.

Based on statistical analysis, the effects of variety, growth stage, and abiotic stress treatments on the different morphological characteristics of the potato crop, e.g., plant height, stem diameter, number of leaves, and percent canopy cover, were highly significant (Figure 5.11 and Appendix 5.2-5.5). The plant height, stem diameter, and canopy cover were generally reduced by abiotic stress, but the intensity was dependent on the different factors i.e., cultivar, growth stage, and stress treatment. The plant height of 'Agria' was more negatively affected than 'Taurus' by abiotic stress. Moreover, the plant height of 'Agria' was more affected when abiotic stress occurred at the vegetative stage than at the reproductive stage, while opposite trend was observed in 'Taurus'. On the abiotic stress effect, DS generally reduced the plant height (up to 23.6%), and the effect was amplified by the combination of drought and heat stress in DHS (up to 27.5%). HS (up to 16.3%) alone had different effects depending on the cultivar. The highest reduction in plant height was recorded in 'Agria' at the vegetative stage under DHS at 27.5% (338 mm) compared with that in the non-stressed treatment or C (466 mm). The highest increase in plant height was recorded in 'Taurus' at the vegetative stage under HS at 10.8% (422 mm) when compared with the non-stressed treatment or C (381 mm). In contrast to plant height, the stem diameter of 'Taurus' was more negatively affected than 'Agria' by abiotic stress. The difference in the negative effect of abiotic stress between the growth stages of 'Taurus' was very minimal. On the abiotic stress effect, DS (up to 15.6%) and DHS (up to 11.6%) generally reduced the stem diameter. HS either maintained the stem diameter at the vegetative stage or enhanced it at the reproductive stage of 'Agria'; meanwhile, HS slightly reduced the stem diameter in 'Taurus' at both growth stages. The highest increase in stem diameter was recorded in 'Agria' at the reproductive stage under HS at 25.2% (16.9 mm) when compared with the non-stressed treatment or C (13.5 mm), while the highest reduction in stem diameter was recorded in 'Taurus' at the reproductive stage under DS at 15.6% (11.4 mm) when compared with the non-stressed treatment or C (13.5 mm).

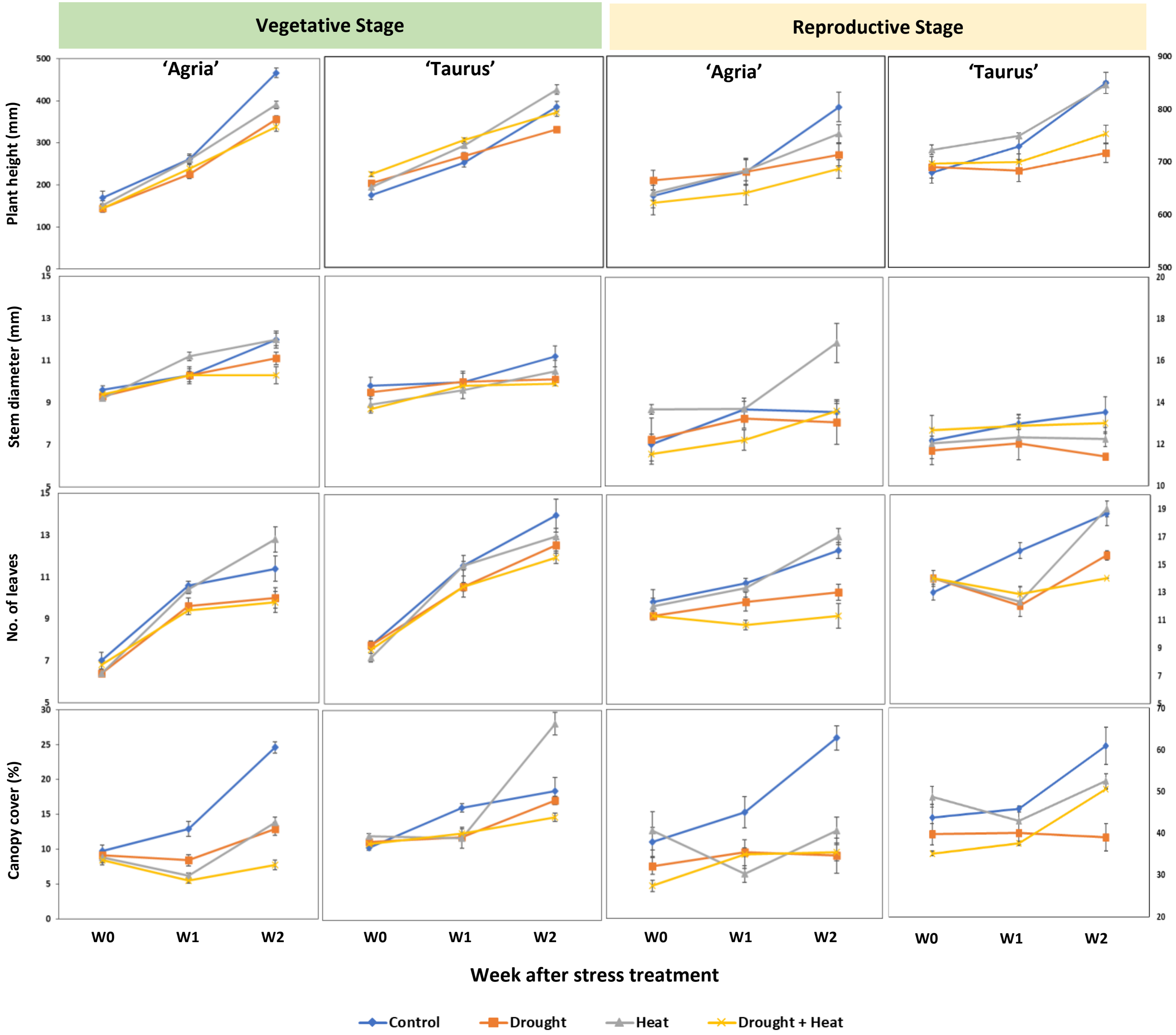


Figure 5.11 Effects of abiotic stress on the different morphological characteristics of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages. Statistical analysis in Appendix 5.2-5.5.

Similr to plant height, the canopy cover of ‘Agria’ was more negatively affected than ‘Taurus’ by abiotic stress and was even more affected when the abiotic stress occurred at the vegetative stage than at the reproductive stage; opposite result was observed in ‘Taurus’. On the abiotic stress effect, DS (up to 47.6%) generally reduced the canopy cover, and the effect was amplified by the combination of drought and heat stress in DHS (up to 68.7%) at the vegetative stage, whereas HS enhanced the canopy cover (up to 51.9%). The highest reduction in canopy cover was recorded in ‘Agria’ under DHS at 68.7% (7.7 mm) when compared with the non-stressed treatment or C (24.6 mm). The canopy cover was greatly enhanced in ‘Taurus’ under HS at 51.9% (28.1%) when compared with the non-stressed treatment or C (18.5%).

For the number of leaves, ‘Taurus’ naturally had higher number of leaves under non-stressed conditions and under abiotic stress effect. Under non-stressed conditions, ‘Taurus’ had a higher number of leaves by 18.6% (14.0) at the vegetative stage and by 14.4% (18.7) at the reproductive stage compared with ‘Agria’ (11.4 and 16.0). However, ‘Agria’ appeared to be more responsive to abiotic stress effects on leaf number than ‘Taurus’, while no clear distinction was found on the effect of abiotic stress during both growth stages. On the abiotic stress effect, DS reduced the number of leaves (up to 18.8%) formed, and this effect was exacerbated in DHS (up to 29.4%); meanwhile, HS (up to 12.3%) enhanced the number of leaves formed. The highest reduction of the number of leaves formed was observed in ‘Agria’ in DHS at 29.4% (from 16.0 to 11.3), while the highest increase in the number of leaves formed was also detected in ‘Agria’ under HS at 12.3% (from 11.4 to 12.8).

The results are consistent with the findings of previous studies, where drought stress reduced the plant height, leaf number, and canopy cover in potato crops (Hirut et al., 2017; Tourneux et al., 2003b). It is noteworthy, however, that plant height and percent canopy cover at the vegetative stage and plant height and the number of leaves at the reproductive stage of ‘Taurus’ increased under HS. The same observation was obtained in past studies (Gawronska et al., 1992; Hastilestari et al., 2018; Lafta & Lorenzen, 1995), where potato crops grown under high temperatures increased the development of the aboveground plant parts. Another distinct morphological characteristic observed under HS in ‘Agria’ and ‘Taurus’ was the development of more numerous but smaller leaves (Figure 5.10f), which could have contributed to the increase in percent canopy cover, especially in ‘Taurus’. This finding was also reported by Gawronska et al. (1992). This response could be an adaptive mechanism of 'Taurus' to HS. 'Agria' also had an increased number of leaves at both developmental stages and increased the stem diameter at the reproductive stage under HS. Furthermore, based on visual observation, lateral shoots that developed from the main stem at the vegetative stage of 'Taurus' were significantly longer than those that developed in 'Agria'. Representative photos on the effects of abiotic stress on vegetative and reproductive stages in 'Agria' and 'Taurus' potato cultivars are presented in Figures 5.12 and 5.13, respectively.

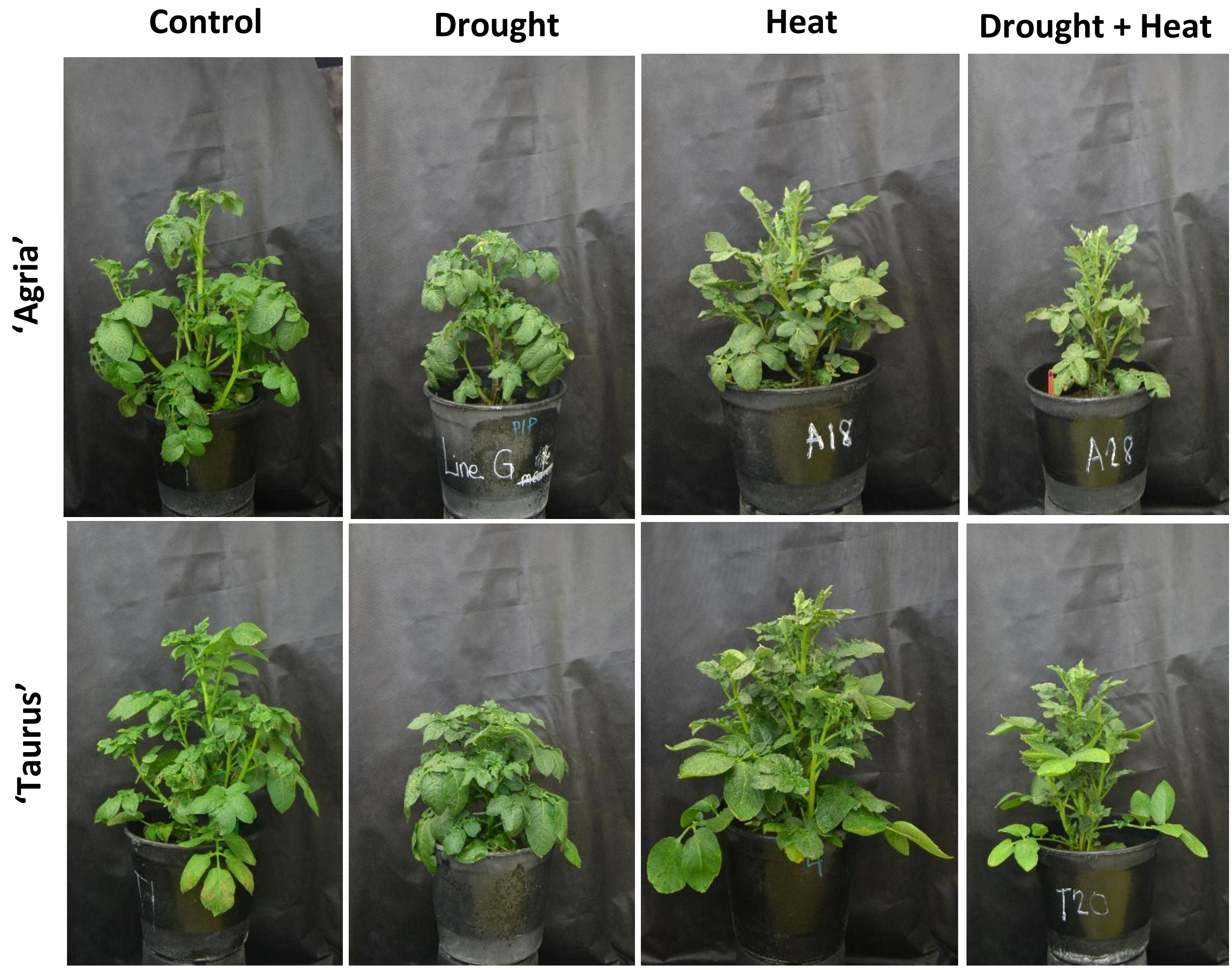


Figure 5.12 Effects of abiotic stress on the growth and development of potato cultivars 'Agria' and 'Taurus' at the vegetative stage 35 DAP (representative photo of treatment effects).

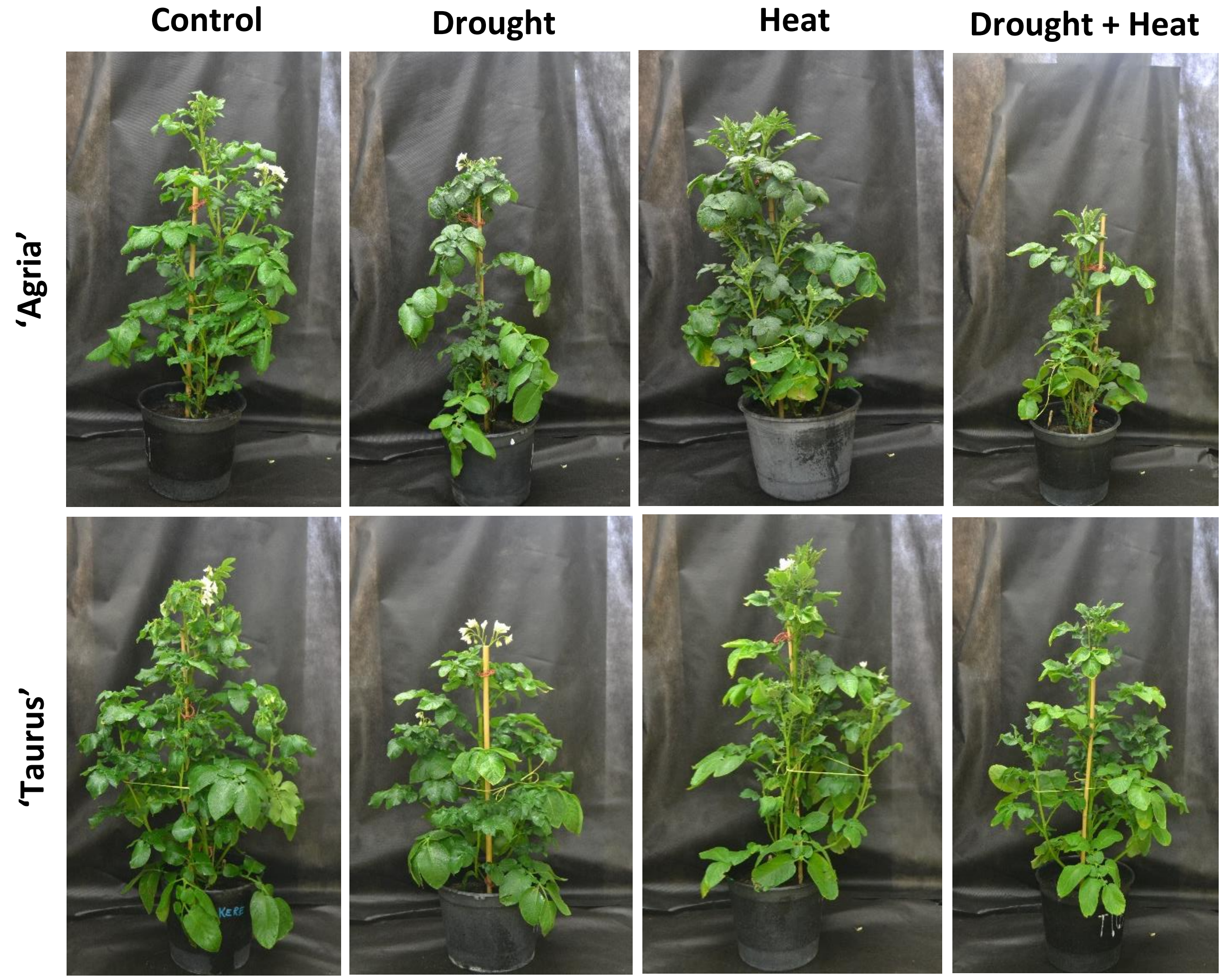


Figure 5.13 Effects of abiotic stress on the growth and development of potato cultivars 'Agria' and 'Taurus' at the reproductive stage 50 DAP (representative photo of treatment effects)

5.3.3.2 Abiotic stress effects on physiological functions of potato crops

The effects of variety, growth stage, and abiotic stress (DS, HS, and DHS) on different physiological parameters, e.g., chlorophyll content (SPAD), net photosynthesis (P_N), transpiration rate (E), and stomatal conductance (g_S), of the potato plant were statistically significant (Figure 5.14 and Appendix 5.6-5.9).

In terms of chlorophyll content, 'Taurus' (91.4 SPAD value) generally was greener than 'Agria' (80.5 SPAD value) at the vegetative stage. However, significant reduction in chlorophyll content was observed at the reproductive stage for 'Taurus' (56.9 SPAD value) and 'Agria' (59.4 SPAD value). This finding can be attributed to the natural breakdown of chlorophyll (Hörtensteiner & Kräutler, 2011) from the early to late growth stage of the plant in relation to the onset of leaf senescence. The same results were observed on other crop species, such as rice (Choubey & Choubey, 1999) and maize (Argenta, Silva, & Sangoi, 2004), where chlorophyll content is higher at the vegetative stage and decreases at the flowering or maturity stages.

Based on the abiotic stress effect on the chlorophyll content of cultivars, 'Taurus' was more negatively affected than 'Agria'. Significant reductions in chlorophyll content at the vegetative and reproductive stages of 'Taurus' were recorded. In the study of Hancock et al. (2014), a 20% reduction was observed in the levels of photosynthetic pigments including chlorophyll *a* and *b* and carotenoids in potato plants under heat stress. However, the long-term effect of heat stress on SPAD value could not be determined in the current trial because heat treatment was applied for only two weeks.

On the other hand, the chlorophyll content in 'Agria' was enhanced by abiotic stress at the reproductive stage. In terms of the growth stage, a greater reduction in chlorophyll content was recorded at the vegetative stage than at the reproductive stage. In contrast to findings in related literature that chlorophyll content is negatively affected by heat stress (Reynolds, 1990) and enhanced by drought stress (Hirut, 2017), the current trial indicated no clear trend. Both DS (up to 31.7%) and HS (up to 45.0%) reduced the chlorophyll content, while DHS enhanced the chlorophyll content (up to 17.1%). Moreover, all abiotic stress enhanced the chlorophyll content in 'Agria' at the reproductive stage. The highest reduction in chlorophyll content was observed in 'Taurus' under HS at 45.0% (from 91.4 to 50.3 SPAD), while the highest increase in chlorophyll content was detected in 'Agria' under HS at 29.3% (from 59.4 to 76.8 SPAD).

In the current trial, before the end of the stress regimen, as transpiration (E) and stomatal conductance (g_S) increased, the net photosynthesis (P_N) increased but only under HS at the vegetative stage. This finding contradicts previous data by Hastilestari (2018), who reported that heat stress was associated with the reduced photosynthetic rate. However, differential susceptibility to heat stress effects on photosynthesis was also observed in past studies (Hancock et al., 2014; Lafta & Lorenzen, 1995; Wolf et al., 1990).

In the findings of Kumar, Minhas, and Singh (2004), higher g_S in the identified potato cultivars showed better evaporative cooling under heat stress, which resulted in improved photosynthesis and plant growth. According to Aien, Khetarpal, and Pal (2011), the enhanced g_S and E under heat stress may reduce the leaf temperature and thus demonstrate high-temperature stress avoidance. Additionally, reduced canopy temperature was found to be associated with higher g_S and E, leading to improved photosynthetic activity (Hirut et al., 2017). The g_S was initially reduced in 'Agria' in week 1 and then increased in week 2 under HS. According to Ku, Edwards, and Tanner (1977), the closing of potato leaf stomata under elevated temperatures is an attribute of a crop that is more adapted in cooler environments, similar to the response of the cultivar 'Agria' in the current trial. Moreover, 'Agria' at the vegetative stage had a significantly greater increase in E at 48.0% (from 5.0 to 7.4 mmol H_2O m^2s^1) and g_S at 51.9% (from 0.260 to 0.395 mol H_2O m^2s^1), compared with 'Taurus' E at 19.7% (from 6.6 to 7.9 mmol H_2O m^2s^1) and g_S at 16.7% (from 0.354 to 0.413 mol H_2O m^2s^1); however, P_N was higher in 'Taurus' (25.3 µmol CO_2 m^2s^1) than in 'Agria' (22.1 µmol CO_2 m^2s^1). This result illustrates the capacity of 'Taurus' to respond more efficiently to HS by controlling E and g_S while improving P_N. In terms of P_N, 'Agria' was more affected at the vegetative stage, while 'Taurus' was more affected at the reproductive stage. On the other hand, the E and g_S of 'Agria' and 'Taurus' were significantly reduced by DS (up to 72.0% and 68.5%, respectively), and the effect was amplified by DHS (up to 82.8% and 89.3%, respectively) at the vegetative and reproductive growth stages. Correspondingly, at the vegetative stage, P_N was reduced by 13.3% (from 19.6 to 17.0 µmol CO_2 m^2s^1) in 'Agria' and by only 3.1% (from 22.8 to 22.1 µmol CO_2 m^2s^1) in 'Taurus' under DS; even larger reductions in P_N of 48.0% (from 19.6 to 10.2 µmol CO_2 m^2s^1) were found in 'Agria' and of 36.4% (from 22.8 to 14.5 µmol CO_2 m^2s^1) in 'Taurus' under DHS. At the reproductive stage, the P_N was reduced by 46.6% (from 20.8 to 11.1 µmol CO_2 m^2s^1) in 'Agria' and by 49.2% (from 17.7 to 9.0 µmol CO_2 m^2s^1) in 'Taurus' under DS, and even larger reductions in P_N of 73.1% (from 20.8 to 5.6 µmol CO_2 m^2s^1) in 'Agria' and of 75.1% (from 17.7 to 4.4 µmol CO_2 m^2s^1) in 'Taurus' under DHS.

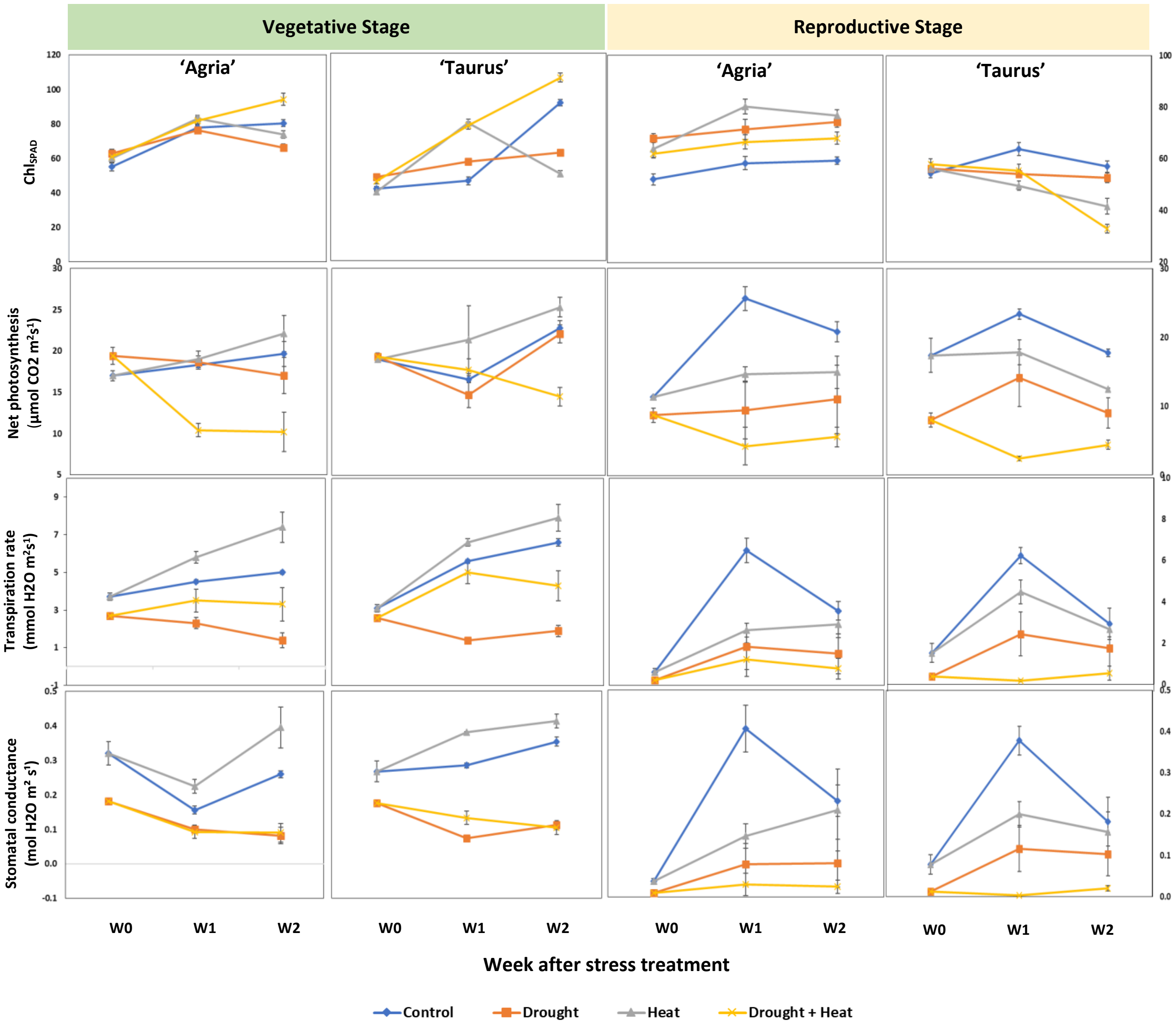


Figure 5.14 Effects of abiotic stress on the different physiological parameters of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages. Statistical analysis in Appendix 5.6-5.9.

Reduced water uptake due to drought stress encourages a series of events in the physiology of the potato crop that affects photosynthetic activity. The decrease in the photosynthesis rate due to drought stress is influenced by stomatal and non-stomatal factors (Li et al., 2017). The regulation of stomatal aperture is usually the initial response of plants to drought stress, where the stomata closed (reduced g_S) and *E* was reduced (Blonquist Jr, Norman, & Bugbee, 2009), affecting the influx of CO_2 into the leaves (Liu, Jensen, Shahanzari, Andersen, & Jacobsen, 2005) and correspondingly hampering the photosynthetic activity. Non-stomatal factors occur in the presence of a prolonged drought period that directly inhibits the photosynthetic capacity (mesophyllic inhibition) by damaging the photosystem II and the antioxidant enzyme system (Li et al., 2017).

In contrast to that in 'Agria', DS in 'Taurus' initially reduced the g_S and *E* in week 1 but increased them in week 2, hence, 'Taurus' showed improved photosynthetic performance (P_N). According to previous studies, the enhanced photosynthesis rate, strong protective enzyme activity (Li et al., 2017), and high stomatal resistance under drought stress (Araghi & Assad, 1998; Pinheiro et al., 2005) are important physiological adaptations for drought tolerance. The capacity of 'Taurus' to better recover from drought stress could suggest its resilience to abiotic stress effects.

The DHS treatment also reduced the g_S, *E*, and P_N in 'Agria' and 'Taurus'; however, 'Taurus' was less affected and performed relatively better under combined stress than 'Agria'. The heat stress component in DHS treatment influenced the increase in *E*, but the drought stress component influenced the reduction in g_S, which led to the reduced P_N particularly in the cultivar 'Agria'. 'Taurus' also had decreased P_N, which was relatively higher than that in 'Agria'. By contrast, the influence of the DHS treatment on the SPAD index of 'Agria' and 'Taurus' was positive. This could be explained by the loss in leaf turgor pressure or reduction of leaf growth (Ramírez et al., 2014) that increases the chlorophyll content of potato leaves under water-stressed conditions (Hirut et al., 2017).

It was apparent that both cultivars could physiologically adapt better when exposed to abiotic stress at an earlier than at the later growth stage in terms of its physiological functions. As observed in this trial, abiotic stress had stronger negative impacts on the reproductive as compared to the vegetative stage. In the control plants (C) at the reproductive stage, P_N, E, and g_S increased in week 1 but drastically decreased in week 2 (potentially due to the incidence of edema), but the reduction in the physiological parameters was stronger under HS, DS, and DHS.

Several studies have reported the reduction in the photosynthetic activity of potato crops under elevated temperatures (>30.0℃) (Dwelle et al., 1981; Sale, 1973; Wolf et al., 1990). In the current trial, the reduction in P_N to heat stress was only observed at the reproductive stage, while a significant increase was observed at the vegetative stage for both 'Agria' and 'Taurus'.

5.3.3.3 Abiotic stress effects on plant water status of potatoes

The capacity of plants to retain moisture in their cells and tissues under adverse environmental conditions i.e., exposed to abiotic stresses such as heat and drought stresses, is a reflection of their resilience and enhanced stress adaptation mechanisms. Water availability influences stomatal functions, which in return regulate the photosynthetic activity of plants.

Relative leaf water content (RWC) is a measurement of the actual water content of leaves about its water holding capacity at full turgidity (Mullan & Pietragalla, 2012). It also describes the balance between water entering the leaf and the plant's transpiration rate (Lugojan & Ciulca, 2011). RWC may indicate the plant's stress level when exposed to abiotic stresses by providing a measurement of water deficit. In the study by Soltys-Kalina, Plich, Strzelczyk-Żyta, Śliwka, and Marczewski (2016a), small reductions in RWC among potato cultivars exposed to drought stress were correlated to better yields compared with those in drought-susceptible cultivars. The extent of the yield reduction was one if not the most considered criterion for stress resistance especially under drought stress among the potato cultivars.

Leaf water potential (ψ_L) is a measurement of the water status of the shoot during the day in response to fluctuations in water absorption by the roots and transpiration of the leaves, which often involves the interactions among soil moisture content, climate, transpiration, and cultivar type (Deloire & Heyns, 2011). In the current trial, RWC and ψ_L have a linear relationship, i.e., decreases in RWC have a corresponding decrease in ψ_L. Even a small reduction in RWC may result in a drastic decline in ψ_L, i.e., from -0.2 to -1.0 MPa (Basu, Sharma, & Sukumaran, 1998). Moreover, even at relatively high ψ_L, a substantial decline in photosynthesis was detected (Sukumaran, Ezekiel, & Perumal, 1989); at relatively low ψ_L, complete inhibition of photosynthesis was observed (Vos & Oyarzun, 1987). The decline in P_N at moderate ψ_L ($\leq$-1.0 MPa) was suggested to be caused by the increase in leaf sugar concentration under low RWC, but the decline in sugar concentration after rewatering of water-stressed leaves resulted in normal photosynthesis (Basu et al., 1998). The minimum ψ_L is generally within the range of -0.7 to -1.0 MPa regardless of soil moisture level because stomatal closure lessens water loss to prevent further dehydration of leaves (Gandar & Tanner, 1976b).

Another factor to consider under drought stress is the production of proline, a low molecular weight amino acid compound (Levy, 1983). Proline is linked to RWC and ψ_L, which may indicate its involvement in osmoregulation (Knipp & Honermeier, 2006). The intensity of proline accumulation strongly correlated with decreasing RWC and ψ_L (Knipp & Honermeier, 2006). In the study of Levy (1983), low ψ_L (-1.0 MPa) of wilting leaves had an 8- to 27-fold increase in proline content, although it was suggested that proline accumulation in potato leaves is activated only under severe stress conditions.

In the current trial, the influence of cultivar, growth stage, and abiotic stress treatment on RWC was found to be highly significant (Figure 5.15 and Appendix 5.10). Under non-stressed conditions (C), the cultivar ‘Taurus’ had a relatively higher RWC by 1.0% (92.5%) at the vegetative stage and by 4.2% (92.8%) at the reproductive stage than ‘Agria’ (91.6% and 88.9%, respectively). ‘Taurus’ had lower reductions in RWC when exposed to abiotic stress at either growth stage compared with ‘Agria’. The cultivars responded differently to the abiotic stress treatment at both growth stages. The abiotic stress reduced the RWC of ‘Agria’ and ‘Taurus’ with reference to C, except for HS in ‘Taurus’ where RWC slightly increased by 0.3% (from 92.5 to 92.8%) at the vegetative stage and by 1.0% (from 92.8 to 93.7%) at the reproductive stage. DS and DHS reduced the RWC, but DS reduced the RWC more at the vegetative stage, while DHS reduced it more at the reproductive stage. DS reduced the RWC by 11.8% (from 91.6 to 80.8%) in ‘Agria’ and by 6.1% (from 92.5 to 86.9%) in ‘Taurus’ at the vegetative stage. DS reduced the RWC by 7.3% (from 88.9 to 82.4%) in ‘Agria’ and by 3.9% (from 92.8 to 89.2%) in ‘Taurus’ at the reproductive stage. DHS reduced the RWC by 3.6%

(from 91.6 to 88.3%) in ‘Agria’ and by 2.9% (from 92.5 to 89.8%) in ‘Taurus’ at the vegetative stage. DHS reduced the RWC by 13.3% (from 88.9 to 77.1%) in ‘Agria’ and by 10.2% (from 92.8 to 83.3%) in ‘Taurus’ at the reproductive stage.

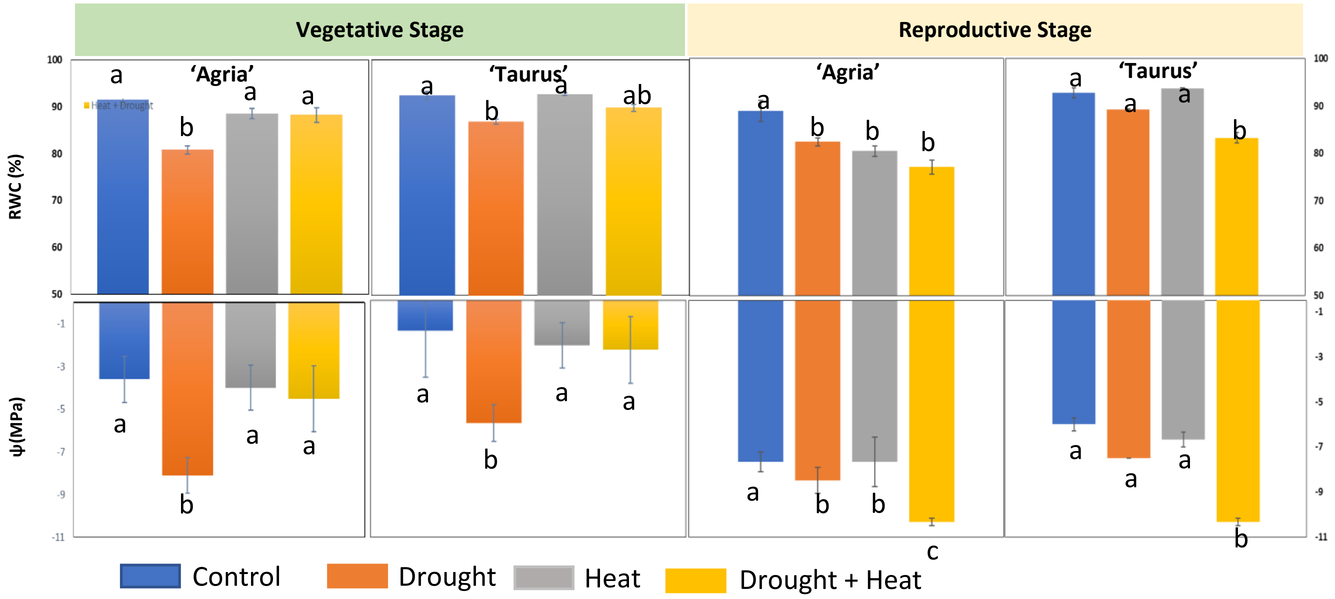


Figure 5.15 Effects of abiotic stress on relative leaf water content (RWC) and leaf water potential (LWP) of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative (35 DAP) and reproductive stages (50 DAP). The columns within a variety and growth stage with the same letters are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.10.

Similar to RWC, ψ_L is also significantly influenced by cultivar, growth stage, and abiotic stress treatment (Figure 5.15 and Appendix 5.11). ‘Agria’ had lower ψ_L at both growth stages and was more affected by the different abiotic stress treatments (i.e., DS, HS, and DHS) than ‘Taurus’, except for the DHS treatment at the reproductive stage, where both cultivars recorded the same ψ_L (-0.98 MPa). Although ‘Taurus’ had higher reductions in ψ_L, the ψ_L values were higher than those in ‘Agria’. Cultivars with the capacity to reduce stress by maintaining turgid leaves under adverse environmental conditions may have physiological advantages because this favors turgor-dependent processes, such as growth, stomatal functions, and maintenance of the photosystem complex.

The vegetative stage had a significantly higher and greater reduction in ψ_L when exposed to abiotic stress, i.e., DS, HS, and DHS, than at the reproductive stage. Hence, potato crops exposed to abiotic stress at the earlier stage have lesser resilience than those exposed at later stages.

The highest reduction in ψ_L was caused by DS at the vegetative stage and by DHS at the reproductive stage. Under DS, the increased pull of water from the soil to the leaves could have resulted in the transpiration flow being under more negative pressure, thereby reducing the ψ_L. DS reduced the ψ_L by 125% (from -0.36 to -0.81 MPa) in 'Agria' and by 307% (from -0.14 to -0.57 MPa) in 'Taurus' at the vegetative stage. DS reduced the ψ_L by only 2.6% (from -0.78 to -0.80 MPa) in 'Agria' and by 27.3% (from -0.55 to -0.70 MPa) in 'Taurus' at the reproductive stage. On the other hand, DHS exacerbated the reducing effect of DS on ψ_L at the reproductive stage for both cultivars. The significantly reduced ψ_L under DHS might have been contributed by the combined heat-stressed plants and low volumetric water content of the substrate in the 10 L pot under the combined drought and heat stress treatment. These results concur with a past study, where constant water stress resulted in reduced ψ_L (Basu et al., 1998; Knipp & Honermeier, 2006). Moreover, reduction in ψ_L as affected by water deficits resulted in aberration in morphological characteristics of the potato crop. Gandar and Tanner (1976a) observed a decline in leaf elongation under low ψ_L and complete cessation of leaf growth and tuber expansion at -0.40 and -0.50 MPa.

5.3.3.4 Abiotic stress effects on stomatal and trichome characteristics of potatoes

Trichomes or plant hairs are "unicellular or multicellular appendages, which originate from epidermal cells only and develop outwards on the surface of various plant organs" (Werker, 2000). There are two major types of trichomes found on the leaf ribs and distributed across the leaf surface: glandular trichomes that have knob-like secretory swellings at the tips of short, uniseriate stalks; and non-glandular simple, uniseriate, or multicellular (two- to four-celled) hairs of varying lengths (McCauley & Evert, 1988). Glandular and non-glandular trichomes in potato cultivars 'Agria' and 'Taurus' are presented in Figures 5.16 and 5.17. Glandular trichomes serve as structures that secrete specialized metabolites that contribute to the plant's increased fitness to the environment, e.g., protection from UV-irradiation (Huchelmann, Boutry, & Hachez, 2017), herbivores and pathogens (Glas et al., 2012); and chemical exudates including terpenoids, methylketones, acyl sugars and flavonoids (Huchelmann et al., 2017). Glandular trichomes play important role in the insect resistance among wild species of potatoes, hence, a great deal of study was done to potentially incorporate the characteristics in potato breeding (Cho et al., 2017; Dimock & Tingey, 1988; Gregory, Tingey, Ave, & Bouthyette, 1986; Tingey, 1991). According to Tingey (1991), pest species such as Colorado potato beetle, green peach aphid, potato leafhopper, potato flea beetle, and spider mites are negatively affected by glandular trichomes.

Non-glandular trichomes, however, are a micromorphological trait that mainly serves as physical protection of plants against abiotic stresses such as low humidity, elevated temperatures, and sun radiation (Peter & Shanower, 1998; Werker, 2000) and against biotic stresses by serving as physical deterrent against feeding insects (Baur, Binder, & Benz, 1991) particularly small-sized insects (Peter & Shanower, 1998). In chickpea, larvae of pod borer (*Helicoverpa armigera*) are prevented from feeding on the seeds by the presence of thick non-glandular trichomes on the pods (Peter & Shanower, 1998). In another study, non-glandular trichomes were found to be a mechanism of resistance to potato leafhopper in red clover (*Trifolium pretense* L.) (Kusmiyati, 1996). In most plant species, non-glandular trichomes increased the radiation reflectance and permitted the formation of microlayer of humid air around the leaf surface, therefore reducing the leaf temperature and transpiration and limiting the moisture loss (Clawson, Specht, Blad, & Garay, 1986; Gausman & Cardenas, 1973) under stressful conditions. In red clovers, non-glandular trichomes significantly improved the leaf water retention under high water deficit by reducing the leaf evaporation (Naydenova & Georgiev, 2013). This can be explained by the xeromorphic characteristics (ability to store water) of plants with dense non-glandular trichomes (Karabourniotis, Liakopoulos, Nikolopoulos, & Bresta, 2020). This illustrates the function of non-glandular trichomes that support the leaf stomatal apparatus in moisture conservation especially under high moisture stress. In *Datura wrightii*, simulations of leaf temperatures showed lower temperature by about 1 °C in velvety plants that produce non-glandular trichomes compared with sticky plants that produce glandular trichomes (Smith II & Hare, 2004). In another study, non-glandular trichomes on the leaves of *Cistus salvifolius* L. were found to filter the shortest solar wavelengths (Tattini et al., 2007). This can be attributed to the phenolic compounds, mainly flavonoids, deposited in the cell wall of the trichomes that provide defense in plant tissues against UV-B radiation (Karabourniotis et al., 2020).

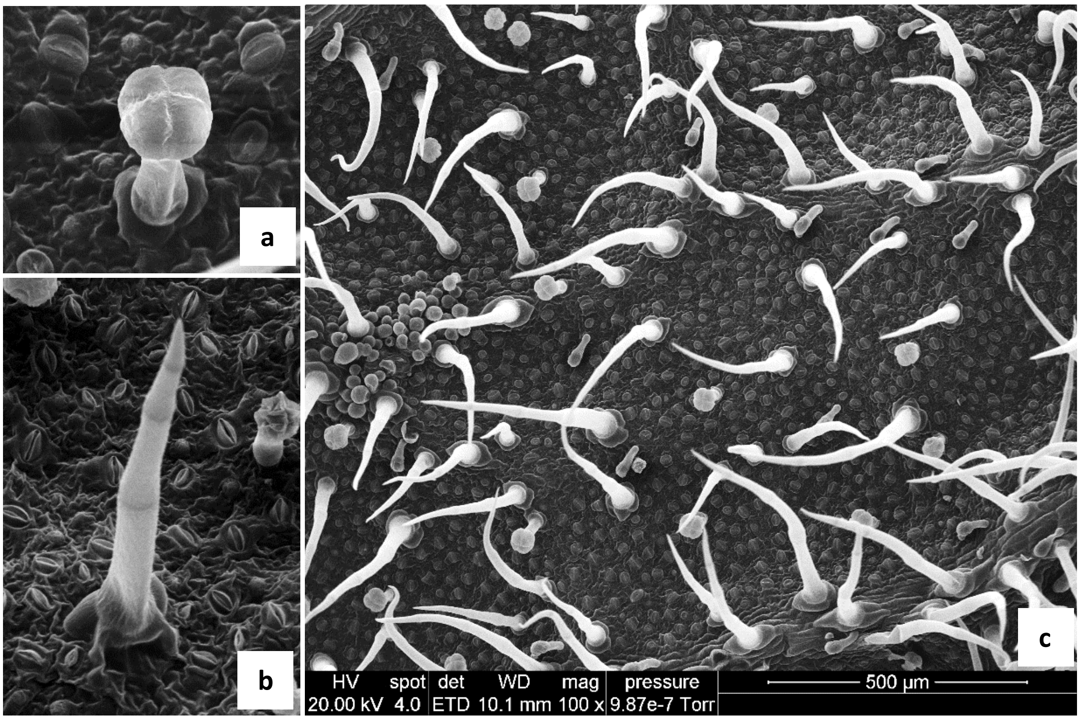


Figure 5.16 Two most common trichomes observed on the leaf surface of the potato cultivars under a scanning electron microscope. Close-up view of (a) glandular and (b) non-glandular trichomes at 400× magnification and (c) glandular and non-glandular trichomes distributed on the abaxial leaf ribs and surface of potato plants at 100× magnification.

In some crops, trichomes had minor effects on gas exchange and water use efficiency or WUE (Amada, Onoda, Ichie, & Kitayama, 2017) as well as on leaf reflectance and absorptance of photosynthetically active radiation or PAR (Smith II & Hare, 2004), suggesting that non-glandular trichomes may have other adaptive functions in plants.

In the current trial, cultivar and abiotic stress treatment apparently influenced the leaf surface morphology of both cultivars on stomata and trichome characteristics (Figure 5.18). The cultivar and abiotic stress treatment had a significant influence on the glandular and non-glandular trichome formation, while only the abiotic stress treatment had a significant effect on the non-glandular trichome formation in potato crops (Appendix 5.12). These observations suggest that the potato crop can adapt in a relatively short time to abiotic stress effects in terms of its leaf surface morphology. Under non-stressed conditions (C), 'Taurus' had 45.1% higher glandular trichome density (21.3 mm^{-2}) than 'Agria' (11.7 mm^{-2}) but had almost the same non-glandular trichome (leaf hairs) density ('Taurus' 16.8 mm^{-2} and 'Agria' 17.7 mm^{-2}).

Among the abiotic stresses, DS significantly enhanced the trichome formation especially non-glandular trichomes. In terms of cultivar, ‘Taurus’ developed more trichomes than ‘Agria’ in response to DS. In particular, DS increased the glandular trichome density by 64.3% (from 21.3 to 35.0 mm^{-2}) in ‘Taurus’ and by 56.4% (from 11.7 to 18.3 mm^{-2}) in ‘Agria’; it also increased the non-glandular trichome density by 138.1% (from 16.8 to 40.0 mm^{-2}) in ‘Taurus’ and by 112.4% (from 17.7 to 37.6 mm^{-2}) in ‘Agria’. HS and DHS also enhanced trichome formation in both cultivars, except for glandular trichomes in ‘Taurus’, where reductions were recorded under HS by 35.7% (from 21.3 to 13.7 mm^{-2}) and DHS by 2.8% (from 21.3 to 20.7 mm^{-2}).

The significant increase in glandular trichome development under DS especially in ‘Taurus’ could be attributed to the cultivar’s adaptive mechanism to increase fitness to the environment through secretion of specialized metabolites, as suggested by Huchelmann et al. (2017). The current trial focused on non-glandular trichomes considering their role on leaf temperature reduction and moisture conservation, which may influence the potato crop’s susceptibility or tolerance to abiotic stress.

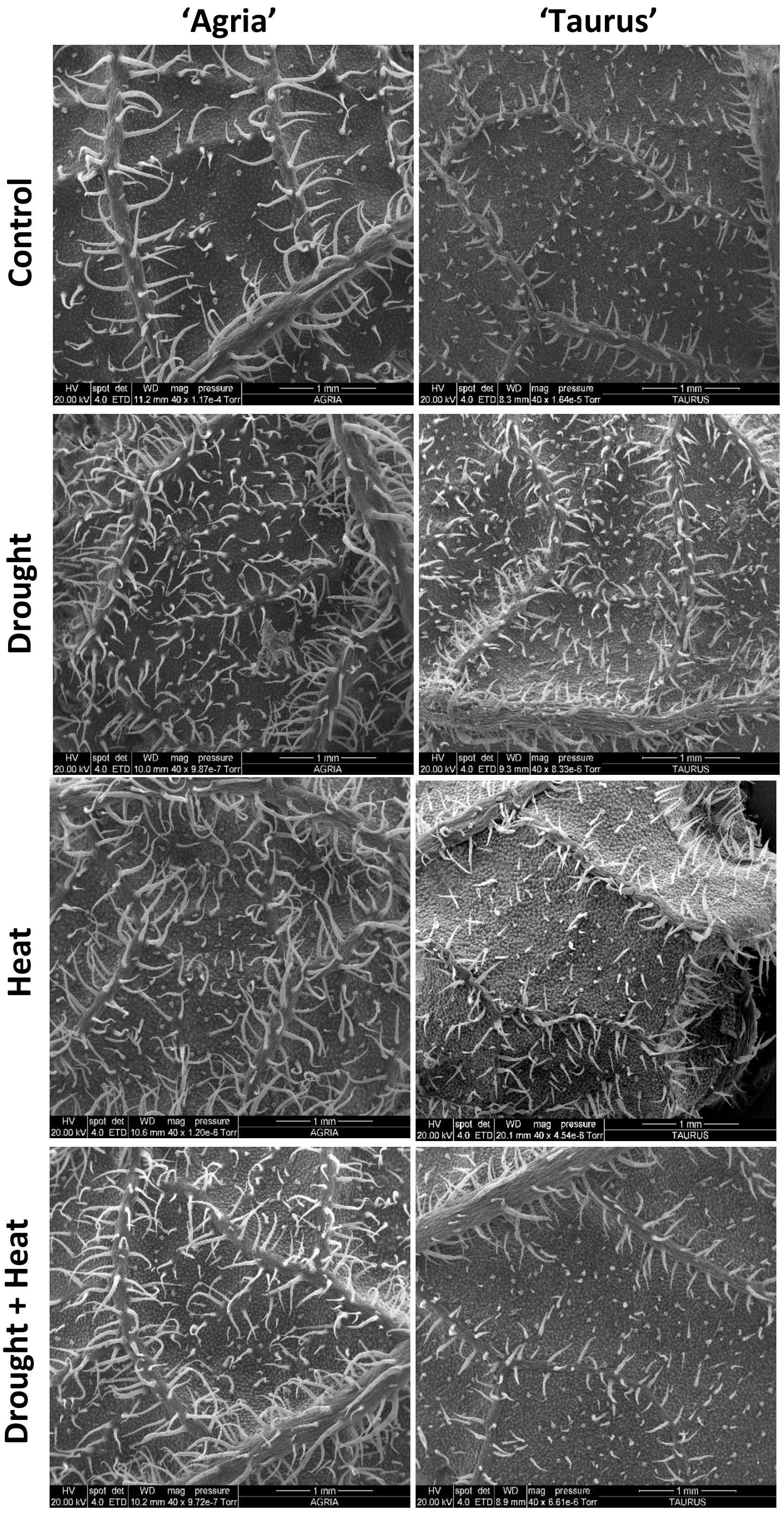


Figure 5.17 Abaxial (lower surface) leaf imprints of potato cultivars 'Agria' and 'Taurus' showing stomata and trichomes under a scanning electron microscope as affected by abiotic stress at 40× magnification at 50 DAP.

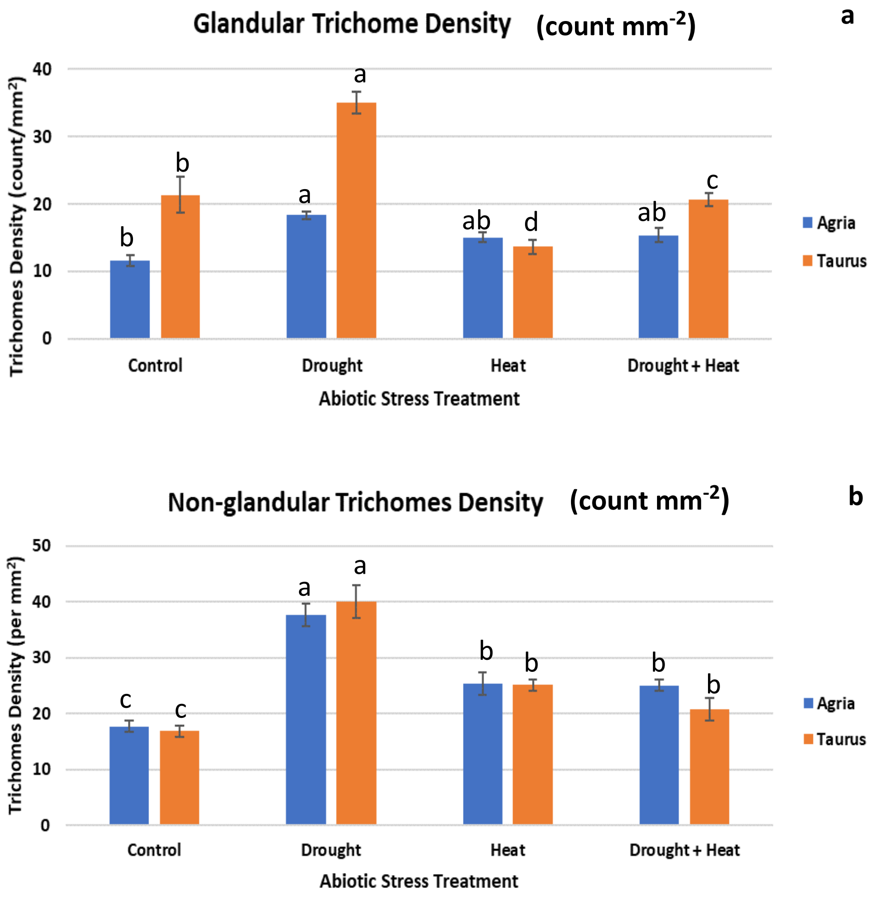
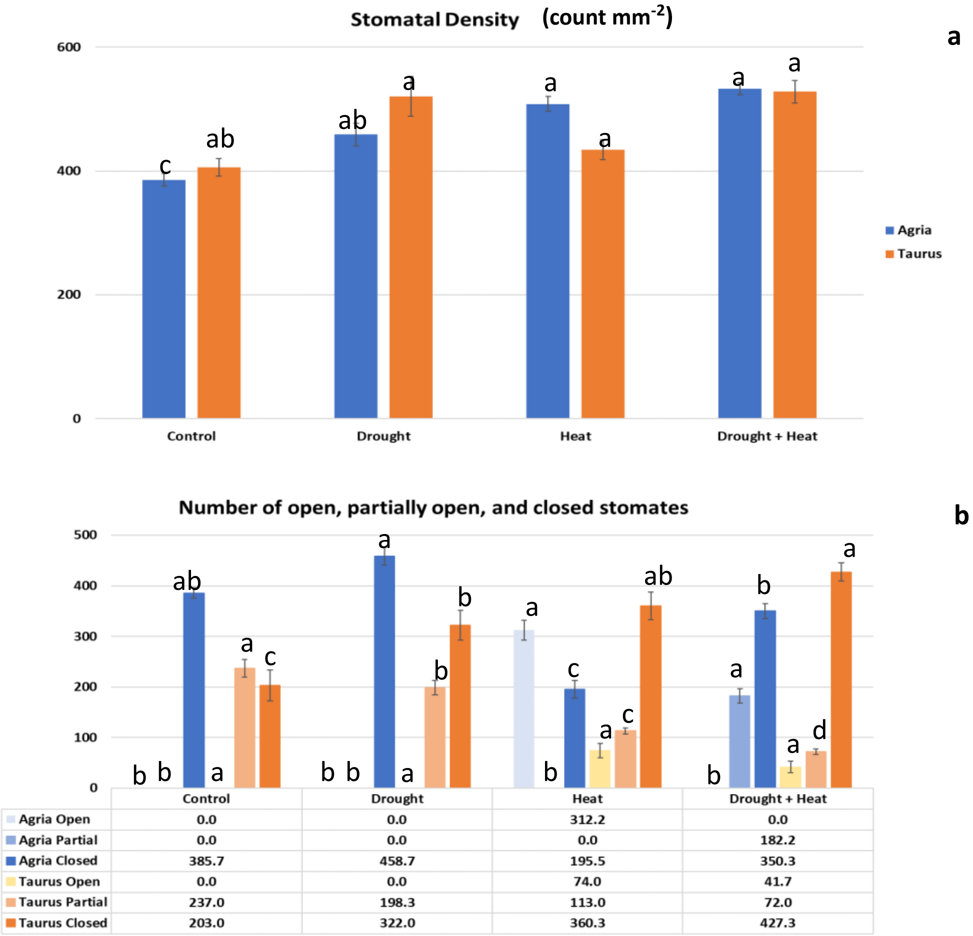


Figure 5.18 Comparison of (a) glandular and (b) non-glandular trichome density between potato cultivars ‘Agria’ and ‘Taurus’ as affected by abiotic stress (50 DAP). The trichome type within each variety with the same letters are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.12.

The higher non-glandular trichome density in ‘Taurus’, particularly under DS, could have significantly improved the leaf water retention of the cultivar by limiting leaf evaporation under high water-deficit conditions (Naydenova & Georgiev, 2013) and translate to the cultivar’s ability to retain higher relative leaf water content or RWC measured at the vegetative and reproductive stages compared with ‘Agria’. The decrease in non-glandular trichome density under HS and DHS in ‘Agria’ and ‘Taurus’ relative to DS could mean that non-glandular trichomes might play an important role in moisture conservation; hence, DS had a greater influence on trichome development. The lower trichome density of ‘Taurus’ under DHS also corresponded with the lowest RWC value among the stress regimens being compared.

In terms of stomatal density (count mm^{-2}) under non-stressed conditions (C), 'Taurus' had 12.3% higher stomatal density (440.0 mm^{-2}) than 'Agria' (385.7 stomata mm^{-2}), although the difference was not statistically different (Figure 5.19a and Appendix 5.13). Abiotic stress treatment also enhanced the formation of stomata, as seen in the increase in stomatal density in 'Agria' and 'Taurus'. Relative to C, HS had the highest increase in stomatal density in 'Taurus' at 24.4% (from 440.0 to 547.3 stomata mm^{-2}), followed by DHS at 22.9% (from 440.0 to 541.0 stomata mm^{-2}), and the least in DS at 18.2% (from 440.0 to 520.3 stomata mm^{-2}), but the differences were not statistically different from one another. In 'Agria', the highest increase in stomatal density was found in DHS at 38.0% (from 385.7 to 532.6 stomata mm^{-2}), followed by HS at 31.6% (from 385.7 to 507.7 stomata mm^{-2}), and the least in DS at 18.9% (from 385.7 to 458.7 stomata mm^{-2}), but the differences were also not statistically significant.

Besides the increase in stomatal density, abiotic stress affected the opening of the stomatal aperture in the potato leaves (Figure 5.19 and Appendix 5.14). Among the abiotic stresses, HS had the most influence on the opening of the stomatal aperture. In Figure 5.20, only in 'Agria' under HS (400x magnification) can be seen that the stomatal apparatus consists of two distinctly enlarged guard cells, which created a large central pore or opening. Moreover, in terms of cultivar, 'Agria' had the most opened stomata constituting an average of 61.5% (312.2 of 507.7 stomata mm^{-2}), while 'Taurus' had only 13.5% (74.0 of 547.3 stomata mm^{-2}) under HS. Although an additional 20.6% (113.0 of 547.3 stomata mm^{-2}) was partially opened under HS in 'Taurus'. At high temperatures under adequate water, plants retain their stomata open for evaporative cooling to keep the leaf temperature at the optimum level (Aien, Chaturvedi, Bahuguna, & Pal, 2017), as in the case of the cultivar 'Agria'. This translates to a decrease in stomatal resistance (Wolf et al., 1990) or higher stomatal conductance, and higher transpiration that could reduce the leaf temperature and therefore result in heat stress avoidance. However, prolonged exposure to higher temperatures translates to a higher transpiration rate, which may lead to moisture depletion and reduced crop WUE (Schleser, 1990; Zhao & Yu, 2008).



	Control	Drought	Heat	Drought + Heat
Agria Open	0.0	0.0	312.2	0.0
Agria Partial	0.0	0.0	0.0	182.2
Agria Closed	385.7	458.7	195.5	350.3
Taurus Open	0.0	0.0	74.0	41.7
Taurus Partial	237.0	198.3	113.0	72.0
Taurus Closed	203.0	322.0	360.3	427.3

Figure 5.19 Comparison of (a) stomatal density and (b) number of open/partially open/closed stomata between the potato cultivars ‘Agria’ and ‘Taurus’ as affected by abiotic stress. The same letters within each variety for stomatal density and stomatal aperture opening/closing are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.13 – 5.14.

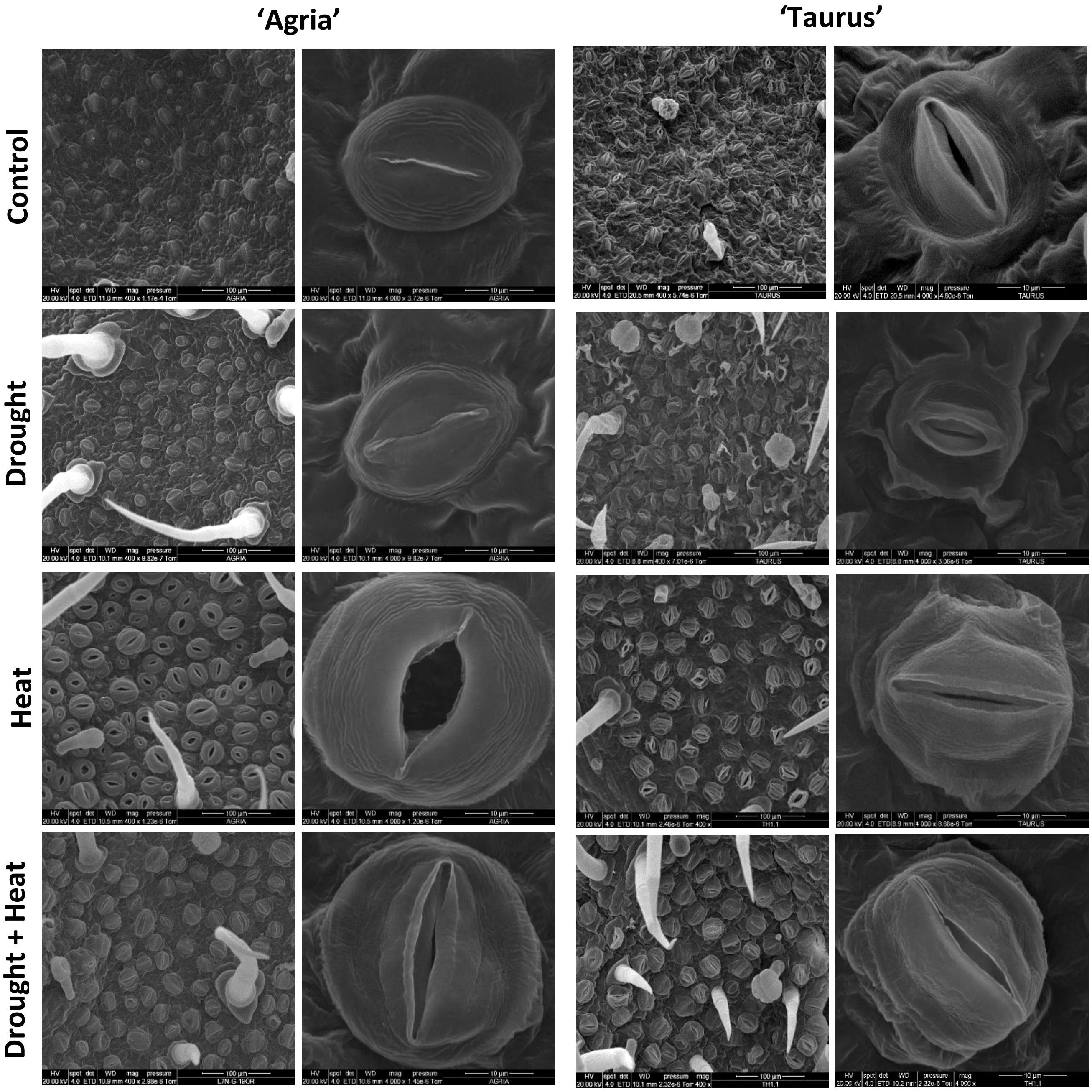


Figure 5.20 Abaxial (underside) leaf imprints of potato cultivars 'Agria' and 'Taurus' showing stomatal characteristics under a scanning electron microscope as affected by abiotic stress at 100× (first and third column) and 400× (second and fourth column) magnification.

In the DS treatment, stomata from the samples collected in 'Agria' were all closed, while in 'Taurus', 61.9% (322.0 of 520.3 stomata mm^{-2}) were closed and 38.1% (198.3 of 520.3 stomata mm^{-2}) were partially opened. According to Nobel (1991), partially opened stomata can enhance WUE by permitting the entry of CO_2 while minimizing water loss through transpiration under drought stress. Liu et al. (2005) suggested that partial closure or partial opening of stomata tends to improve the photosynthetic water use efficiency, that is, the ratio of photosynthesis to stomatal conductance. Further, Jones (2013) proposed that the optimum stomatal aperture opening is between fully opened and those that will allow the most water use efficiency. In the current trial, partially opened stomata were observed in the cultivar 'Taurus' not only under DS but also under HS 20.6% (113.0 of 547.3 stomata mm^{-2}) and DHS 13.3% (72.0 of 541.0 stomata mm^{-2}). In 'Agria', partially opened stomata were observed only under DHS at 34.2% (182.2 of 532.6 stomata mm^{-2}), which is potentially more influenced by the heat stress component rather than a cultivar characteristic.

The initial response of plants to drought stress is stomatal closure (Yordanov, Velikova, & Tsonev, 2000), which is commonly linked with a decline in leaf turgor as a consequence of low water potential (Kramer, 1988). Stomatal and non-stomatal factors control photosynthesis in the leaves (Liu et al., 2005). In the study by Li et al. (2017a), under mild to medium drought stress, potato varieties compensated photosynthesis through a reduction in light capture, dissipation of heat, and regulation of enzyme activities, which were identified as the stomatal limitation factor. However, under severe drought stress, the photosystem II and antioxidant enzyme systems are damaged, which constitute the non-stomatal limitation factor (Li et al., 2017a). Closing of the stomata decreases the stomatal conductance (Chaves et al., 2002), which then reduces the transpiration and increases the leaf temperature (Blonquist Jr et al., 2009). However, this also reduces the influx of CO_2 into the leaves (Liu et al., 2005), thereby reducing the photosynthesis (Chaves et al., 2002), growth rate, and final yield, which is an intrinsic trade-off mechanism within most drought-tolerant plants (Obidiegwu et al., 2015). The closure of stomata under drought stress is regulated by abscisic acid, a plant hormone that is synthesized in the root tips in response to drought stress (Shahnazari et al., 2007). The plant response to drought stress is likewise dependent on other factors including genotype, drought history, and other environmental conditions (Schulze & Hall, 1982; Tardieu & Simonneau, 1998).

In the DHS treatment, the drought stress component influenced the closure of stomatal aperture in 'Agria', as only partially opened stomata at 34.2% (182.2 of 532.6 stomata/mm^2) was observed, while the rest were closed. On the other hand, 'Taurus' had 7.7% (41.7 of 541.0 stomata/mm^2) and 13.3% (72.0 of 541.0 stomata/mm^2) opened and partially opened stomata, respectively.

In C, stomata from the samples collected in 'Agria' were all closed, while in 'Taurus', they were either closed or partially opened. Stomata are typically open during the day to allow photosynthesis to occur and closed at night to conserve moisture. In C, the incidence of edema could have stressed the plants and triggered the stomates to close to conserve plant water even during the day. The reduced plant moisture status of the control plants can be seen in the reduction of RWC at the second week under stress especially at the vegetative stage. Besides abiotic stress, CO_2 concentration regulates stomatal aperture opening/closing, where high CO_2 concentrations close the stomatal aperture, while low concentrations cause stomata to open (Negi, Hashimoto-Sugimoto, Kusumi, & Iba, 2014).

Another distinct effect of abiotic stress was on stomatal size, that is, area (µm^2) as well as and length and width (µm) (Figure 5.21a and b). Based on statistical analysis, stomatal size was significantly affected by cultivar, abiotic stress treatment, and the interaction of both factors (Appendix 5.15 and 5.16). 'Taurus' had a statistically larger average stomatal area (404.3 µm^2) ($p < 0.001$) than 'Agria' (377.6 µm^2) in C. The stomatal area was significantly reduced under DS but was significantly enlarged under HS, followed by DHS. It is a possibility that the drought stress component in DHS contributed to the reducing effect on stomatal size. DS reduced the stomatal area in 'Agria' by 13.8% (from 377.6 to 325.8 µm^2) and that 'Taurus' by 22.8% (from 404.3 to 312.3 µm^2). HS increased the stomatal area in 'Agria' by 149.2% (from 377.6 to 941.7 µm^2) and that in 'Taurus' only by 86.9% (from 404.3 to 754.8 µm^2). DHS increased the stomatal area in 'Agria' by 73.5% (from 377.6 to 655.7 µm^2) and that in 'Taurus' by only 34.4% (from 404.3 to 533.5 µm^2). The same trend was observed with regard to the effect of abiotic stress on stomatal length and width in 'Agria' and 'Taurus'. The average stomatal length and width are almost the same for 'Taurus' (23.7 and 17.9 µm, respectively) and 'Agria' (24.0 and 18.2 µm, respectively) in C. 'Taurus' had a greater reduction in stomatal length and width than 'Agria' under DS but a lesser increase in stomatal length and width than 'Agria' under HS and DHS. Under DS, the stomatal length and width were reduced in 'Taurus' by 15.2% (from 23.7 to 20.1 µm) and 10.6% (from 17.9 to 16.0 µm), respectively, and in 'Agria' by 6.3% (from 24.0 to 22.5 µm) and 6.6% (from 18.2 to 17.0 µm), respectively. Under HS, the stomatal length and width were increased in 'Taurus' by 27.4% (from 23.7 to 30.2 µm) and 48.0% (from 17.9 to 26.5 µm), respectively, and in 'Agria' by 41.2% (from 24.0 to 33.9 µm) and 68.7% (from 18.2 to 30.7 µm), respectively. Under DHS, the stomatal length and width were increased in 'Taurus' by 11.0% (from 23.7 to 26.3 µm) and 22.3% (from 17.9 to 21.9 µm), respectively, and in 'Agria' by 18.8% (from 24.0 to 28.5 µm) and 40.1% (from 18.2 to 25.5 µm), respectively. A different response was observed in the study of Handayani and Watanabe (2020), who reported that drought, heat, and their combination significantly reduced the size of stomata, i.e., stomatal length and width, and pore length and width. However, the stomata pore width decreased under drought stress.

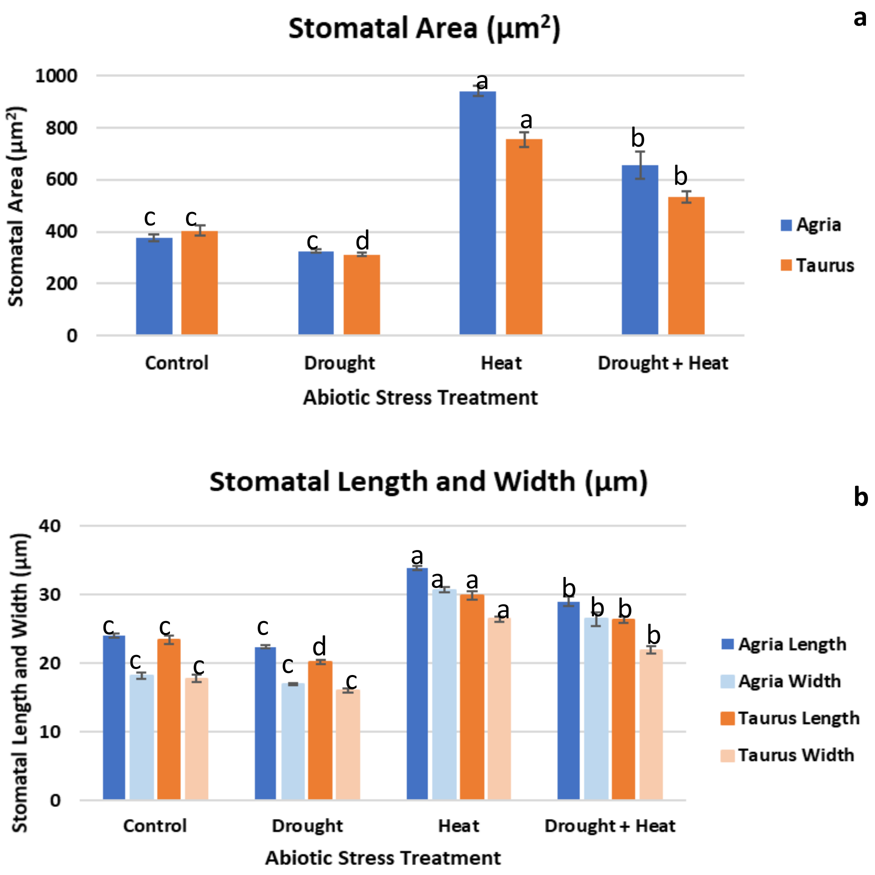


Figure 5.21 Comparison of stomatal (a) area, and (b) length and width between the potato cultivars 'Agria' and 'Taurus' as affected by abiotic stress. The same letters within each variety for stomatal area, and stomatal length and width are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.15 – 5.16.

The increase in stomatal density, partial opening of stomata, and reduction in stomatal size under DS in ‘Taurus’ could mean an enhanced adaptation through stomatal regulation over moisture loss (Jefferies & MacKerron, 1997), better ability to maintain plant water potential during water stress (Levy, Coleman, & Veilleux, 2013), and increased stress avoidance strategy to reduce moisture loss through transpiration (Zhang, 2007). Drought stress also encouraged more but smaller stomata to develop with smaller pore sizes in a potato study conducted by Banik et al. (2016). In another study done by Ristic and Jenks (2002), drought-resistant lines in maize showed higher stomatal density but smaller stomatal apparatus.

5.3.4 Abiotic stress effects on yield and tuber quality of potato crops under controlled environment conditions

5.3.4.1 Abiotic stress effects on yield and tuber quality of potato crops

Abiotic stress (DS, HS, and DHS) at either the vegetative or reproductive stage had significant effects on the different yield and tuber quality parameters of the potato cultivars ‘Agria’ and ‘Taurus’ including the total tuber fresh weight (TFW), marketable tuber fresh weight (MFW), total number of tubers (TNT), and number of marketable tubers (NMT) per pot, and percent dry matter content (DMC) (Figure 5.22 and 5.23, and Appendix 5.17-5.21). In general, TFW and TNT were more affected by abiotic stress at the vegetative stage than at the reproductive stage. This finding could be due to the reduction in the number of tubers formed when crops were exposed to abiotic stress early in their growth stage. In previous studies, heat stress was found to completely inhibit tuber initiation at the early growth stage of the potato crop (Ghosh et al., 2000; Levy et al., 1991). In this trial, the average TFW was lower by about 9.0% at the vegetative stage (871 g) compared with that at the reproductive stage (956 g). The average TNT was lower by 20.9% at the vegetative stage (12.5 tubers/plant) compared with that at the reproductive stage (15.8 tubers/plant). Abiotic stress had a more negative impact on DMC at the reproductive stage than at the vegetative stage. DMC was slightly higher at the vegetative stage (21.2%) than that at the reproductive stage (20.1%). Heat stress can reduce the dry matter partitioning from the above-ground parts (shoot) to the tubers and negatively affect tuber quality by reducing specific gravity (Ghosh et al., 2000), which is closely related to the dry matter content. Drought stress, on the other hand, could hasten haulm senescence (van Loon, 1981) and crop maturity (Robins & Domingo, 1956) that potentially reduces the time for the crop to accumulate dry matter in the tubers compared with that under normal conditions.

No considerable differences were found between 'Agria' and 'Taurus' with regard to the effect of abiotic stress on TFW. Even though 'Taurus' had more substantial TNT per plant than 'Agria', the naturally larger and heavier tubers of 'Agria' compensated for its fewer TNT per plant (Figure 5.24 and 5.25). However, 'Taurus' had higher MFW and NMT than 'Agria' when crops were exposed to abiotic stress at the reproductive stage due to the lower incidence of tuber physiological disorders, as discussed in the succeeding chapters. 'Taurus' also had higher DMC than 'Agria'.

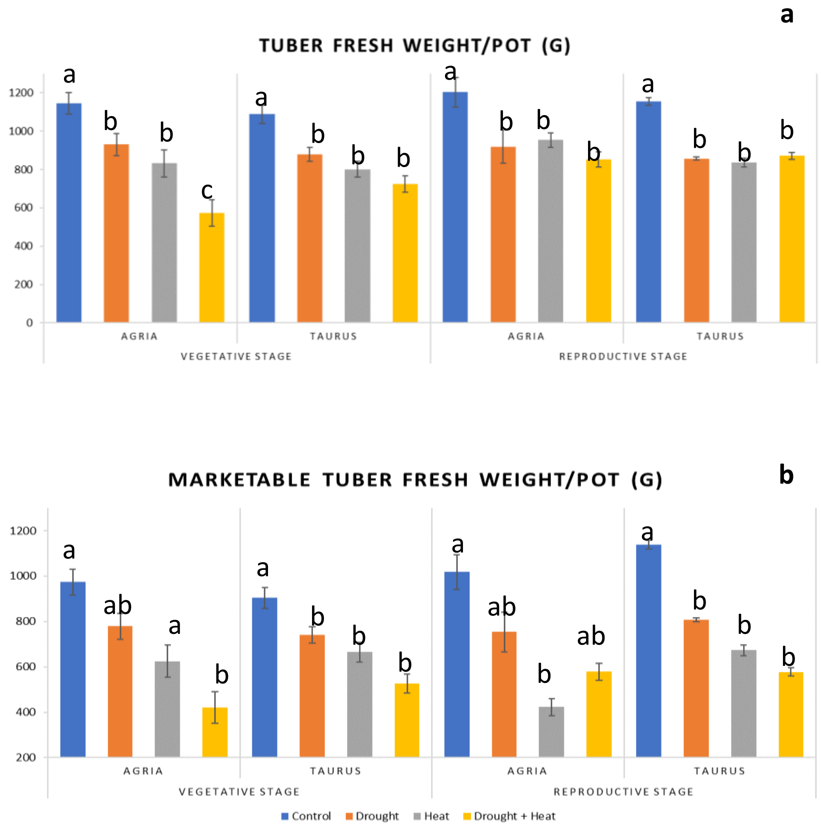


Figure 5.22 Yield parameters (a) total tuber fresh weight, and (b) marketable tuber fresh weight per pot at final harvest (100 DAP) in potato cultivars 'Agria' and 'Taurus' as affected by abiotic stress. The same letters within each variety for tuber fresh weight and marketable tuber fresh weight are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.17 – 5.18.

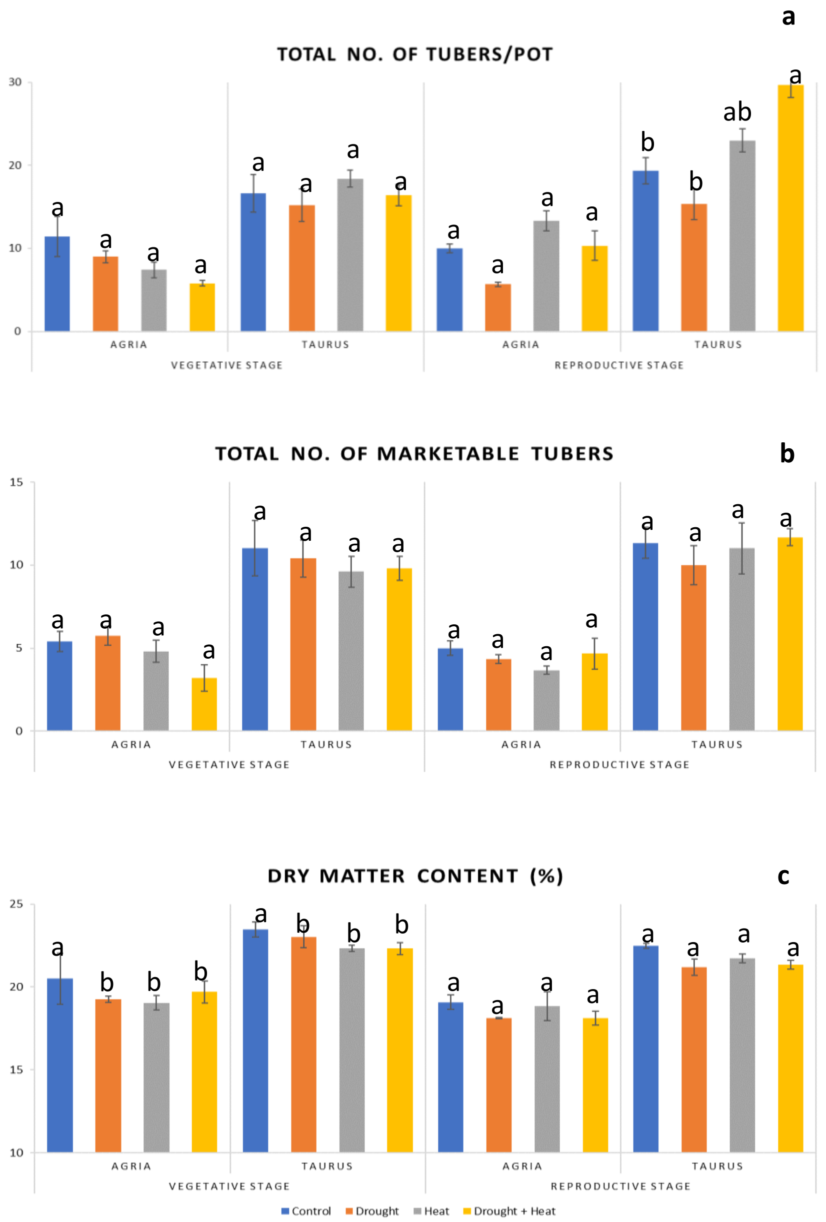


Figure 5.23 (a) Total number of tubers - TNT, (b) total number of marketable tubers NMT, (c) dry mater content -DMC per pot at final harvest (100 DAP) in potato cultivars 'Agria' and 'Taurus' as affected by abiotic stress. The same letters within each variety for the total number of tubers, total number of marketable tubers, and dry matter content are not statistically different (LSD 0.05). Statistical analysis in Appendix 5.19 – 5.21.

The DS treatment had the least reduction in the TFW compared with C in ‘Agria’ at 18.7% (from 1145.0 g to 930.6 g) and in ‘Taurus’ at 19.3% (from 1088.0 g to 877.9 g), followed by HS in ‘Agria’ at 27.4% (from 1145.0 g to 831.5 g) and in ‘Taurus’ at 26.4% (from 1088.0 g to 801.2 g), and DHS had the most reduction in ‘Agria’ at 50.0% (from 1145.0 g to 572.8 g) and in ‘Taurus’ at 33.4% (from 1088.0 g to 724.4 g) at the vegetative stage. The HS treatment had the least reduction in TFW of ‘Agria’ at 20.7% (from 1203.0 g to 953.8 g), while DHS in ‘Taurus’ at 24.6% (from 1156 g to 871.2 g), followed by DS in ‘Agria’ at 23.6% (from 1203.0 g to 919.4 g) and in ‘Taurus’ at 25.9% (from 1156.0 g to 856.8 g). DHS had the most reduction in ‘Agria’ at 29.1% (from 1203.0 g to 852.9 g) and HS in ‘Taurus’ at 27.7% (from 1156.0 g to 835.5 g) at the reproductive stage. Almost the same trend was observed for MTFW in ‘Agria’ and ‘Taurus’. The overall trend showed that DS had the least reduction in MTFW, followed by HS, while the greatest reduction was observed in DHS at the vegetative and reproductive stages. MTFW was particularly low in ‘Agria’ under HS at the reproductive stage due to the cultivar’s apparent susceptibility to second growth, specifically heat sprouts, which made the tubers unmarketable, as observed in the previous season’s field trial.

In general, DS had a negative effect, while HS had a positive effect on TNT. The DHS treatment also reduced TNT, except in ‘Taurus’ at the reproductive stage, wherein TNT significantly increased. According to Deblonde and Ledent (2001), potato plants adapt to water deficit by increasing assimilate partitioning to tubers, producing larger tubers, or developing more tubers. For DMC, no particular trend was observed in the current trial except that abiotic stress reduced the DMC compared with C.

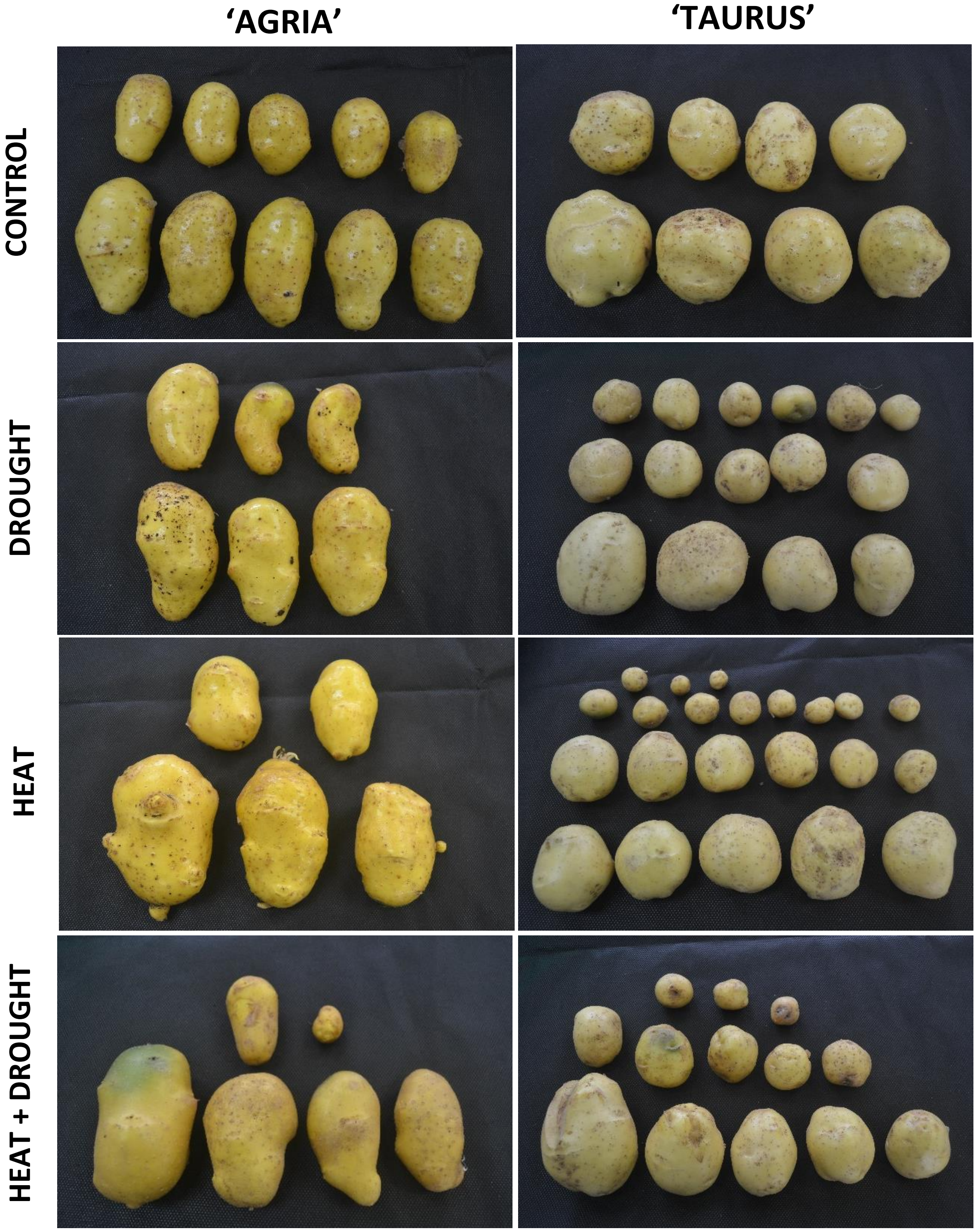


Figure 5.24 Characteristics of potato cultivars 'Agria' and 'Taurus' at 100 DAP, as affected by abiotic stress at the vegetative stage.

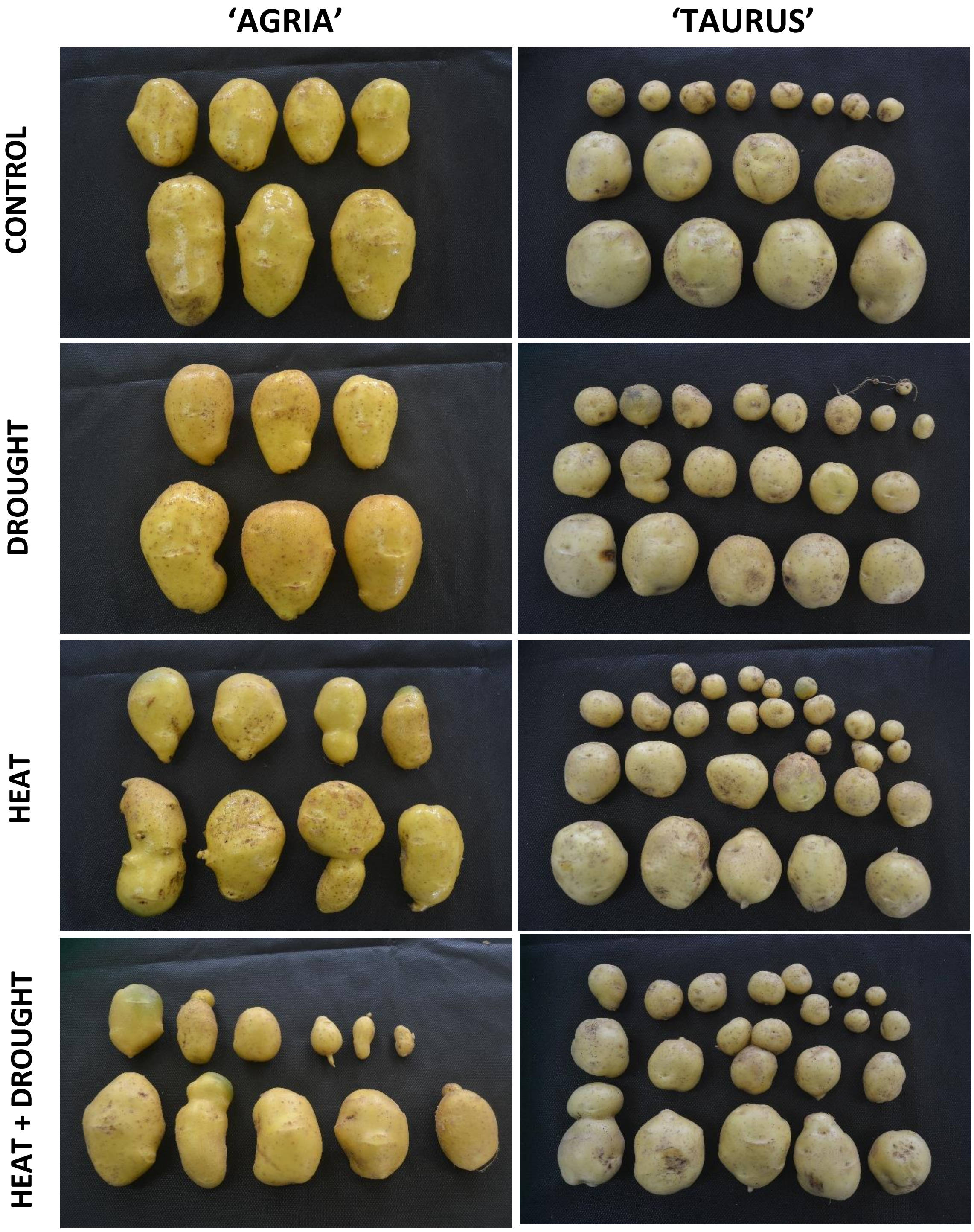


Figure 5.25 Characteristics of potato cultivars 'Agria' and 'Taurus' at 100 DAP, as affected by abiotic stress at the reproductive stage.

5.3.4.2 Abiotic stress effects on tuber size distribution of potato crops

In general, abiotic stress applied at the reproductive stage resulted in smaller tuber sizes than at the vegetative stage (Table 5.1 and Appendix 5.22). This finding can be attributed to the reducing effect of abiotic stress on the bulking of tubers at the reproductive stage. In the study by MacKerron and Jefferies (1988), drought increased the number of small tubers <35 mm and reduced the number of larger tubers >55 mm. The same trend was observed in the study by Shock et al. (1992), where early season water deficit resulted in the formation of larger tubers that are connected to the reduced number of tubers per plant. On the other hand, heat stress reduced the tuber size even among potato cultivars showing heat tolerance (Rykaczewska, 2015).

In the current trial, ‘Agria’ produced more large-sized tubers (>90 mm), while ‘Taurus’ produced more of the table- (51–90 mm), gourmet- (31–50 mm), and undersized (<30 mm) tubers. This finding can be attributed to cultivar characteristics rather than potential abiotic stress effect. The overall trend is that DS increased the number of large-sized tubers and HS increased the number of table-sized tubers in ‘Agria’ and ‘Taurus’; and DHS increased the gourmet- (31–50 mm) and undersized (<30 mm) tubers in ‘Taurus’ but decreased those in ‘Agria’.

Table 5.1 Tuber size distribution of 'Agria' and 'Taurus' at the final harvest at 100 DAP as affected by abiotic stress, drought (D), and heat (H) at vegetative and reproductive growth stages.

Cultivars	Tuber Size Distribution^a							
	Large (>90 mm)***		Table (51–90 mm)**		Gourmet (31–50 mm)^{ns}		Undersize (<30 mm)^{ns}	
	Ave. No./plant	%	Ave. No. /plant	%	Ave. No. /plant	%	Ave. No. /plant	%
'Agria' – Vegetative Growth Stage								
Control	1.4±0.4 bc	12.3	4.4±0.8 a	38.6	2.4±1.4 a	21.1	3.2±1.4 a	28.1
Drought	2.6±0.4 a	28.9	2.6±0.4 a	28.9	1.8±0.2 a	20.0	2.0±0.0 a	22.2
Heat	2.0±0.4 b	27.0	3.4±1.0 a	45.9	0.6±0.2 a	8.1	1.4±0.6 a	18.9
D + H	1.0±0.3 c	17.2	3.0±0.3 a	51.7	0.4±0.0 a	6.9	1.4±0.7 a	24.1
'Taurus' – Vegetative Growth Stage								
Control	0.2±0.2 a	1.2	7.4±1.4 a	44.6	7.2±1.7 a	43.4	1.8±1.1 a	10.8
Drought	0.2±0.2 a	1.3	7.6±0.7 a	50.0	5.0±1.6 a	32.9	2.4±1.0 a	15.8
Heat	0.0±0.0 a	0.0	8.6±1.3 a	46.7	5.0±0.5 a	27.2	4.8±0.8 a	26.1
D + H	0.0±0.0 a	0.0	6.0±0.4 a	36.6	5.4±0.8 a	32.9	5.0±1.1 a	30.5
'Agria' – Reproductive Growth Stage								
Control	2.0±0.0 ab	20.0	5.3±0.7 a	53.3	2.0±0.6 a	20.0	0.7±0.3 a	6.7
Drought	2.0±0.6 ab	35.3	2.7±0.3 a	47.1	1.0±0.6 a	17.6	0.0±0.0 a	0.0
Heat	1.7±0.3 c	12.5	3.3±0.9 a	25.1	3.7±1.5 a	27.6	4.7±0.9 a	35.1
D + H	3.0±0.0 a	29.0	3.3±0.9 a	32.3	1.0±0.6 a	9.7	3.0±1.7 a	29.0
'Taurus' – Reproductive Growth Stage								
Control	0.0±0.0 a	0.0	7.3±0.7 a	37.9	3.7±1.5 a	19.0	8.3±0.7 a	43.1
Drought	0.0±0.0 a	0.0	5.7±0.9 a	37.0	4.7±0.9 a	30.4	5.0±1.2 a	32.6
Heat	0.0±0.0 a	0.0	5.0±1.5 a	21.7	7.3±1.3 a	31.9	10.7±1.5 a	46.4
D + H	0.0±0.0 a	0.0	4.7±0.7 a	15.7	8.0±1.5 a	26.9	17.0±3.0 a	57.2

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

5.3.4.3 Abiotic stress effects on tuber physiological disorders of potato crops

As discussed for the 2018/19 field trial, tuber physiological disorders were observed in the 2019/20 controlled condition trial (Figure 5.26). Tuber physiological disorders were observed in all treatments, including control plants in 'Agria' at the reproductive stage; however, the incidence was intensified by heat and drought stress and their combination (Table 5.2 and Appendix 5.23). In terms of the percent of the total number of tubers, tuber physiological disorders were more frequent when abiotic stress occurred at the vegetative stage than at the reproductive stage. This concurs with the findings of Rykaczewska (2017a), who reported that the most substantial impact of stress was observed in the earlier growth stage of the potato crop. In another study by Rykaczewska (2013), heat stress under favorable soil moisture in the early growth stage of potato crops promoted second-growth formation. In terms of cultivars, 'Taurus' was less susceptible to tuber physiological disorders, as observed in the previous field trials (Salinger, Diamond, Behrens, Fernandez, Fitzharris, Herold, Johnstone, Kerckhoffs, Mullan, Parker, Renwick, Scofield, et al., 2020; Siano, Roskruge, Kerckhoffs, & Sofkova-Bobcheva, 2018) but succumbed more to superficial disorders such as the enlargement of lenticels. On the other hand, 'Agria' was more susceptible to tuber physiological disorders, especially tuber malformation (i.e., knobby, bottleneck, and pointed tubers) and second growth (i.e., heat sprouts and secondary tuber) that greatly affected the tuber quality. In DS, tuber malformation (e.g., knobby and pointed tubers) was the most common tuber physiological disorder at the vegetative (48.9%) and reproductive (47.1%) stages in 'Agria'. In HS, tuber malformation (e.g., knobby, pointed, and bottleneck tubers) and second growth (i.e., heat sprouts) were the most common tuber physiological disorder at the vegetative (48.6% and 40.5%, respectively) and reproductive (62.7% and 12.5%, respectively) stages. The high tuber malformation at the reproductive stage in this trial due to heat stress coincides with the observation of Rykaczewska (2017b). Potato tubers may exhibit various types of malformation depending on the timing of the stress in the growing season, and cultivars with naturally elongated tuber shape are more prone to tuber malformation (Potatoes South Africa, 2016).

In DHS, tuber malformation (e.g., knobby and pointed tubers) was also the most common tuber physiological disorder at the vegetative (69.0%) and reproductive (48.4%) stages in 'Agria'. According to Hillerm and Thornton (2008), tuber malformation is caused by either moisture or heat stress that impedes tuber growth through various ways, such as reduced growth rate, increased respiration, decreased cell division, deviated hormone levels, and reduced carbohydrates. Besides heat and moisture stress, nutrient shortage may also play a part, but each of the factors mentioned above can cause tuber malformation (Potatoes South Africa, 2016).

Figure 5.26 Tuber physiological disorders observed in the glasshouse and plant growth chamber trial in potato cultivar ‘Agria’: (a) tuber malformation (i.e. knobby tuber), (b) second growth (i.e. heat sprout), (c) tuber malformations (combination of knobby, bottleneck, and pointed tubers); and in ‘Taurus’: (d) tuber malformations (bottleneck tubers) and second growth (secondary tubers) as affected by abiotic stress.

In earlier studies, second growth (e.g., heat sprouts, tuber chaining or gemmation, and secondary tubers) was induced by high temperature (28 °C) regardless of soil moisture but not by drought stress (Bodlaender, Lugt, & Marinus, 1964). Moreover, prolonged exposure to high atmospheric temperatures increased the number of secondary tubers compared with a shorter period of exposure (Bodlaender et al., 1964). In another study, heat sprout or preharvest sprouting was enhanced by heat and drought stresses, with variability among cultivars (Levy, 1986). Shock et al. (1992) suggested that preharvest tuber sprouting is an indirect effect of incomplete canopy coverage due to drought stress. The incomplete canopy coverage in field studies exposes the soil to a very high temperature, which then increases the soil temperature, breaks the dormancy of tubers (Bodlaender et al., 1964), and promotes sprout development. Preharvest sprouting in this trial could have been caused by the exposure of the potato plants to high atmospheric temperatures inside the glasshouse at its later growth stages. Rykaczewska (2017a) observed that preharvest sprouting was more distinct when heat stress was applied at the beginning of plant maturity. On the other hand, frequent watering to achieve the optimum moisture level (following the two-week abiotic stress treatment) might have promoted the incidence of enlargement of lenticels in almost all treatments in ‘Agria’ and ‘Taurus’. ‘Agria’ was more susceptible to the enlargement of lenticels than ‘Taurus’.

Table 5.2 Tuber physiological disorders in 'Agria' and 'Taurus' as affected by abiotic stress at vegetative and reproductive growth stages.

Treatments	Tuber Physiological Disorders					
	Tuber Malformation		Second Growth		Enlarged Lenticels	
	Ave. No.	%	Ave. No.	%	Ave. No.	%
			'Agria' – Vegetative			
Control	0.0±0.0 b	0.0	0.0±0.0 c	0.0	5.0±0.8 a	43.9
Drought	4.4±0.9 a	48.9	0.0±0.0 c	0.0	3.0±0.4 ab	33.3
Heat	3.6±0.4 a	48.6	3.0±0.3 a	40.5	5.0±0.6 a	67.6
D + H	4.0±0.8 a	69.0	1.4±0.4 b	24.1	1.4±0.2 b	24.1
			'Taurus' – Vegetative			
Control	0.0±0.0 a	0.0	0.0±0.0 a	0.0	6.0±0.8 a	36.1
Drought	1.8±0.6 a	11.8	0.0±0.0 a	0.0	4.2±1.0 ab	27.6
Heat	0.0±0.0 a	0.0	0.0±0.0 a	0.0	5.2±1.1 a	28.3
D + H	2.0±0.4 a	12.2	0.0±0.0 a	0.0	1.8±1.1 b	11.0
			'Agria' – Reproductive			
Control	3.7±0.3 b	36.7	0.0±0.0 b	0.0	3.0±0.6 a	30.0
Drought	2.7±0.7 b	47.1	0.0±0.0 b	0.0	1.7±0.3 a	29.4
Heat	8.3±1.0 a	62.7	1.7±0.7 a	12.5	4.0±0.0 a	30.1
D + H	5.0±0.6 b	48.4	0.0±0.0 b	0.0	1.0±1.0 a	9.7
			'Taurus' – Reproductive			
Control	0.0±0.0 b	0.0	0.0±0.0 a	0.0	3.3±0.9 ab	17.2
Drought	1.3±0.0 ab	8.7	0.0±0.0 a	0.0	6.0±1.5 a	39.1
Heat	4.0±1.2 a	17.4	0.0±0.0 a	0.0	6.3±1.5 a	27.5
D + H	2.0±1.0 ab	6.7	0.0±0.0 a	0.0	0.0±0.0 b	0.0

Means ± standard error are presented; Different letters in a column within each trial site and each cultivar indicate means are statistically different on Tukey's HSD test (P ≤ 0.05.

5.4 Summary and conclusions

This study compared the yield and morpho-physiological responses of two selected commercial potato cultivars (‘Agria’ and ‘Taurus’) known to have susceptibility and tolerance to abiotic stress (based on the results from the 2018/19 multi-environment trial) with a focus on drought, heat, and their combination under controlled environment conditions in a glasshouse and plant growth chamber. The morpho-physiological characteristics of the two cultivars that contributed to either susceptibility or tolerance to abiotic stress were closely examined in relation to the final yield and several other physiological growth parameters.

The cultivar ‘Taurus’ exhibited various morpho-agronomic characteristics and physiological functions that may have contributed to its apparent abiotic stress tolerance in contrast to the reference cultivar ‘Agria’. These include its non-susceptibility to leaf curling, a form of wilting potentially due to the declined leaf water and turgor potential; higher number of leaves (18.6%) and percent canopy cover (51.9%) that may enhance photosynthetic capacity; and reduced transpiration rate (E) and stomatal conductance (g_S) but higher net photosynthesis (P_N) (under heat stress). This result illustrates the capacity of ‘Taurus’ to respond efficiently to HS by controlling the E and g_S while improving P_N. Moreover, ‘Taurus’ had relatively higher RWC by 1.0%–4.2% and ψ_L by 40%–150% and was less affected by abiotic stress that may have physiological advantages, because this allows turgor-dependent processes, e.g., growth, stomatal functions and maintenance of the photosystem complex. Furthermore, ‘Taurus’ may have adapted its natural leaf surface morphology, i.e., stomatal and trichome characteristics, as an adaptive mechanism that contributed to its abiotic stress tolerance. ‘Taurus’ had significantly greater glandular trichome density (45.1%) that is involved in the secretion of specialized metabolites that contribute to the plant’s increased fitness to the environment. Under abiotic stress, especially under drought stress, ‘Taurus’ produced significantly higher glandular (47.7%) and non-glandular (6.0%) trichomes than ‘Agria’. On stomatal characteristics, ‘Taurus’ developed denser but smaller stomatal size, i.e., area, length, and width in response to abiotic stress. Under non-stressed conditions, ‘Taurus’ had 12.3% higher stomatal density, although this was not statistically different from ‘Agria’. ‘Taurus’ also could reduce the stomatal area, length, and width by 22.7%, 15.2%, and 10.6%, respectively, in response to DS potentially to conserve moisture.

Under HS, 20.6% of the stomata were partially opened in 'Taurus', which according to Nobel (1991) can enhance water use efficiency (WUE) by permitting the entry of CO_2 while minimizing water loss through transpiration under drought stress. These different morpho-physiological characteristics may have contributed to the better adaptation of 'Taurus' to abiotic stress, hence, maintaining its yield and tuber quality in comparison with 'Agria'.

An abiotic stress-tolerant cultivar reduces the size of the stomata and keeps the opening partially open under stress conditions; under heat stress, it increases the size of stomata but is kept partially open to conserve moisture loss through transpiration. Under DHS, it produces large stomata but is kept close. Susceptible cultivars could not reduce the size of stomata in response to drought stress and have to shut the stomata to conserve moisture. They respond to heat stress by producing enlarged stomata that are kept open to reduce heat but may lead to excessive moisture loss. Under DHS, it produces large stomata that are partially open, which could be its response to the heat component of the treatment.

Drought stress (DS) generally caused reductions in plant height, number of leaves, and canopy cover. With regard to the leaf surface morphology, glandular and non-glandular trichome formation was enhanced, and more but smaller stomata were developed under DS. In this experiment, DS stimulated the closing of the stomatal aperture to potentially reduce water loss. On physiological parameters, DS reduced the net photosynthesis (P_N), transpiration rate (E), and stomatal conductance (g_S).

Heat stress (HS) increased the development of the aboveground plant parts, including the plant height and percent canopy cover, and increased the number of leaves. Its effect on glandular trichome formation differed depending on the cultivar, while it increased the non-glandular trichome formation but was not as enhanced as in the DS. HS enhanced the stomatal formation more than DS and developed even larger stomata. HS also stimulated stomatal opening, thereby increasing E and g_S. On the other hand, the combination of drought and heat stress exacerbated the negative effects on the different morpho-physiological parameters brought about by each stress.

Based on the results of this controlled environment, 'Taurus' also performed better than 'Agria' in terms of the volume of marketable tuber fresh weight (MFW) and the number of marketable tubers (NMT) when crops were exposed to the different abiotic stresses. This was attributed to the lower incidence of tuber physiological disorders in ‘Taurus’, hence, the lower volume of unmarketable tubers. ‘Agria’ was more susceptible to tuber physiological disorders, especially tuber malformation and second growth, which greatly affected the tuber quality. These tuber physiological disorders are caused by either moisture or heat stress that impedes tuber growth through various ways such as reduced growth rate, increased respiration, decreased cell division, deviated hormone levels, and reduced carbohydrates (Hillerm & Thornton, 2008).

CHAPTER 6

General Discussion and Conclusion

Potato remains the top vegetable crop of New Zealand in terms of volume produced and area planted. It is also the fifth highest horticultural export product of New Zealand valued, after kiwifruit, grape wine, apples, and onions. Being a temperate crop, potato is affected by current fluctuations in different climate factors expressing increasing periods of extreme temperatures and rainfall events. In the latest IPCC report (Reisinger et al., 2014), New Zealand is already experiencing climate change with projected long-term trends toward higher temperatures and shifting rainfall patterns. The variation in local climate patterns exacerbated by climate change significantly affects potato marketable yield and tuber quality.

The expected direct impact of climate change on global potato production is mainly on the reduction of crop yield. At present, there is a paucity of studies done on the effect of abiotic stress (e.g., drought and heat stress) often associated with climate change on the cropping performance, tuber yield, and tuber quality of commercial potato cultivars in New Zealand. Climate change is unequivocal, and the effects of abiotic stress commonly associated with climate change such as heat, moisture, and their combination on the development of potato crops have been the topic of this study. In several field trials, the influence of the environment on yield variation of potato crops was significant. Under experimental and production conditions, environmental factors significantly contributed to the variability of the potato crop yield by 20%–60% and 40%–80%, respectively (Kalbarczyk, 2004). In another study, the variation in potato yield due to the environment was 40% (Trawczynski, 2009).

The literature review in Chapter 2 highlights the potential effects of different abiotic stresses commonly associated with climate change, such as drought, heat, and their combinations, on potato production. Abiotic stress is estimated to cause about 70% of yield loss in crop production (Acquaah, 2012). Adaptation strategies can provide about 10%–15% yield advantage over situations without adaptation strategies (Lotze-Campen, 2011); hence, it is crucial to alleviate the negative impacts of climate change on potato production. Adaptation strategies can be categorized as either agronomic or genetic. Agronomic options include shifting of planting schedules and adjustments in crop rotation, water management, and irrigation. While genetic options involve the introduction of new cultivars with better tolerance to heat, moisture, and salinity stresses. According to George et al. (2017), the characteristics of prospective potato cultivar ideotype include: (1) early maturing to avoid heat and drought stress late in the season, (2) capable of rapid canopy growth and closure for maximum photosynthesis, (3) capable of efficiently using water and carbon per unit of water used, and (4) maintains tuberization even under heat, moisture, and salinity stress.

This can be achieved through breeding and selection of new elite cultivars. Before releasing a new cultivar, genotypes of high potential are typically evaluated at different locations over several years to determine the degree of adaptation (Acquaah, 2012). Multilocation trial is a practice used to evaluate such cultivars or strains (Piepho, 1996).

Given the unique environmental and climatic conditions of New Zealand alongside already identified issues related to climate change, limited studies were done to quantify and qualify the potential effects of abiotic stress associated with climate change on existing potato cultivars. Thus, it is crucial to address these knowledge gaps that can contribute to improved climate change resilience of the New Zealand potato industry.

6.1 Climate change in New Zealand potato production system

Climate change is expected to have an impact on potato production by reducing crop yield and associated yield components. The global potato production under climate change is estimated to decrease by 18%–32% (without adaptations) and by 9%–18% (with adaptations) (Hijmans, 2003). In the latest IPCC report (Reisinger et al., 2014), New Zealand has warmed by about 0.9 °C since the 1900s and the temperature is expected to keep rising throughout this century by about 3.5 °C above the 1986–2005 average under high-carbon emission scenario. The major potato production areas in New Zealand would either experience extreme heat and water scarcity or excessive rain in the coming years (New Zealand Climate Change Centre, 2014).

The analysis of the baseline data collection activity in Chapter 3 focused on the analysis of secondary climate and weather data including the mean temperature and total rainfall in the past 60 years (1958–2018) during the potato growing months (October to March) in the trial sites including Ohakune, Opiki, and Hastings, representing the three major potato production areas in New Zealand. A general increasing trend for temperature but a decreasing trend for rainfall were observed. Moreover, the comparison of the mean temperature and total rainfall in the last 30 years (1988–2017) and the previous 30 years (1958–1987) during the potato growing months showed variability among the trial sites. The average temperature showed an increasing trend across the trial sites, with Ohakune having the highest increase, agreeing with the projection of the Ministry for the Environment (2016) that warming in New Zealand will be the most significant at higher elevations. The total rainfall was significantly reduced in Hastings, consistent with the IPCC report that reduced soil moisture will be experienced in many parts of eastern New Zealand (Reisinger et al., 2014).

The atmospheric temperature recorded during the 2017/18 potato growing season across the trial sites of the baseline data set showed an above-historical average (1981–2010) trend. Across the trial sites, mid-summer (January 2018) was the hottest month with an average increase in all temperature parameters (average, maximum, and minimum temperatures) in Ohakune, Opiki, and Hastings. According to NIWA (2018a), the 2017/18 summer was New Zealand's hottest summer on record, which is 2.1 °C above the 1981–2010 average, based on NIWA's seven-station temperature series. Similar observations were recorded during the multi-environment trial in Chapter 4 during the 2018/19 potato growing season. Distinct variations and extreme weather patterns were observed in each of the three trial sites, and the daily maximum temperature was more affected than the average and minimum temperatures. The 2018/19 summer was the third hottest summer recorded (after 2017/18 and 1934/35) in New Zealand (NIWA, 2020b). The national average temperature for the 2018/19 summer was recorded at 17.9 °C that is 1.2 °C above the 1981–2010 average, based on NIWA's seven-station temperature series that began in 1909 (NIWA, 2020b).

The abnormal increase in atmospheric temperature during the 2017/18 and 2018/19 potato growing seasons resulted in the increase in the number of days with supra-optimal temperatures for potato crops that are believed to delay (>25 °C) (Levy & Veilleux, 2007) or even inhibit (>30 °C) tuber growth (FAO, 2008c). In the 2017/18 growing season, the highest number of days with supra-optimal temperatures was recorded in Hastings at 57 days, with 10 days reaching temperatures >30 °C. This was followed by Opiki at 56 days with only a day recorded with temperature >30 °C. The least number of days with supra-optimal temperatures was recorded in Ohakune, with 21 days without any day reaching temperature >30 °C. In the 2018/19 growing season, the highest number of days with supra-optimal temperatures was recorded in Opiki at 103 days, with 24 days reaching temperatures >30 °C. This was followed by Hastings at 49 days, with 8 days recorded with temperatures >30 °C. The least number of days with supra-optimal temperatures was again recorded in Ohakune at 20 days, with only a day recorded with temperature >30 °C. Supra-optimal temperatures lasted for 2–6 hours in the Ohakune trial site, 6–11 hours in the Opiki trial site, and 7–12 hours in the Hastings trial site at any given day when extreme or elevated atmospheric temperatures occurred.

The increase in temperature was distinct during the summer months of December, January, and February. In contrast, rainfall in the trial sites during the 2017/18 growing season was all below the historical 30-year average (1981–2010). The most considerable rainfall reduction was detected in the eastern (Hastings) and northern (Ohakune) regions of the North Island.

6.2 Abiotic stress effects on morpho-agronomic and physiological characteristics of potato

The results of the baseline data collection, multi-environment trial, and controlled environment trials described in Chapters 3, 4, and 5, respectively, established that abiotic stresses associated with climate change such as drought, heat, and their combination had a significant influence on the morpho-agronomic characteristics and physiological functions of potato crops and could potentially affect the marketable yield and tuber quality.

6.2.1 Effects of abiotic stress on potato morpho-agronomic characteristics

In the 2018/19 growing season, based on the multi environmental trial (MET) described in Chapter 4, the heat stress due to extreme weather conditions was aggravated by mesh covering practice as a physical barrier to manage the tomato-potato psyllid or TPP in the organic Hastings trial site, resulting in increases in plant height, whole plant leaf area, and number of stems per plant. This is accompanied by the increase in the dry matter content of the haulm and roots, suggesting an enhanced dry matter partitioning to the haulm and thus promoting vegetative growth (Levy & Veilleux, 2007). Younger leaves could compete better for limited assimilates due to their proximity to source leaves (Marinus & Bodlaender, 1975). Stem diameter, however, was the smallest in Hastings. This decrease in stem diameter could be attributed to the relatively rapid vegetative growth, leading to the development of slender plants in the process. Conversely, the drier conditions in Opiki reduced the plant height, whole plant leaf area, and number of stems per plant. Either or both the lowered leaf water potential that acts as a hydraulic signal and the hormonal signals (abscisic acid) produced in the root tips of potato crops may reduce the leaf area expansion under drought conditions (Shahnazari, Liu, Andersen, Jacobsen, & Jensen, 2007). Stem diameter was the thickest in Opiki, a typical response of crops under drought stress. In other crop species, stem diameter was enhanced as a plant response to drought stress by accumulating assimilates and conserving water into the stem (Ohashi, Nakayama, Saneoka, Mohapatra, & Fujita, 2008).

The MET findings in the 2018/19 growing season are consistent with the results obtained in the 2019/20 glasshouse trial, where individual potato plants were exposed to abiotic stress treatments simulated in a controlled plant growth chamber. The drought stress generally caused the reduction in plant height, number of leaves, and canopy cover; furthermore, the drought and heat stress combination exacerbated these negative effects. The heat stress increased the plant height, percent canopy cover, and number of leaves. Another distinct morphological characteristic observed under heat stress was the development of numerous but smaller leaves that could have contributed to the increase in percent canopy cover.

The heat stress in the Hastings trial site resulted in the increase in haulm and root DMC, relative to the Ohakune trial site. However, the stem diameter was reduced in Hastings compared with that in the Ohakune trial site. In contrast, the hot and drier conditions of Opiki reduced the plant height and total plant leaf area but increased the stem diameter and root DMC. Drought stress reduced the maximum leaf area index of potato crops in the field and in the greenhouse (Lahlou et al., 2003).

In terms of the cultivar influence, significant variation was observed in the morphological responses of the potato cultivars to abiotic stress in the MET. Across the sites, 'Fianna' seemed to have the most considerable vigor in terms of plant height and stem diameter but had the least number of stems per plant. On the other hand, 'Hermes' had the highest number of stems per plant and total plant leaf area, while 'Taurus' had the highest dry matter content of haulm and roots. Based on these results, ‘Taurus’, which had potential abiotic stress tolerance across multiple environments, was further tested under controlled conditions in a glasshouse and plant growth chamber alongside cultivar ‘Agria’ as a reference cultivar. In the glasshouse trial, less variation in morpho-agronomic characteristics was observed as influenced by the different abiotic stress treatments in ‘Taurus’ than in ‘Agria’.

In Chapter 5, in the controlled environment experiment, upon close examination of the abiotic stress-treated potato leaf samples observed under a scanning electron microscope, distinct changes in the leaf surface morphology were detected with regard to stomatal and trichome characteristics. Drought stress (DS) generally enhanced the glandular and non-glandular (leaf hairs) trichome formation and produced more but smaller stomata. DS also stimulated the closing of the stomatal aperture, thereby potentially reducing the water loss. The effect of heat stress (HS) on glandular trichome formation differed depending on the cultivar, while it increased the non-glandular trichome formation but was not as enhanced as in the DS treatment. HS enhanced the formation of stomata more than in DS and developed even larger stomatal apertures. HS also stimulated the opening of the stomata potentially as a thermoregulation adaptive mechanism of the plant. The combination of drought and heat stress exacerbated the negative effects on the different morpho-physiological parameters brought about by each stress.

‘Taurus’ may have natural leaf surface morphology, i.e., stomatal and trichome characteristics, and adaptive mechanisms that contributed to its abiotic stress tolerance. ‘Taurus’ had significantly greater glandular trichome density that is involved in the secretion of specialized metabolites that contribute to the plant’s increased fitness to the environment. Under abiotic stress, especially under drought stress, ‘Taurus’ produced significantly higher glandular and non-glandular trichomes than ‘Agria’. On stomatal characteristics, ‘Taurus’ developed denser but smaller stomatal size, i.e., area, length, and width, in response to abiotic stress. ‘Taurus’ partially opened the stomata under stress conditions, which according to Nobel (1991) could enhance the water use efficiency (WUE) by permitting the influx of CO_2 while minimizing water loss through transpiration under drought stress. These different morpho-physiological characteristics may have contributed to the adaptation of 'Taurus' to abiotic stress, leading to its ability to maintain its yield and tuber quality.

6.2.2 Effects of abiotic stress on potato physiological characteristics

In the baseline data collection in Chapter 3, abiotic stress experienced during the 2017/18 growing season may have a significant influence on the different physiological functions of the potato crop and could be responsible for the reduction in yield and tuber quality. This assumption was validated in the multi-environment trial (MET) in the following 2018/19 season in Chapter 4. Coincidently, both growing seasons were featured as the first and third hottest year on record in New Zealand. Physiological parameters measured during the MET including net photosynthesis, transpiration rate, and stomatal conductance were significantly affected by abiotic stresses in the environment during the 2018/19 season. The elevated temperatures or heat stress (HS) in the Hastings trial site increased the transpiration rate and stomatal conductance and reduced the net photosynthesis. In the water-deficit or drought-stressed (DS) Opiki trial site, the transpiration rate (E) and stomatal conductance (g_S) increased, whereas the net photosynthesis (P_N) decreased.

A similar result was observed on the effect of HS on the physiological parameters in the controlled environment conditions trial in Chapter 5. HS also had positive effects on the different physiological parameters, but the effects were observed to be cultivar-dependent. HS enhanced the E and g_S and therefore improved P_N in 'Agria' and 'Taurus'. 'Taurus' had greater g_S and E, resulting in higher P_N.

These findings are consistent with the results of previous studies whereby elevated atmospheric temperatures impaired the crop's photosynthetic activity in source leaves and increased the transpiration rate and stomatal conductance (Hammes & De Jager, 1990; Hastilestari et al., 2018; Reynolds et al., 1990; Wolf et al., 1990). Burton (1981) suggested that for every 5 °C rise in the leaf temperature of European potato cultivars above the optimum (20.0 °), the photosynthetic rate decreases by 25%. Besides the negative impact of high temperature on photosynthesis, higher leaf temperatures affected photosynthate allocation, shifting away from the developing tubers toward the vegetative organs (Hastilestari et al., 2018).

6.3 Abiotic stress effects on yield and tuber quality

The effects of abiotic stress on the morpho-agronomic characteristics and physiological functions of the potato crop ultimately impact the final yield and tuber quality. In the baseline data collection, multi-environment trial, and glasshouse trial, significant yield losses due to reduced quality of tubers were observed. However, considerable variability in terms of yield response to abiotic stress effects among the tested commercial potato cultivars was also noted.

6.3.1 Tuber yield and quality

As observed in the 2017/18 growing season baseline data in Chapter 3, the tuber yield was the highest in Ohakune, where the temperature and rainfall were close to the optimum levels for potato growth and development. The tuber yield was significantly lower in the Opiki and Hastings trial sites, where drought and a more significant number of days with supra-optimal atmospheric temperatures >25 °C and >30 °C were experienced, which were believed to either delay or inhibit tuber growth, combined with supra-optimal soil temperatures >18 °C recorded. This result was validated in the detailed multi-environment trial in Chapter 4. The total and marketable yield, number of tubers per plant, harvest index (HI), dry matter content (DMC) content, and specific gravity (SG) were the highest in Ohakune as compared with the hot and hot and dry environment of the Hastings and Opiki trial sites, respectively, during the 2018/19 growing season. The total yield was reduced by more than 40% in the Hastings and Opiki trial sites.

In the controlled environment trial in Chapter 5, the tuber fresh weight and total number of tubers were negatively affected by abiotic stress due to the reduction in the number of tubers formed especially when exposed early in their growth stage. In previous studies, heat stress was found to completely inhibit tuber initiation at the early growth stage of the potato crop (Ghosh et al., 2000; Levy et al., 1991).

The decline in tuber yield was primarily attributed to the reduction in photosynthetic activity, especially under heat stress. Burton (1981) cited that for every 5 °C rise in leaf temperature above the optimum, a 25% reduction in the rate of photosynthesis was observed. Heat stress also impairs water use efficiency (Guoju et al., 2013) and enhances dry matter partitioning to the haulm, thereby promoting vegetative growth over tuber development (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018). Therefore, fresh tuber weight, dry weight, dry matter, and harvest index (Ghosh et al., 2000; Hancock et al., 2014; Hastilestari et al., 2018) decrease, eventually reducing the final yield. By contrast, plants grown under drought stress have lower stomatal conductance, which conserves and maintains an adequate leaf water status, thereby reducing leaf internal CO_2 concentration and photosynthesis (Chaves et al., 2002). Additionally, faster accumulation of growing degree days (GDD) was observed in Opiki and Hastings, which could have resulted in faster plant development and therefore earlier maturity of plants but lesser time for tuber bulking.

Another major cause of tuber yield decline was the high volume of unmarketable tubers exhibiting an array of tuber physiological disorders, as discussed in the succeeding section. Data gathered from randomly collected potato tubers from the different trial sites revealed that yield was primarily affected by the increase in the volume of defective or unmarketable tubers. Unmarketable tubers could reach as high as 85% of the total volume of tubers collected. The increase in the volume of unmarketable tubers is primarily due to the incidence of a wide array of underlying tuber physiological disorders such as enlarged lenticels, growth cracks, netting, malformations, and pre-harvest sprouting. The initial findings showed clearly that commercial potato cultivars have differential susceptibility to abiotic stress and related tuber physiological disorders. Tubers of ‘Nadine’, ‘Snowden’, and ‘Taurus’ showed the least defects, while ‘Fianna’, ‘Hermes’, ‘Agria’, ‘Vivaldi’, ‘Victoria’, and ‘Moonlight’ exhibited greater susceptibility.

6.3.2 Tuber size distribution

In the baseline data described in Chapter 3, there seemed to be no clear effects of drought or heat stress in Opiki and Hastings on the reduction of tuber size in the 2017/18 growing season. However, according to the grower in Opiki, usually, there are 8–10 tubers produced per plant, but since the potato crops were exposed to drought and heat stress during the tuber initiation stage, only 2–6 tubers per plant were formed.

The MET described in Chapter 4 showed a significant reduction in the percentage of large, table-, and gourmet-sized tubers in the hot and the hot and dry conditions of Hastings and Opiki, respectively, when compared with the Ohakune trial site with cooler conditions. This was validated in the controlled environment trial in Chapter 5, where abiotic stress caused the development of smaller tuber size distribution especially when the stress was applied at the reproductive stage. This can be attributed to the reducing effect of abiotic stress on the bulking of tubers at the reproductive stage. In the study by MacKerron and Jefferies (1988), drought increased the number of small tubers <35 mm and reduced the number of larger tubers >55 mm. Similar results were observed in the study by Shock et al. (1992), who reported that early season water deficit resulted in the formation of larger tubers that are connected to a reduced number of tubers per plant. In another study conducted by Aliche et al. (2018), drought stress resulted in the downshifting of tuber sizes; the more severe the drought condition is, the lesser number of large tubers are. On the other hand, heat stress reduced the tuber size even among the potato cultivars showing heat tolerance (Rykaczewska, 2015).

6.3.3 Tuber physiological disorders

In the baseline data in Chapter 3, as high as 85% of the tubers collected in a particular cultivar (i.e., 'Moonlight') were unmarketable due to the very high incidence of a wide array of tuber physiological disorders such as enlarged lenticels, growth cracks, netting, malformations, and pre-harvest sprouting. The literature strongly suggests that many tuber physiological disorders are influenced by unfavorable environmental factors, including air and soil temperature, rainfall, and humidity (Hiller et al., 1985; Lugt et al., 1964; Rykaczewska, 2015b, 2017b). Moreover, the changing pattern and increasing incidence of extreme weather events promoted the incidence of tuber physiological disorders in the potato field during the 2018/19 and 2019/20 seasons. The type and severity of tuber physiological disorders were greater under heat stress in Hastings and under combined drought and heat stress in Opiki as compared with an area with close to the optimum water and temperature levels for potato growth and development in Ohakune.

In the MET in Chapter 4, the results of the baseline data collection were validated, where the environment or trial sites significantly affected the occurrence of tuber physiological disorders at final harvest (130DAP) during the 2018/19 growing season. The occurrence of a particular type or type of tuber physiological disorder depends on the environment and types of abiotic stress present during the growing season. In the cooler environment of the Ohakune, feathering, which is characterized by having a thin skin that can easily be torn at harvest and during handling, was the most common physiological disorder. The probable cause of the feathering of tubers in Ohakune was the slower GDD (growing degree days) accumulation rate due to the relatively cooler environment during the growing season. In the hotter conditions of Opiki, growth cracks and second growth were the greatest tuber physiological disorders recorded. The arid spring (October–November 2018) followed by a very wet early summer (December 2018) that was almost 100% above the historical average rainfall may have encouraged the growth crack formation of tubers. The moisture stress combined with supra-optimal temperatures (>25 °C) that was 3 °C–6°C higher than the historical average during the summer months (December 2018–February 2019) may have caused the premature breaking of tuber dormancy, resulting in second-growth formation, e.g., heat sprouts, chain tubers, and secondary tuber formation. According to Levy (1986), heat and drought stresses may enhance tuber preharvest sprouting, but there could be variability among cultivars depending on the physiological status of the seed tubers. Shock et al. (1992) also suggested that preharvest tuber sprouting can be an indirect effect of incomplete canopy coverage, which exposes the soil to a very high temperature, thereby increasing its temperature and inducing heat sprouting. In the Hastings trial site, the most common tuber physiological disorder observed was the enlargement of lenticels and second growth potentially caused by the extremely high atmospheric temperatures (>25 °C). This was aggravated by the mesh covering practice as a physical barrier to manage TPP pest occurrence and additional irrigation necessary to manage the temperature extremes in the Hastings trial site. Frequent and heavy irrigation resulted in waterlogging and heavy soils that promoted the enlargement of lenticels on the tuber surface. In the Opiki trial site, the moisture stress combined with elevated temperatures caused the pre-mature breaking of tuber dormancy and resulted in the second-growth formation, e.g., heat sprouts, chain tubers, and secondary tuber formation as seen in the Hastings trial site.

In the controlled environment trial in Chapter 5, tuber physiological disorders were observed in all abiotic stress treatments (i.e., drought, heat, and drought + heat), including control plants in the cultivar ‘Agria’ at the reproductive stage; however, the incidence was aggravated by heat and drought stress treatments. In terms of the percent of the total number of tubers, tuber physiological disorders were more frequent when abiotic stress occurred at the vegetative stage than at the reproductive stage. This concurs with the findings of Rykaczewska (2017a), who stated that the most substantial impact of stress occurred in the earlier growth stage of the potato crop.

Differential susceptibility was evident among the cultivars in response to abiotic stress and associated tuber physiological disorders. In the baseline data collected, cultivars ‘Nadine’, ‘Snowden’, and ‘Taurus’ showed the least defects even under adverse environmental conditions, while ‘Fianna’, ‘Hermes’, ‘Agria’, ‘Vivaldi’, ‘Victoria’, and ‘Moonlight’ exhibited greater susceptibility. In the multi-environment trial, the tested cultivars that showed relative tolerance or susceptibility to tuber physiological disorders were arranged in the following order of tolerance: ‘Taurus’ > ‘Snowden’ > ‘Hermes’; while the following order of susceptibility: ‘Agria’ > ‘Ilam Hardy’ > ‘Rua’ > ‘Fianna’.

6.4 Genotype x environment

The differential susceptibility of the different commercial potato cultivars to abiotic stress that ultimately affected the final yield in the multi-environment and glasshouse trials in Chapters 4 and 5, respectively, illustrates the variable response of plants to their environment. Potentially, there can be cultivars that are well suited across a wide range of environments (wide adaptation), and there are also cultivars that perform relatively better than others under a limited set of conditions (specific adaptation). Through genotype-by-environment interaction (GEI) analysis, cultivars with wide and specific adaptation can be identified.

In the multi-environment trial, the genotype x environment (GxE) interaction was found to be highly significant. The significant effect of the G×E interaction showed that the genotypes had differential performance in the trial sites or test environments. Further analysis showed strong location-specific adaptation (agronomic zoning) among the tested commercial potato cultivars during the 2018/19 growing season. The cultivar ‘Hermes’ is tolerant to the combination of heat and drought stress in Opiki but less tolerant to heat stress alone in Hastings, while ‘Snowden’ is tolerant to heat stress in Hastings. The cultivar ‘Taurus’, on the other hand, is the most stable and widely adaptable cultivar across all the trial sites/test environments during the 2018/19 growing season.

6.5 Practical implications of the study for potato growers in New Zealand

As demonstrated in this research over three growing seasons (2017–2020), the different abiotic stresses associated with climate change showed a significant effect on the morpho-agronomic and physiological functions of the potato crop that ultimately influenced the tuber yield and quality. Based on the climate forecasts and simulations of future climate scenarios from international and local climate institutions, there will be long-term trends toward higher temperatures with shifting rainfall patterns, with more associated extreme events (droughts/flooding) in New Zealand (Reisinger et al., 2014). The western and southern regions of the country will receive more rain and warmer temperature, while the eastern and northern regions will have double to triple frequency of periods of severe droughts by 2040 (New Zealand Agricultural Greenhouse Gas Research Centre, 2012). Water scarcity in the Canterbury, Marlborough, Hawke's Bay, Waikato, and Northland regions will prominently feature as a potential problem.

Current farmer's practices in potato production in New Zealand, such as ground storage, could be negatively affected by extreme weather conditions and may not be a viable option in the future. Ground storing of ready-to-harvest potatoes is often conduced for weeks or months until the weather and/or market conditions are suitable before harvesting (Whenua Māori, 2020). Potato crops in the ground are exposed to heat and moisture stress (i.e., drought and flooding), which may dramatically affect tuber quality and ultimately the marketable yield. Some rather unique cultural practices in the New Zealand potato production systems are also affected by changing climate. The use of mesh covering to protect crops as a non-chemical means from the tomato-potato psyllid or TPP was found to increase the average temperature by 1 °C under the Canterbury growing conditions (Merfield et al., 2015). In the current trial, a microclimate was established under the mesh that caused temperatures to rise about 1 °C higher than the ambient temperature in the Hastings trial site. Moreover, the potato crops under the mesh senesced earlier, indicating that their growth and development were enhanced compared with the control plants.

Future warmer temperatures may promote crop yields as a result of faster emergence and rapid canopy development, especially in situations where cooler temperatures inhibited potato cropping. As an example, the temperature rise is generally expected to increase potato yields in England and Wales (Davies et al., 1997), Scotland (Peiris et al., 1996), the

Netherlands (Wolf, 2002), and Finland (Carter et al., 1996) mainly due to an extended growing season and an increase in the suitable arable land for potato production. However, the accelerated crop growth and development will inadvertently shorten the crop cycle, thereby reducing the time for photosynthesis and ultimately negatively impacting the final tuber yield as a general rule (Clark et al., 2012).

Another risk is the scarcity or surplus of water due to the extreme weather events influenced by climate change. The demand for water may increase as a result of increased evapotranspiration as affected by higher temperatures and a reduction in average rainfall (Gavin, 2001), especially in the eastern regions of New Zealand. Rainfed farming may not be viable due to variability in precipitation, often within extreme events interspersed with drought conditions, under future climate change scenarios. Water deficit leads to reduced leaf area duration that negatively impacts tuber yield when irrigation is unavailable (Millner et al., 2013). Supplemental irrigation will be needed in future farming to achieve economically viable yields under new agro-climatic conditions. However, in addition to the already limiting irrigation water resources (e.g., rivers and aquifers) and associated legislation, the need for irrigation may increase the capital costs and therefore hinder any expansion of its use and increase the likelihood of losses for crops under drought conditions (Gavin, 2001). Potatoes are very sensitive to drought stress, and the tuber yield may be considerably reduced by soil moisture deficits. Therefore, ensuring a sufficient water supply is essential to the production of potatoes. However, as the available water resource is decreasing, optimum irrigation strategies must be established to increase water use efficiency (Liu 2005).

The predicted changes in temperature and rainfall patterns may alter the spread and distribution of existing pests and diseases and enable the emergence of new ones that may create new biosecurity challenges. The drier and warmer conditions in the east of New Zealand may lower the prevalence of some cereal crop diseases, while the warm and humid conditions in the west may aggravate some diseases, such as leaf blight in maize (Gavin, 2001). The use of plant protection products against pests and diseases will most likely intensify in some cropping systems, aggravating environmental contamination and increasing the issues of chemical residues in food products (Lake et al., 2018). The use of biocontrol agents as an integral component of integrated pest management in New Zealand to reduce reliance on synthetic pesticides and promote more sustainable pest control will be challenged in the future with changing climate. The limited genetic variability of biocontrol agent populations may hinder their ability to adjust to new agro-climatic conditions (Gerard et al., 2010); hence, new cultivars with greater tolerance to important pests and diseases should be developed.

The predicted excess rainfall will increase the frequency of flooding events that may damage crops and increase losses, especially in the western regions of New Zealand. Flooding may also affect the timely scheduling of farm activities, such as land preparation, planting, spraying, and harvesting, and may entail additional expense due to its negative impact on the ease of doing the activities. Moreover, increased flooding events may have related negative effects, such as increase incidences of contaminating land with fertilizer and chemical residues, spread of antibiotic-resistant microorganisms, spread of pathogens from animal waste to crops, and increased risk of pathogen outbreak (Lake et al., 2018).

6.6 General conclusions

Based on the analysis of historical (60-year period) climate data and the extreme weather events experienced in the past three seasons during this study, there is apparent evidence that abiotic stress, i.e., heat, drought, and their combination, associated with climate change is affecting the current potato production system in New Zealand. Moreover, based on the baseline data collection (Chapter 3), multi-environment trial (Chapter 4), and controlled environment trial (Chapter 5), these abiotic stresses significantly affect the morpho-agronomic characteristics and physiological functions of the potato crop that ultimately impacts tuber yield and quality.

The climate in New Zealand has shifted toward a warmer atmosphere and varying rainfall patterns for the past 60 years, bringing associated abiotic stresses, such as drought, heat, and their combination into the potato production fields. Each stress stimulates a different morpho-agronomic and physiological response from the potato crop and cultivars. On the morpho-agronomic response to abiotic stress, drought stress reduces the plant height, whole plant leaf area, number of leaves, canopy cover, and number of stems per plant but increases the stem diameter. In contrast, heat stress promotes vegetative growth, thereby increasing the plant height, whole plant leaf area, number of leaves, canopy cover, and number of stems per plant, but reduces the stem diameter. This is accompanied by the increase in the dry matter content of the haulm and roots, suggesting an enhanced dry matter partitioning to the vegetative parts of the plant. The combination of drought and heat stress exacerbates the effects on the different morpho-physiological parameters brought about by each stress.

The elevated temperatures or heat stress (HS) in the Hastings trial site resulted in an increase in transpiration rate by 61.8% and stomatal conductance by 129.5% and a reduction in net photosynthesis by 16.5%. In the water-deficit or drought-stressed (DS) Opiki trial site, transpiration rate and stomatal conductance also increased by 55.9% and 52.3%, respectively, with a reduction in net photosynthesis by 8.3%.

The same result was observed on the effect of HS on the physiology of both potato cultivars in the controlled environment trial in Chapter 5. HS also had positive effects on the different physiological parameters, but the effects were observed to be cultivar-dependent. HS enhanced the transpiration rate and stomatal conductance and therefore improved the net photosynthesis in ‘Agria’ and ‘Taurus’. ‘Taurus’ had greater stomatal conductance and transpiration rate that resulted in higher net photosynthesis.

6.7 Limitations of the research

There are several identified limitations of this research. For the baseline data collection and multi-environment trial, the potential effects of the different soil characteristics across sites were not part of the scope of the study. Moreover, there was limited sampling for some measured parameters, e.g., number of measurements or replications for physiology data, i.e., net photosynthesis, transpiration rate, and stomatal conductance, due to time constraints and distance of sites. Furthermore, for the controlled environment trial, there was a limited number of commercial potato cultivars that were tested, and sample plants were measured due to the small space in the plant growth chamber and glasshouse.

6.8 Future research

Besides the current research, only a limited number of studies were conducted on the response of commercial potato cultivars to abiotic stress associated with climate change under New Zealand conditions. There is a need to test other existing and/or new cultivars in a wider range of environments in the country to identify those that will exhibit wide adaptation and location-specific adaptation or breed new cultivars with tolerance to abiotic stress. The output of this research will provide potato growers with options of cultivars that are better suited to obtain higher yield and better tuber quality in their respective regions.

With an increasingly projected shortage of water and the predicted likelihood of more and severe droughts in the near future, it is important to conduct further research on improved water management and precision irrigation to improve the water use efficiency of the crops.

The farmer’s practice of ground storage of potato tubers could be affected by extreme weather conditions and may reduce the yield and tuber quality; hence, it may not be a viable option in the future. Research on better-controlled storage conditions may be conducted as an alternative to ground storage.

In addition, as part of the long-term strategies, suitability land-use mapping of new areas for potato production might prove useful, considering the predicted regional changes in future climate scenarios for regional New Zealand, where areas currently not suitable for potato production may now become more suitable due to the changing climate and vice versa. According to NIWA (2020b), the 2020 drought highlights the projections of climate modeling for New Zealand’s northern and eastern regions, which will become more prone to drought with the ongoing climate change over the 21st century.

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Appendices

Appendix 2.1 Growth stages of the potato crop.

Growth stage	Developmental Process (Miller & Hopkins, 2008)	Days After Planting (DAP)
I. Sprout Development	Small sprouts erupt from the eyes on seed pieces and emerge from the soil.	10-15
II. Stolon Initiation/ Vegetative	Sprouts that emerged from the soil have all vegetative parts formed. Leaves and stem formed aboveground, while roots and stolons formed below ground. Besides the seed piece as the source of nutrients, the leaves also start to produce carbohydrates through photosynthesis.	30-45
III. Tuber Initiation/ Reproductive	Stolon-ends start to swell and turn into tubers, although not yet substantially enlarging. This is when the plant starts to transport excess carbohydrates from the aboveground parts to the tubers. Several factors may control the process of tuber initiation, including plant hormones, temperature, soil moisture and nitrogen levels. This process often coincides with the formation of the first flowers, although each process is unrelated.	45-65
IV. Tuber Bulking	Tubers begin to increase in size and weight due to cell division and elongation, with corresponding increase in accumulation with water, starch, and nutrients.	65-105
V. Tuber Maturation	Tubers reach its dry matter content to maximum and undergo dormancy. The rate of photosynthesis declines. The leaves senesces from stems and vines gradually die.	105-130

Gamboa, B.C. 2002; Miller & Hopkins, 2008; Rowe and Powelson, 2008.

Appendix 3.1 Standardized grower interview guide.

FARMER INTERVIEW GUIDE

I. BASIC INFORMATION

Respondent's name:	
Company Name:	
Contact number/s:	
Email address:	
Address:	
No. of years in business:	
Production scheme:	

II. THE FARM

Total area of farm:	
Total area planted to potatoes:	
Crops planted other than potato:	
No. of cropping/ year:	
Crop rotation practiced:	
Sources of seed potatoes:	
Target market/s for potatoes:	
Marketing system for potatoes:	

III. POTATO VARIETIES

1. Potato varieties planted in the farm

Varieties/ Maturity	Volume produced (t) and production (%)/ cropping	End-use (fresh, chips, fries)	Planting schedule	Harvesting schedule	Strengths/ weaknesses/ reasons for choosing the variety

2. Criteria and ranking in selecting potato varieties for production

Criteria	Ranking

IV. CULTURAL PRACTICES (previous season)

1. Land preparation

Activity	No. of times	Timing	Remarks

2. Planting

Depth:	
Spacing b/w hill:	
Row spacing:	
Row length:	
Timing:	
Average amount of seed potatoes planted per hectare:	

3. Fertilizer application

Kind (formulation)	Amount	Method of application (foliar, basal)	Time of application (days after planting or DAP)	Remarks

4. Irrigation

Type (irrigated, non-irrigated)	Method of application (drip, sprinkler)	Frequency/ growth stage of potato	Rate	Water source	Remarks

5. Weed Management

Method	Frequency/ Interval	Remarks

IV. PESTS AND DISEASE MANAGEMENT

1. Pest Problems

Pests and diseases	Severity				Growth stage observed (vegetative, reproductive)	Management (crop rotation, BCA, chemical etc.)
	None	Low	Mod	High		

V. POSTPRODUCTION

1. Harvesting

Varieties	Date harvested	Total yield	Remarks

VI. QUALITY PROFILE OF HARVESTED POTATO TUBERS

1. System of buying:

Marketing System	Please check	Price

Where sorting is done, please check:

________________ Field
________________ Farm packing house
________________ Exporter’s packinghouse
________________ Others, specify

2. Proportions of marketable potato tubers

Grade	Volume (t)/ percent (%)

3. Quality profile

Type of Rejects	Percent (%)/ Remarks

4. Size Classification (if classified by size)

Size Category	Percent (%)

VII. MARKETING OPERATIONS

1. Type of buyer:

Type	Name of Buyer/Company	Volume (t)

VII. WEATHER/CLIMATE FACTORS

1. Sources of weather data

Sources of weather data	Tick appropriate item/s	Frequency of access (daily, weekly, need-based)

2. Weather/climate factors considered in the implementation of farm activities

Farm activities	Weather/climate factors (temperature, soil moisture, rainfall, degree days etc.)	Remarks

3. Perception of climate change in potato production __/_ Yes ___ No

4. Perception of effects of climate change in potato production

Perceived effects of climate change	Check appropriate item/s in this column

5. Perception of consequences of climate change in potato production

Perceived effects of climate change	Check appropriate item/s in this column/ Remarks

6. Extreme weather/climate events affecting different growth stages of potato and adaptation strategies

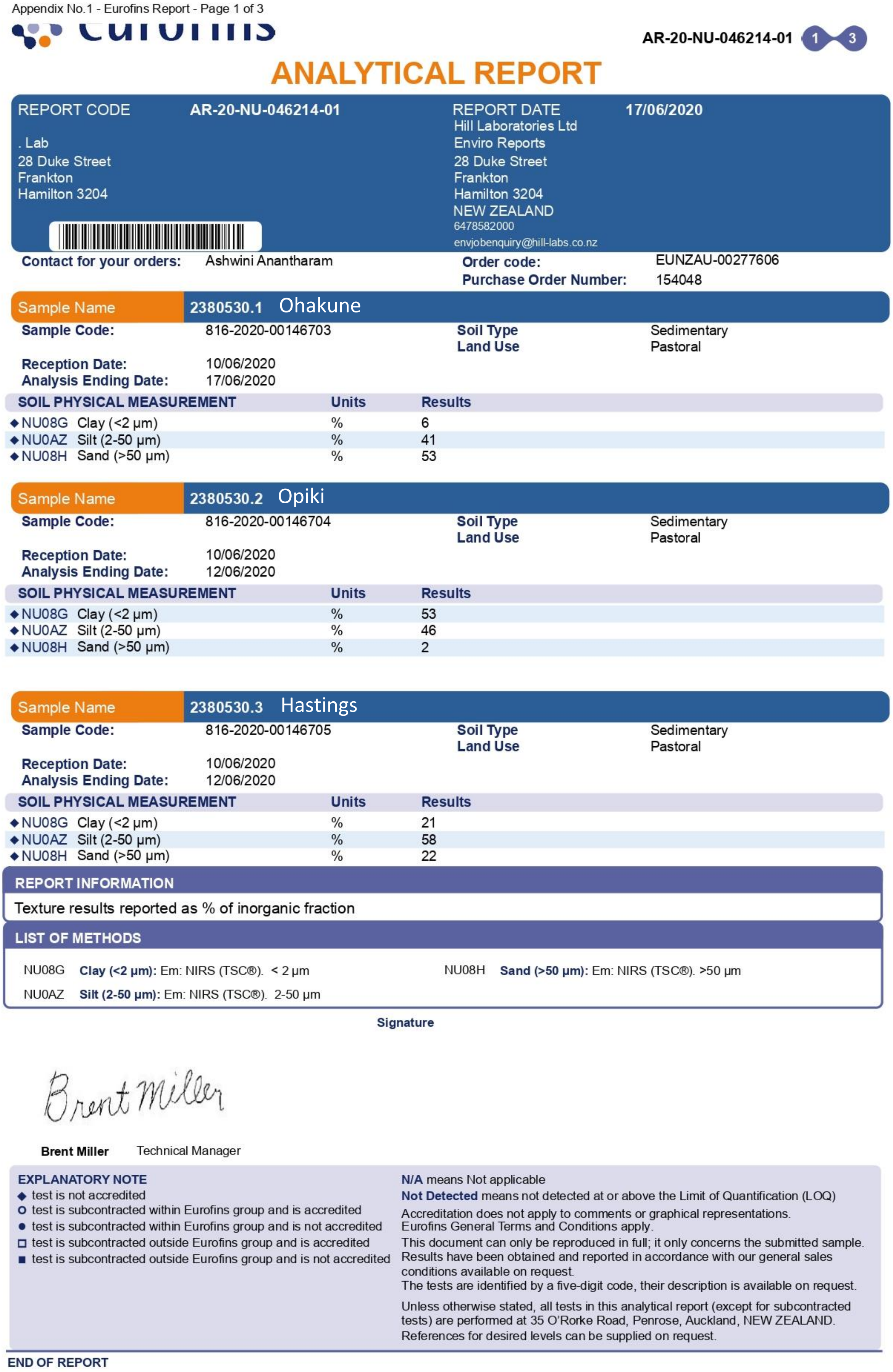
Stages	Extreme weather/climate events[a]	Estimated losses (%)	Adaptation strategies[c]	Remarks

Appendix 3.2 List of weather stations as sources of climate and weather data.

Weather Parameter	Test Environments	Weather Station	Latitude	Longitude	Elevation (masl)	Observing Authority
Mean atmospheric temperature – 1958-2018	Ohakune	Ohakune Ohakune Junction 2 Ohakune EWS Ohakune 'Rua'pehu College	-39.419 -39.402 -39.418 -39.419	175.414 175.416 175.413 175.412	610 629 607 610	NIWA
	Opiki	Palmerston N EWS Palmerston N Aero Palmerston N Palmerston N AWS	-40.381 -40.327 -40.382 -40.318	175.609 175.616 175.609 175.614	21 45 34 40	NIWA/ AGRESEARCH
	Hastings	Hastings AWS Hastings Hastings Fire Station	-39.648 -39.633 -39.647	176.841 176.845 176.842	16 14 12	-
Total rain – 1958-2018	Ohakune	Ohakune Ohakune Junction 2 Ohakune EWS Ohakune 'Rua'pehu College	-39.419 -39.402 -39.418 -39.419	175.414 175.416 175.413 175.412	610 629 607 610	NIWA
	Opiki	Palmerston N EWS Palmerston N	-40.381 -40.382	175.609 175.609	21 34	NIWA/ AGRESEARCH
	Hastings	Hastings AWS Hastings Hastings Fire Station	-39.648 -39.633 -39.647	176.841 176.845 176.842	16 14 12	-
Atmospheric temperature – 2017/18	Ohakune	Ohakune EWS	-39.418	175.413	607	NIWA
	Opiki	Palmerston N EWS	-40.381	175.609	21	NIWA/ AGRESEARCH
	Hastings	Hastings AWS	-39.648	176.841	16	-
Soil temperature – 2017/18	Ohakune	Ohakune EWS	-39.418	175.413	607	NIWA
	Opiki	Palmerston N EWS	-40.381	175.609	21	NIWA/ AGRESEARCH
	Hastings*	Bridge Pa Climate	-39.648	176.750	25	Hawke's Bay Reg Council
Total rainfall – 2017/18	Ohakune	Ohakune EWS	-39.418	175.413	607	NIWA
	Opiki	Palmerston N EWS	-40.381	175.609	21	NIWA/ AGRESEARCH
	Hastings	Hastings AWS	-39.648	176.841	16	-
Sunshine hours – 2017/18	Ohakune	Ohakune EWS	-39.418	175.413	607	NIWA
	Opiki	Palmerston N EWS	-40.381	175.609	21	NIWA/ AGRESEARCH
	Hastings	Napier EWS	-39.498	176.911	7	NIWA
Growing degree days – 2017/18	Ohakune	Ohakune EWS	-39.418	175.413	607	NIWA
	Opiki	Palmerston N EWS	-40.381	175.609	21	NIWA/ AGRESEARCH
	Hastings	Hastings AWS	-39.648	176.841	16	-

Retrieved through CliFlo-NIWA; *Retreived from the Hawke's Bay Reg Council

Appendix 4.1 Soil texture analysis from soil samples collected in the Ohakune, Opiki, and Hastings trial sites for the multi-environment trial during the 2018/19 potato growing season.



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ANALYTICAL REPORT

REPORT CODE	**AR-20-NU-046214-01**	REPORT DATE	**17/06/2020**

. Lab
28 Duke Street
Frankton
Hamilton 3204

Hill Laboratories Ltd
Enviro Reports
28 Duke Street
Frankton
Hamilton 3204
NEW ZEALAND
6478582000
envjobenquiry@hill-labs.co.nz

Contact for your orders: Ashwini Anantharam

Order code: EUNZAU-00277606
Purchase Order Number: 154048

Sample Name **2380530.1** Ohakune

Sample Code:	816-2020-00146703	**Soil Type**	Sedimentary
		Land Use	Pastoral
Reception Date:	10/06/2020		
Analysis Ending Date:	17/06/2020		

SOIL PHYSICAL MEASUREMENT	**Units**	**Results**
◆NU08G Clay (<2 µm)	%	6
◆NU0AZ Silt (2-50 µm)	%	41
◆NU08H Sand (>50 µm)	%	53

Sample Name **2380530.2** Opiki

Sample Code:	816-2020-00146704	**Soil Type**	Sedimentary
		Land Use	Pastoral
Reception Date:	10/06/2020		
Analysis Ending Date:	12/06/2020		

SOIL PHYSICAL MEASUREMENT	**Units**	**Results**
◆NU08G Clay (<2 µm)	%	53
◆NU0AZ Silt (2-50 µm)	%	46
◆NU08H Sand (>50 µm)	%	2

Sample Name **2380530.3** Hastings

Sample Code:	816-2020-00146705	**Soil Type**	Sedimentary
		Land Use	Pastoral
Reception Date:	10/06/2020		
Analysis Ending Date:	12/06/2020		

SOIL PHYSICAL MEASUREMENT	**Units**	**Results**
◆NU08G Clay (<2 µm)	%	21
◆NU0AZ Silt (2-50 µm)	%	58
◆NU08H Sand (>50 µm)	%	22

REPORT INFORMATION

Texture results reported as % of inorganic fraction

LIST OF METHODS

NU08G **Clay (<2 µm):** Em: NIRS (TSC®). < 2 µm
NU0AZ **Silt (2-50 µm):** Em: NIRS (TSC®). 2-50 µm
NU08H **Sand (>50 µm):** Em: NIRS (TSC®). >50 µm

Signature

Brent Miller

Brent Miller Technical Manager

EXPLANATORY NOTE
- ◆ test is not accredited
- o test is subcontracted within Eurofins group and is accredited
- ● test is subcontracted within Eurofins group and is not accredited
- ☐ test is subcontracted outside Eurofins group and is accredited
- ■ test is subcontracted outside Eurofins group and is not accredited

N/A means Not applicable
Not Detected means not detected at or above the Limit of Quantification (LOQ)
Accreditation does not apply to comments or graphical representations.
Eurofins General Terms and Conditions apply.
This document can only be reproduced in full; it only concerns the submitted sample.
Results have been obtained and reported in accordance with our general sales conditions available on request.
The tests are identified by a five-digit code, their description is available on request.
Unless otherwise stated, all tests in this analytical report (except for subcontracted tests) are performed at 35 O'Rorke Road, Penrose, Auckland, NEW ZEALAND.
References for desired levels can be supplied on request.

END OF REPORT

Appendix 4.2 Details of the trial site's primary and secondary data and sources of information.

Unit	When to measure and sources of data/information		
	Before	**During**	**At harvest**
Plot	- Soil nutrient level/ soil analysis from the grower	- Pests and disease occurrence/ actual observations - Observations and notes	- Crop yield and tuber quality data/ actual measurements - Grower's assessment of crop
Farm	- History of land use (i.e., previous crops planted, farming system)/ interview with grower	- Schedule, rates, and types of inputs (e.g., irrigation, fertilizer & other chemicals) - Observations and notes	
Site	- Average rainfall, temperature, and growing degree days (GDD)/ on-site temp loggers or nearest weather station (NIWA)	- Daily rainfall, maximum/ minimum temperatures, and GDD/ on-site temp loggers or nearest weather station (NIWA) - Observations and notes	

Appendix 4.3 Analysis of variance for the genotype x environment interaction in the Ohakune, Opiki, and Hastings trial sites during the 2018/19 potato growing season.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Environment (Env)	2	91166	45583	59.0470	6.692e-06	***
Rep Env	9	6948	772	2.9399	0.0021451	**
Genotype (Gen)	6	16242	2707	10.3090	1.165e-10	***
Env x Gen	12	10608	884	3.3666	0.0001043	***
Residuals	419	110022	263			

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Appendix 5.1 Daily average soil temperature for the two weeks under optimum atmospheric temperature or control, drought, heat, and drought and heat stress combination in potted plants in the plant growth chamber.

Particulars	**Soil Temperature (℃)**			
	Control	**Drought**	**Heat**	**Drought + Heat**
Vegetative Stage				
Ave	18.5	21.2	27.6	28.1
Max	19.2	23.6	33.7	34.4
Min	17.3	17.8	24.1	24.5
Reproductive Stage				
Ave	18.9	20.1	28.1	28.8
Max	20.3	21.7	36.1	36.9
Min	17.1	18.1	24.5	25.1

Appendix 5.2 Effects of abiotic stress on the plant height of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**PLANT HEIGHT (mm)**					
	'AGRIA'			**'TAURUS'**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
Vegetative Stage						
Control	170±15.5 a	261±12.5 a	466±11.2 a	172±11.7 b	249±10.9 b	381±12.5 ab
Drought (D)	144±9.7 a	226±10.8 a	356±8.1 bc	200±6.4 ab	264±8.7 ab	328±6.6 c
Heat (H)	152±10.2 a	260±10.0 a	390±8.9 b	190±5.5 ab	289±5.6 ab	422±11.6 a
D + H	145±10.4 a	239±11.78 a	338±10.2 c	221±5.8 a	302±4.9 a	368±9.2 bc
Reproductive Stage						
Control	670.0± 28.9 a	726.7± 31.8 a	880.0± 35.1 a	680.0± 20.0 a	730.0± 25.2 b	850.0± 20.0 a
Drought (D)	706.7± 23.3 a	726.7± 29.6 a	766.7± 26.0 bc	690.0± 20.8 a	683.3± 20.3 c	716.7± 17.6 b
Heat (H)	676.7± 17.6 a	730.0± 25.2 a	816.7± 21.9 b	723.3± 8.8 a	750.0± 5.8 a	846.7± 6.7 a
D + H	653.3± 29.1 a	676.7± 28.5 a	733.3± 21.9 c	696.7± 13.3 a	700.0± 15.3 b	753.3± 16.7 b
ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	9605	9605	11.5492	0.0008768	***
Growth Stage (GS)	1	9542251	9542251	11473.7248	< 2.2e-16	***
Stress Treatment (ST)	3	50335	16778	20.1744	5.682e-11	***
C x GS	1	2558	2558	3.0753	0.0816199	.
C x ST	3	34458	11486	13.8107	5.764e-08	***
GS x ST	3	11930	3977	4.7816	0.0033100	**
C x GS x ST	3	11070	3690	4.4369	0.0051500	**
Residuals	144	119759	832			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.3 Effects of abiotic stress on the stem diameter of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**STEM DIAMETER (mm)**					
	‘AGRIA’			**‘TAURUS’**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
Vegetative Stage						
Control	9.6±0.2 a	10.3±0.3 a	12.0±0.4 a	9.8±0.4 a	10.0±0.4 a	11.2±0.5 a
Drought (D)	9.3±0.2 a	10.3±0.4 a	11.1±0.3 ab	9.5±0.3 a	10.0±0.5 a	10.1±0.3 a
Heat (H)	9.2±0.1 a	11.2±0.2 a	12.0±0.3 a	8.9±0.4 a	9.6±0.4 a	10.5±0.5 a
D + H	9.4±0.2 a	10.3±0.2 a	10.3±0.4 b	8.7±0.1 a	9.8±0.1 a	9.9±0.1 a
Reproductive Stage						
Control	12.0±0.5 ab	13.7±0.5 a	13.5±0.4 b	12.2±0.1 a	13.0±0.3 a	13.5±0.7 a
Drought (D)	12.2±1.0 ab	13.2±0.5 a	13.1±1.1 b	11.7±0.7 a	12.0±0.2 a	11.4±0.1 b
Heat (H)	13.7±0.2 a	13.7±0.4 a	16.9±0.9 a	12.0±0.7 a	12.3±1.1 a	12.2±0.3 ab
D + H	11.5±0.5 b	12.2±0.5 a	13.6±0.5 b	12.7±0.7 a	12.9±0.5 a	13.0±0.5 ab
ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	22.76	22.76	30.6949	1.395e-07	***
Growth Stage (GS)	1	335.31	335.31	452.2871	< 2.2e-16	***
Stress Treatment (ST)	3	15.75	5.25	7.0816	0.0001794	***
C x GS	1	0.89	0.89	1.1944	0.2762659	
C x ST	3	16.48	5.49	7.4115	0.0001188	***
GS x ST	3	6.77	2.26	3.0422	0.0309350	*
C x GS x ST	3	8.94	2.98	4.0207	0.0087920	**
Residuals	144	106.76	0.74			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.4 Effects of abiotic stress on the number of leaves of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**NUMBER OF LEAVES**					
	‘AGRIA’			**‘TAURUS’**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
Vegetative Stage						
Control	7.0±0.4 a	10.6±0.2 a	11.4±0.6 ab	7.8±0.2 a	11.6±0.5 a	14.0±0.8 a
Drought (D)	6.4±0.2 a	9.6±0.4 a	10.0±0.5 c	7.8±0.2 a	10.6±0.2 a	12.6±0.4 ab
Heat (H)	6.4±0.2 a	10.4±0.2 a	12.8±0.6 a	7.2±0.2 a	11.6±0.2 a	13.0±0.4 ab
D + H	6.8±0.2 a	9.4±0.2 a	9.8±0.5 c	7.6±0.2 a	10.6±0.5 a	12.0±0.3 b
Reproductive Stage						
Control	12.3±0.9 a	13.7±0.3 a	16.0±0.6 a	13.0±0.6 a	16.0±0.6 a	18.7±0.9 a
Drought (D)	11.3±0.3 a	12.3±0.7 ab	13.0±0.6 b	14.0±0.6 a	13.3±0.2 b	15.7±0.3 b
Heat (H)	12.0±0.6 a	13.3±0.7 a	17.0±0.6 a	14.0±0.6 a	15.7±1.1 a	19.0±0.6 a
D + H	11.3±0.3 a	10.7±0.3 b	11.3±0.9 b	14.0±0.6 a	14.7±0.5 ab	14.0±0.0 b
ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	136.69	136.69	157.3801	< 2.2e-16	***
Growth Stage (GS)	1	770.87	770.87	887.5666	< 2.2e-16	***
Stress Treatment (ST)	3	87.69	29.23	33.6541	< 2.2e-16	***
C x GS	1	11.00	11.00	12.6668	0.0005046	***
C x ST	3	4.10	1.37	1.5752	0.1979817	
GS x ST	3	18.33	6.11	7.0368	0.0001897	***
C x GS x ST	3	3.63	1.21	1.3929	0.2474232	ns
Residuals	144	125.07	0.87			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.5 Effects of abiotic stress on percent canopy cover of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**CANOPY COVER (%)**					
	‘AGRIA’			**‘TAURUS’**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
			Vegetative Stage			
Control	9.7±1.5 a	12.9±1.5 a	24.6±1.5 a	10.4±1.5 a	16.1±1.5 a	18.5±1.5 b
Drought (D)	9.1±1.5 a	8.4±1.5 ab	12.9±1.5 bc	11.2±1.5 a	11.9±1.5 a	17.1±1.5 b
Heat (H)	8.8±1.5 a	6.2±1.5 b	13.8±1.5 b	12.0±1.5 a	11.7±1.5 a	28.1±1.5 a
D + H	8.4±1.5 a	5.5±1.5 b	7.7±1.5 c	10.9±1.5 a	12.4±1.5 a	14.7±1.5 b
			Reproductive Stage			
Control	38.3±1.9 ab	45.4±1.9 a	63.2±1.9 a	43.8±1.9 ab	45.8±1.9 a	60.9±1.9 a
Drought (D)	32.6±1.9 c	35.8±1.9 b	35.1±1.9 b	39.8±1.9 c	40.1±1.9 ab	39.0±1.9 c
Heat (H)	41.0±1.9 a	30.6±1.9 b	41.0±1.9 b	48.7±1.9 a	43.0±1.9 ab	52.6±1.9 b
D + H	27.8±1.9 c	35.4±1.9 b	35.9±1.9 b	35.1±1.9 c	37.6±1.9 b	50.6±1.9 b

ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	1128	1128	99.7316	< 2.2e-16	***
Growth Stage (GS)	1	37908	37908	3352.7404	< 2.2e-16	***
Stress Treatment (ST)	3	1905	635	56.1717	< 2.2e-16	***
C x GS	1	56	56	4.9950	0.0269610	*
C x ST	3	506	169	14.9155	1.655e-08	***
GS x ST	3	490	163	14.4422	2.818e-08	***
C x GS x ST	3	3	1	0.0867	0.9672167	ns
Residuals	144	1628	11			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.6 Effects of abiotic stress on the chlorophyll content of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**CHLOROPHYLL (SPAD)**					
	'AGRIA'			**'TAURUS'**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
Vegetative Stage						
Control	55.1±2.3 b	77.8±1.5 a	80.5±1.9 b	41.5±1.5 ab	46.1±2.2 c	91.4±1.9 b
Drought (D)	63.0±2.2 a	76.5±2.3 a	66.2±2.1 d	48.5±1.7 a	57.3±1.8 b	62.4±1.9 c
Heat (H)	60.2±2.3 ab	83.2±1.6 a	73.9±2.0 c	39.7±1.0 b	79.8±2.0 a	50.3±1.8 d
D + H	60.9±2.5 ab	82.0±2.1 a	94.3±3.5 a	45.8±1.3 ab	78.2±2.2 a	105.9±2.6 a
Reproductive Stage						
Control	52.2±2.1 b	58.4±2.5 b	59.4±1.4 b	54.2±1.7 a	63.6±2.5 a	56.9±2.2 a
Drought (D)	68.0±1.8 a	71.5±3.8 a	74.3±2.1 a	56.2±1.1 a	54.1±1.6 b	52.6±1.9 a
Heat (H)	63.9±3.4 a	80.2±2.8 a	76.8±2.2 a	56.1±2.5 a	49.6±1.8 b	41.6±3.0 b
D + H	62.0±1.6 ab	66.6±2.8 b	68.1±2.3 ab	57.9±2.1 a	55.3±2.6 ab	32.9±1.7 b
ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	24570	24569.9	323.998	< 2.2e-16	***
Growth Stage (GS)	1	8967	8966.9	118.244	< 2.2e-16	***
Stress Treatment (ST)	3	9515	3171.5	41.822	< 2.2e-16	***
C x GS	1	881	881.1	11.619	0.0006904	***
C x ST	3	5969	1989.6	26.236	4.372e-16	***
GS x ST	3	11440	3813.2	50.284	< 2.2e-16	***
C x GS x ST	3	3073	1024.3	13.507	1.419e-08	***
Residuals						

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.7 Effects of abiotic stress on the net photosynthesis of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**NET PHOTOSYNTHESIS (μmol CO_2 m^2s^1)**					
	‘AGRIA’			**‘TAURUS’**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
Vegetative Stage						
Control	17.0±0.6 a	18.3±0.5 a	19.6± 0.5 a	19.0±0.4 a	16.6±0.4 ab	22.8±0.9 a
Drought (D)	19.4±1.0 a	18.6±0.8 a	17.0±2.2 b	19.3±0.5 a	14.7±1.5 b	22.1±1.1 a
Heat (H)	17.0±0.6 a	19.0±1.0 a	22.1±2.2 a	19.0±0.4 a	21.4±4.1 a	25.3±1.2 a
D + H	19.4±1.0 a	10.4±0.8 b	10.2±2.4 b	19.3±0.5 a	17.7±1.4 ab	14.5±1.1 b
Reproductive Stage						
Control	11.4±0.1 a	25.6±1.7 a	20.8±1.5 a	17.4±2.5 a	23.4±0.7 a	17.7±0.6 a
Drought (D)	8.7±1.0 a	9.5±2.0 bc	11.1±2.0 bc	8.0±1.0 b	14.1±2.0 b	9.0±2.0 bc
Heat (H)	11.4±0.1 a	14.7±1.1 b	15.0±2.0 ab	17.4±2.5 a	17.8±1.8 ab	12.5±0.1 ab
D + H	8.7±1.0 a	4.3±2.7 c	5.6±1.4 c	8.0±1.0 b	2.4±0.3 c	4.4±0.7 c
ANOVA						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	125.62	125.62	9.8797	0.002030	**
Growth Stage (GS)	1	1471.33	1471.33	115.7207	< 2.2e-16	***
Stress Treatment (ST)	3	1581.83	527.28	41.4707	< 2.2e-16	***
C x GS	1	50.01	50.01	3.9331	0.049247	*
C x ST	3	28.79	9.60	0.7549	0.521241	ns
GS x ST	3	812.24	270.75	21.2944	1.790e-11	***
C x GS x ST	3	45.04	15.01	1.1808	0.319252	ns
Residuals	144	1830.88	12.71			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.8 Effects of abiotic stress on the transpiration rate of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**TRANSPIRATION RATE (mmol H_2O m^2s^1)**					
	‘AGRIA’			**‘TAURUS’**		
	Week after stress treatment			**Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
			Vegetative Stage			
Control	3.7±0.2 a	4.5±0.1 ab	5.0±0.1 b	3.1±0.2 a	5.6±0.1 ab	6.6±0.1 a
Drought (D)	2.7±0.1 a	2.3±0.3 c	1.4±0.4 c	2.6±0.1 a	1.4±0.1 c	1.9±0.3 c
Heat (H)	3.7±0.2 a	5.8±0.3 a	7.4±0.8 a	3.1±0.2 a	6.6±0.2 a	7.9±0.7 a
D + H	2.7±0.1 a	3.5±0.6 bc	3.3±0.9 c	2.6±0.1 a	5.0±0.6 b	4.3±0.8 b
			Reproductive Stage			
Control	0.6±0.2 a	6.5±0.6 a	3.6±0.4 a	1.5±0.5 a	6.2±0.4 a	2.9±0.8 a
Drought (D)	0.3±0.0 a	1.9±1.1 b	1.5±1.0 bc	0.4±0.1 a	2.4±1.1 b	1.7±0.9 ab
Heat (H)	0.6±0.2 a	2.7±0.3 b	2.9±0.6 ab	1.5±0.5 a	4.5±0.6 a	2.7±0.4 a
D + H	0.3±0.0 a	1.2±0.8 b	0.8±0.5 c	0.4±0.1 a	0.2±0.1 c	0.5±0.3 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	5.672	5.672	6.1633	0.014191	*
Growth Stage (GS)	1	119.887	119.887	130.2736	< 2.2e-16	***
Stress Treatment (ST)	3	202.528	67.509	73.3581	< 2.2e-16	***
C x GS	1	0.990	0.990	1.0759	0.301353	ns
C x ST	3	2.291	0.764	0.8297	0.479581	ns
GS x ST	3	107.064	35.688	38.7798	< 2.2e-16	***
C x GS x ST	3	7.655	2.552	2.7727	0.043701	ns
Residuals	144	132.519	0.920			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.9 Effects of abiotic stress on the stomatal conductance of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**STOMATAL CONDUCTANCE (mol H_2O m^2s^1)**					
	‘AGRIA’ Week after stress treatment			**‘TAURUS’ Week after stress treatment**		
	0	**1**	**2**	**0**	**1**	**2**
	Vegetative Stage					
Control	0.320±0.034 a	0.156±0.011 ab	0.260±0.010 b	0.268±0.030 a	0.285±0.007 b	0.354±0.014 b
Drought (D)	0.181±0.009 b	0.101±0.011 b	0.082±0.024 c	0.175±0.005 a	0.075±0.007 c	0.112±0.013 b
Heat (H)	0.320±0.034 a	0.225±0.020 a	0.395±0.060 a	0.268±0.030 a	0.381±0.002 a	0.413±0.020 a
D + H	0.181±0.009 b	0.092±0.018 b	0.090±0.027 c	0.175±0.005 a	0.133±0.019 c	0.104±0.020 b
	Reproductive Stage					
Control	0.038±0.006 a	0.407±0.057 a	0.233±0.038 a	0.078±0.024 a	0.378±0.035 a	0.182±0.059 a
Drought (D)	0.010±0.001 a	0.079±0.051 b	0.082±0.058 b	0.013±0.004 a	0.116±0.056 bc	0.103±0.053 b
Heat (H)	0.038±0.006 a	0.147±0.030 b	0.210±0.099 a	0.078±0.024 a	0.199±0.030 b	0.156±0.049 a
D + H	0.010±0.001 a	0.030±0.027 a	0.025±0.016 b	0.013±0.004 a	0.003±0.001 c	0.020±0.006 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	0.01839	0.01839	5.5329	0.020016	*
Growth Stage (GS)	1	0.30618	0.30618	92.1240	< 2.2e-16	***
Stress Treatment (ST)	3	0.98015	0.32672	98.3040	< 2.2e-16	***
C x GS	1	0.00859	0.00859	2.5837	0.110159	ns
C x ST	3	0.00787	0.00262	0.7890	0.501919	ns
GS x ST	3	0.30834	0.10278	30.9253	1.715e-15	***
C x GS x ST	3	0.01353	0.00451	1.3568	0.258477	ns
Residuals	144	0.47859	0.00332			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.10 Effects of abiotic stress on the leaf relative water content of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**LEAF RELATIVE WATER CONTENT (%)**	
	‘AGRIA’	**‘TAURUS’**
	Vegetative Stage	
Control	91.6±1.1 a	92.5±0.8 a
Drought (D)	80.8±0.8 b	86.9±0.6 b
Heat (H)	88.6±1.1 a	92.8±0.3 a
D + H	88.3±1.6 a	89.8±0.7 ab
	Reproductive Stage	
Control	88.9±1.1 a	92.8±1.1 a
Drought (D)	82.4±1.6 b	89.2±0.2 a
Heat (H)	80.5±0.7 b	93.7±0.2 a
D + H	77.1±1.0 b	83.3±1.1 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	541.45	541.45	87.2852	8.083e-15	***
Growth Stage (GS)	1	92.16	92.16	14.8574	0.00022	***
Stress Treatment (ST)	3	330.82	110.27	17.7770	4.176e-09	***
C x GS	1	35.64	35.64	5.7461	0.01864	*
C x ST	3	30.79	10.26	1.6547	0.18262	ns
GS x ST	3	260.34	86.78	13.9892	1.551e-07	***
C x GS x ST	3	13.02	4.34	0.6994	0.55489	ns
Residuals	88	545.88	6.20			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.11 Effects of abiotic stress on the leaf water potential of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**LEAF WATER POTENTIAL ψ_L (MPa)**	
	‘AGRIA’	**‘TAURUS’**
	Vegetative Stage	
Control	-3.6±0.2 a	-1.4±0.2 a
Drought (D)	-8.1±0.6 b	-5.7±0.3 b
Heat (H)	-4.0±0.3 a	-2.1±0.3 a
D + H	-4.5±0.3 a	-2.3±0.3 a
	Reproductive Stage	
Control	-7.8±0.4 a	-5.5±0.3 a
Drought (D)	-8.00±0.6 b	-7.0±0.0 a
Heat (H)	-7.2±1.1 b	-6.2±0.3 a
D + H	-9.8±0.2 c	-9.8±0.2 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	0.12	0.123	0.1804	0.6722	ns
Growth Stage (GS)	1	57.27	57.276	84.3357	5.950e-14	***
Stress Treatment (ST)	3	349.06	116.354	171.3465	< 2.2e-16	***
C x GS	1	53.23	53.232	78.3906	2.543e-13	***
C x ST	3	33.08	11.027	16.2387	2.998e-08	***
GS x ST	3	198.66	66.219	97.5156	< 2.2e-16	***
C x GS x ST	3	182.27	60.758	89.4743	< 2.2e-16	***
Residuals	76	51.61	0.679			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \le 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.12 Effects of abiotic stress on the glandular and non-glandular trichomes density of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**Glandular and Non-glandular Trichomes Density (count/mm^2)**			
	Glandular Trichomes		**Non-glandular Trichomes**	
	'Agria'	**'Taurus'**	**'Agria'**	**'Taurus'**
Control	11.7±0.8 b	21.3±2.7 b	17.7±1.0 c	16.8±1.0 c
Drought (D)	18.3±0.6 a	35.0±1.6 a	37.6±2.0 a	40.0±3.0 a
Heat (H)	15.0±0.7 ab	13.7±1.0 c	25.3±2.0 b	24.1±1.0 b
D + H	15.3±1.0 ab	20.7±1.0 b	25.0±1.0 b	20.7±2.0 b

ANOVA – Glandular Trichome

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	1380.2	1380.17	63.656	5.129e-12	***
Stress Treatment (ST)	3	2105.8	701.94	32.375	3.396e-14	***
C x ST	3	1028.5	342.83	15.812	2.628e-08	***
Residuals	88	1908.0	21.68			

ANOVA – Non-glandular Trichome

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	13.5	13.50	0.3717	0.5436	ns
Stress Treatment (ST)	3	6283.2	2094.39	57.6678	<2e-16	***
C x ST	3	137.8	45.94	1.2651	0.2914	ns
Residuals	88	3196.0	36.32			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.13 Effects of abiotic stress on the stomatal density of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**Stomatal Density (count/mm^2)**	
	'Agria'	**'Taurus'**
Control	385.7±10.0 c	440.0±27.4 ab
Drought (D)	458.7±18.0 ab	520.3±38.7 a
Heat (H)	508.0±12.0 a	547.3±22.6 a
D + H	532.6±9.9 a	541.0±20.2 a

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	655	655	0.1139	0.7365350	ns
Stress Treatment (ST)	3	110111	36704	6.3863	0.0005764	***
C x ST	3	96379	32126	5.5899	0.0014801	**
Residuals	88	505758	5747			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.14 Effects of abiotic stress on the number of open, partial, and closed stomata of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**Number of open, partial, and closed stomata (count/mm^2)**					
	‘Agria’			**‘Taurus’**		
	Open	**Partial**	**Closed**	**Open**	**Partial**	**Closed**
Control	0.0±0.0 b	0.0±0.0 b	385.7±10.4 ab	0.0±0.0 b	237.0±17.4 a	203.0±30.8 c
Drought (D)	0.0±0.0 b	0.0±0.0 b	458.7±17.8 a	0.0±0.0 b	198.3±14.2 b	322.0±29.6 b
Heat (H)	312.2±19.9 a	0.0±0.0 b	195.5±17.2 c	74.0±14.4 a	113.0±5.9 c	360.3±27.8 ab
D + H	0.0±0.0 b	182.2±13.7 a	350.3±14.7 b	41.7±11.2 a	72.0±6.0 d	427.3±17.9 a

ANOVA – Open stomata

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	57928	57928	53.020	1.325e-10	***
Stress Treatment (ST)	3	630659	210220	192.409	< 2.2e-16	***
C x ST	3	292876	97625	89.354	< 2.2e-16	***
Residuals	88	96146	1093			

ANOVA – Partially opened stomata

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	287897	287897	245.768	< 2.2e-16	***
Stress Treatment (ST)	3	71282	23761	20.284	4.432e-10	***
C x ST	3	434656	144885	123.683	< 2.2e-16	***
Residuals	88	103085	1171			

ANOVA – Closed stomata

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	9004	9004	1.5512	0.2163	
Stress Treatment (ST)	3	260162	86721	14.9405	6.090e-08	***
C x ST	3	501901	167300	28.8230	4.486e-13	***
Residuals	88	510788	5804			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.15 Effects of abiotic stress on the stomatal area of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	**Stomatal Area (μm^2)**	
	‘Agria’	**‘Taurus’**
Control	377.6±13.3 c	404.3±18.9 c
Drought (D)	325.8±5.5 c	312.3±5.7 d
Heat (H)	941.7±19.2 a	754.8±29.9 a
D + H	655.7±50.5 b	533.5±21.0 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	131232	131232	18.0175	5.406e-05	***
Stress Treatment (ST)	3	4056460	1352153	185.6440	< 2.2e-16	***
C x ST	3	173231	57744	7.9279	9.711e-05	***
Residuals	88	640955	7284			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.16 Effects of abiotic stress on the stomatal length and width of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the plant growth chamber during the 2019/2020 season.

Stress Treatment	Stomatal Length and Width (µm)			
	‘Agria’		‘Taurus’	
	Length	Width	Length	Width
Control	24.0±0.28 c	18.2±0.47 c	23.5±0.62 c	17.8±0.53 c
Drought (D)	22.4±0.23 c	17.0±0.18 c	20.1±0.30 d	16.1±0.31 c
Heat (H)	33.9±0.31 a	30.7±0.38 a	29.9±0.64 a	26.4±0.40 a
D + H	29.0±0.73 b	26.4±0.95 b	26.3±0.50 b	21.9±0.53 b

ANOVA – Stomatal length

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	134.19	134.19	47.1590	8.883e-10	***
Stress Treatment (ST)	3	1553.57	517.86	181.9929	< 2.2e-16	***
C x ST	3	36.83	12.28	4.3146	0.006908	**
Residuals	88	250.40	2.85			

ANOVA – Stomatal width

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	152.26	152.26	48.313	6.067e-10	***
Stress Treatment (ST)	3	2241.01	747.00	237.029	< 2.2e-16	***
C x ST	3	85.56	28.52	9.050	2.758e-05	***
Residuals	88	277.33	3.15			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.17 Effects of abiotic stress on the tuber fresh weight of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	Tuber Fresh Weight (wt/pot)			
	Vegetative		Reproductive	
	‘Agria’	‘Taurus’	‘Agria’	‘Taurus’
Control	1145.0±56.1 a	1088.0±46.7 a	1203.0±76.7 a	1156.0±20.2 a
Drought (D)	930.6±57.1 b	877.9±36.0 b	919.4±87.0 b	856.8±7.6 b
Heat (H)	831.5±71.1 b	801.2±42.2 b	953.8±38.0 b	835.5±23.0 b
D + H	572.8±69.0 c	724.4±41.6 b	852.9±38.2 b	871.2±18.9 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	2687	2687	0.2144	0.64546	ns
Growth Stage (GS)	1	117809	117809	9.3985	0.00356	**
Stress Treatment (ST)	3	1441669	480556	38.3373	8.583e-13	***
C x GS	1	15016	15016	1.1979	0.27920	ns
C x ST	3	71449	23816	1.9000	0.14220	ns
GS x ST	3	91073	30358	2.4219	0.07736	.
C x GS x ST	3	10593	3531	0.2817	0.83834	ns
Residuals	48	601678	12535			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.18 Effects of abiotic stress on the marketable tuber fresh weight of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	Marketable Tuber Fresh Weight (wt/pot)			
	Vegetative		Reproductive	
	‘Agria’	‘Taurus’	‘Agria’	‘Taurus’
Control	973.5±53.8 a	904.2±30.9 a	1017.9±98.9 a	1138.9±24.2 a
Drought (D)	779.3±95.9 ab	741.2±40.6 b	754.3±54.1 ab	808.0±13.0 b
Heat (H)	625.5±50.5 ab	664.6±55.5 b	423.2±75.9 b	673.2±75.9 b
D + H	420.5±98.3 b	526.2±48.2 b	578.3±40.6 ab	578.0±17.9 b

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	131896	131896	5.1329	0.028026	*
Growth Stage (GS)	1	74142	74142	2.8853	0.095865	.
Stress Treatment (ST)	3	771735	257245	10.0110	3.093e-05	***
C x GS	1	4820	4820	0.1876	0.666896	ns
C x ST	3	136607	45536	1.7721	0.165077	ns
GS x ST	3	419537	139846	5.4422	0.002652	**
C x GS x ST	3	59693	19898	0.7743	0.514078	ns
Residuals	48	1233424	25696			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.19 Effects of abiotic stress on the number of tubers of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	No. of Tubers (count/pot)			
	Vegetative		Reproductive	
	‘Agria’	‘Taurus’	‘Agria’	‘Taurus’
Control	11.4±2.4 a	16.6±2.3 a	10.0±0.5 a	19.3±1.6 b
Drought (D)	9.0±0.6 a	15.2±2.1 a	5.7±0.3 a	15.3±1.9 b
Heat (H)	7.4±0.9 a	18.4±1.3 a	13.3±1.8 a	23.0±1.6 ab
D + H	5.8±0.3 a	16.4±1.4 a	10.3±1.8 a	29.7±4.3 a

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	1491.89	1491.89	110.2382	5.014e-14	***
Growth Stage (GS)	1	164.18	164.18	12.1312	0.001068	**
Stress Treatment (ST)	3	112.80	37.60	2.7782	0.051159	.
C x GS	1	52.73	52.73	3.8966	0.054153	.
C x ST	3	126.42	42.14	3.1138	0.034757	*
GS x ST	3	248.14	82.71	6.1119	0.001315	**
C x GS x ST	3	47.72	15.91	1.1754	0.328956	ns
Residuals	48	649.60	13.53			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.20 Effects of abiotic stress on the number of marketable tubers of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**No. of Marketable Tubers (count/pot)**			
	Vegetative		**Reproductive**	
	‘Agria’	**‘Taurus’**	**‘Agria’**	**‘Taurus’**
Control	5.4±0.6 a	11.0±1.7 a	5.0±0.4 a	11.3±0.9 a
Drought (D)	5.8±0.6 a	10.4±1.1 a	4.3±0.3 a	10.0±1.2 a
Heat (H)	4.8±0.7 a	9.6±0.9 a	3.7±0.3 a	11.0±1.5 a
D + H	3.2±0.8 a	9.8±0.7 a	4.7±0.9 a	11.7±0.5 a

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	546.39	546.39	128.4785	3.581e-15	***
Growth Stage (GS)	1	0.65	0.65	0.1531	0.6973	ns
Stress Treatment (ST)	3	11.42	3.81	0.8952	0.4505	ns
C x GS	1	5.25	5.25	1.2347	0.2720	ns
C x ST	3	6.17	2.06	0.4838	0.6951	ns
GS x ST	3	13.10	4.37	1.0270	0.3890	ns
C x GS x ST	3	2.49	0.83	0.1949	0.8994	ns
Residuals	48	204.13	4.25			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.21 Effects of abiotic stress on the dry matter content of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Stress Treatment	**Dry Matter Content (%)**			
	Vegetative		**Reproductive**	
	‘Agria’	**‘Taurus’**	**‘Agria’**	**‘Taurus’**
Control	20.5±1.5 a	23.5±0.5 a	19.1±0.4 a	22.5±0.1 a
Drought (D)	19.3±0.2 b	23.0±0.7 b	18.1±0.0 a	21.2±0.5 a
Heat (H)	19.0±0.4 b	22.3±0.2 b	18.8±0.9 a	21.7±0.3 a
D + H	19.7±0.7 b	22.3±0.4 b	18.1±0.4 a	21.4±0.3 a

ANOVA

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	236.006	236.006	117.004	1.820e-14	***
Growth Stage (GS)	1	20.798	20.798	10.311	0.002362	**
Stress Treatment (ST)	3	260.639	86.880	43.072	1.174e-13	***
C x GS	1	4.579	4.579	2.270	0.138451	
C x ST	3	22.220	7.407	3.672	0.018414	*
GS x ST	3	223.246	74.415	36.892	1.630e-12	***
C x GS x ST	3	10.354	3.451	1.711	0.177243	ns
Residuals	48	96.820	2.017			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.22 Effects of abiotic stress on the tuber size distribution of potato cultivars 'Agria' and 'Taurus' at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Cultivars	Tuber Size Distribution[a]							
	Large (>90 mm)***		Table (51–90 mm)**		Gourmet (31–50 mm)^{ns}		Undersize (<30 mm) ^{ns}	
	Ave. No. /plant	%	Ave. No. /plant	%	Ave. No. /plant	%	Ave. No. /plant	%
'Agria' – Vegetative								
Control	1.4±0.4 bc	12.3	4.4±0.8 a	38.6	2.4±1.4 a	21.1	3.2±1.4 a	28.1
Drought	2.6±0.4 a	28.9	2.6±0.4 a	28.9	1.8±0.2 a	20.0	2.0±0.0 a	22.2
Heat	2.0±0.4 b	27.0	3.4±1.0 a	45.9	0.6±0.2 a	8.1	1.4±0.6 a	18.9
D + H	1.0±0.3 c	17.2	3.0±0.3 a	51.7	0.4±0.0 a	6.9	1.4±0.7 a	24.1
'Taurus' – Vegetative								
Control	0.2±0.2 a	1.2	7.4±1.4 a	44.6	7.2±1.7 a	43.4	1.8±1.1 a	10.8
Drought	0.2±0.2 a	1.3	7.6±0.7 a	50.0	5.0±1.6 a	32.9	2.4±1.0 a	15.8
Heat	0.0±0.0 a	0.0	8.6±1.3 a	46.7	5.0±0.5 a	27.2	4.8±0.8 a	26.1
D + H	0.0±0.0 a	0.0	6.0±0.4 a	36.6	5.4±0.8 a	32.9	5.0±1.1 a	30.5
'Agria' – Reproductive								
Control	2.0±0.0 ab	20.0	5.3±0.7 a	53.3	2.0±0.6 a	20.0	0.7±0.3 a	6.7
Drought	2.0±0.6 ab	35.3	2.7±0.3 a	47.1	1.0±0.6 a	17.6	0.0±0.0 a	0.0
Heat	1.7±0.3 c	12.5	3.3±0.9 a	25.1	3.7±1.5 a	27.6	4.7±0.9 a	35.1
D + H	3.0±0.0 a	29.0	3.3±0.9 a	32.3	1.0±0.6 a	9.7	3.0±1.7 a	29.0
'Taurus' – Reproductive								
Control	0.0±0.0 a	0.0	7.3±0.7 a	37.9	3.7±1.5 a	19.0	8.3±0.7 a	43.1
Drought	0.0±0.0 a	0.0	5.7±0.9 a	37.0	4.7±0.9 a	30.4	5.0±1.2 a	32.6
Heat	0.0±0.0 a	0.0	5.0±1.5 a	21.7	7.3±1.3 a	31.9	10.7±1.5 a	46.4
D + H	0.0±0.0 a	0.0	4.7±0.7 a	15.7	8.0±1.5 a	26.9	17.0±3.0 a	57.2

Continuation Appendix 5.22…

ANOVA – Large size

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	54.391	54.391	156.645	< 2e-16	***
Growth Stage (GS)	1	0.376	0.376	1.083	0.30324	
Stress Treatment (ST)	3	1.547	0.516	1.485	0.23046	
C x GS	1	1.001	1.001	2.883	0.09599	.
C x ST	3	1.172	0.391	1.125	0.34832	
GS x ST	3	4.228	1.409	4.059	0.01193	*
C x GS x ST	3	3.603	1.201	3.459	0.02344	*
Residuals	48	16.667	0.347			

ANOVA – Table size

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	172.266	172.266	51.7228	3.738e-09	***
Growth Stage (GS)	1	7.526	7.526	2.2597	0.13933	
Stress Treatment (ST)	3	27.422	9.141	2.7445	0.05320	.
C x GS	1	15.759	15.759	4.7318	0.03457	*
C x ST	3	10.172	3.391	1.0180	0.39297	
GS x ST	3	9.986	3.329	0.9995	0.40122	
C x GS x ST	3	3.236	1.079	0.3239	0.80804	
Residuals	48	159.867	3.331			

ANOVA – Gourmet size

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	284.766	284.766	67.3116	1.083e-10	***
Growth Stage (GS)	1	2.926	2.926	0.6916	0.40972	ns
Stress Treatment (ST)	3	6.922	2.307	0.5454	0.65363	ns
C x GS	1	0.459	0.459	1.0772	0.74319	ns
C x ST	3	13.672	4.557	1.0772	0.36766	ns
GS x ST	3	49.720	16.573	3.9175	0.01397	*
C x GS x ST	3	13.203	4.401	1.0403	0.38327	ns
Residuals	48	203.067	4.231			

ANOVA – Undersize

	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	256.00	256.00	36.7171	2.034e-07	***
Growth Stage (GS)	1	175.10	175.104	25.1145	7.753e-06	***
Stress Treatment (ST)	3	114.06	38.021	5.4532	0.002621	**
C x GS	1	166.67	166.667	23.9044	1.174e-05	***
C x ST	3	79.62	26.542	3.8068	0.015822	*
GS x ST	3	91.84	30.612	4.3906	0.008263	**
C x GS x ST	3	37.98	12.658	1.8155	0.156919	ns
Residuals	48	334.67	6.972			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test ($P \leq 0.05$); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

Appendix 5.23 Effects of abiotic stress on the tuber physiological disorders of potato cultivars ‘Agria’ and ‘Taurus’ at the vegetative and reproductive stages in the glasshouse during the 2019/2020 season.

Treatments	**Tuber Physiological Disorders**					
	Tuber Malformation		**Second Growth**		**Enlarged Lenticels**	
	Ave. No. /plant	**%**	**Ave. No. /plant**	**%**	**Ave. No. /plant**	**%**
‘Agria’ – Vegetative						
Control	0.0±0.0 b	0.0	0.0±0.0 c	0.0	5.0±0.8 a	43.9
Drought	4.4±0.9 a	48.9	0.0±0.0 c	0.0	3.0±0.4 ab	33.3
Heat	3.6±0.4 a	48.6	3.0±0.3 a	40.5	5.0±0.6 a	67.6
D + H	4.0±0.8 a	69.0	1.4±0.4 b	24.1	1.4±0.2 b	24.1
‘Taurus’ – Vegetative						
Control	0.0±0.0 a	0.0	0.0±0.0 a	0.0	6.0±0.8 a	36.1
Drought	1.8±0.6 a	11.8	0.0±0.0 a	0.0	4.2±1.0 ab	27.6
Heat	0.0±0.0 a	0.0	0.0±0.0 a	0.0	5.2±1.1 a	28.3
D + H	2.0±0.4 a	12.2	0.0±0.0 a	0.0	1.8±1.1 b	11.0
‘Agria’ – Reproductive						
Control	3.7±0.3 b	36.7	0.0±0.0 b	0.0	3.0±0.6 a	30.0
Drought	2.7±0.7 b	47.1	0.0±0.0 b	0.0	1.7±0.3 a	29.4
Heat	8.3±1.0 a	62.7	1.7±0.7 a	12.5	4.0±0.0 a	30.1
D + H	5.0±0.6 b	48.4	0.0±0.0 b	0.0	1.0±1.0 a	9.7
‘Taurus’ – Reproductive						
Control	0.0±0.0 b	0.0	0.0±0.0 a	0.0	3.3±0.9 ab	17.2
Drought	1.3±0.0 ab	8.7	0.0±0.0 a	0.0	6.0±1.5 a	39.1
Heat	4.0±1.2 a	17.4	0.0±0.0 a	0.0	6.3±1.5 a	27.5
D + H	2.0±1.0 ab	6.7	0.0±0.0 a	0.0	0.0±0.0 b	0.0

Continuation Appendix 5.23…

ANOVA – Tuber Malformation						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	95.063	95.063	53.1405	2.648e-09	***
Growth Stage (GS)	1	29.400	29.400	16.4348	0.0001837	***
Stress Treatment (ST)	3	74.750	24.917	13.9286	1.163e-06	***
C x GS	1	4.004	4.004	2.2384	0.1411709	
C x ST	3	13.188	4.396	2.4573	0.0742354	.
GS x ST	3	60.183	20.061	11.2143	1.077e-05	***
C x GS x ST	3	11.546	3.849	2.1514	0.1060315	ns
Residuals	48	85.867	1.789			

ANOVA – Second Growth						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	11.3906	11.3906	69.5021	6.854e-11	***
Growth Stage (GS)	1	1.7510	1.7510	10.6843	0.002001	**
Stress Treatment (ST)	3	16.6719	5.5573	33.9089	6.486e-12	***
C x GS	1	1.7510	1.7510	10.6843	0.002001	**
C x ST	3	16.6719	5.5573	33.9089	6.486e-12	***
GS x ST	3	1.7531	0.5844	3.5657	0.020767	*
C x GS x ST	3	1.7531	0.5844	3.5657	0.020767	*
Residuals	48	7.8667	0.1639			

ANOVA – Enlarged Lenticels						
	df	Sum Sq	Mean Sq	F value	Pr (>F)	
Cultivar (C)	1	16.000	16.000	5.8359	0.01956	*
Growth Stage (GS)	1	9.204	9.204	3.3571	0.07312	.
Stress Treatment (ST)	3	147.063	49.021	17.8799	6.285e-08	**
C x GS	1	2.400	2.400	0.8754	0.35415	ns
C x ST	3	12.875	4.292	1.5653	0.20997	ns
GS x ST	3	15.971	5.324	1.9417	0.13543	ns
C x GS x ST	3	13.325	4.442	1.6201	0.19704	ns
Residuals	48	131.600	2.742			

Means ± standard error are presented; Different letters in a column within each cultivar and each growth stage indicate means are statistically different on Tukey's HSD test (P ≤ 0.05); Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'ns' not significant.

PUBLICATIONS

1. Siano, A.B., N. Roskruge, L.H.J., Kerchkhoffs, and S. Sofkova-Bobcheva. (2018) Yield and tuber quality variability in commercial potato cultivars under abiotic stress in New Zealand. Agron N Z 48:149–163.

2. Salinger, M. J., Diamond, H. J., Behrens, E., Fernandez, D., Fitzharris, B. B., Herold, N., Johnstone, P., Kerckhoffs, L. H. J., Mullan, A. B., Parker, A. K., Renwick, J., Scofield, C., Siano, A. B., Smith, R. O., South, P. M., Sutton, P. J., Teixeira, E., Thomsen, M. S., & Trought, M. C. T. (2020). Unparalleled coupled ocean-atmosphere summer heatwaves in the New Zealand region: drivers, mechanisms and impacts. Climatic Change, 162, 485-506.