UNIVERSIDADE FEDERAL DE PELOTAS
Faculdade de Agronomia Eliseu Maciel
Programa de Pós-Graduação em Agronomia
Área de Concentração Fitomelhoramento

Tese

Identification of morpho-physiological parameters for selection of heat tolerant potato genotypes

Ruth Elena Guzmán Ardiles

Pelotas, 2023

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Tese apresentada ao Programa de Pós-Graduação em Agronomia da Universidade Federal de Pelotas, como requisito parcial à obtenção do título de Doutora em Ciências (área de conhecimento: Fitomelhoramento)

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Pelotas, 2023

Universidade Federal de Pelotas / Sistema de Bibliotecas
Catalogação na Publicação

G993i Guzmán-Ardiles, Ruth Elena

Identification of morpho-physiological parameters for selection of heat tolerant potato genotypes / Ruth Elena Guzmán-Ardiles ; Caroline Marques Castro, orientadora ; Antônio Costa de Oliveira, Luciano Carlos da Maia, coorientadores. — Pelotas, 2023.

122 f.

Tese (Doutorado) — Agronomia, Faculdade de Agronomia Eliseu Maciel, Universidade Federal de Pelotas, 2023.

1. *Solanum tuberosum*. 2. Temperatura supraótima. 3. Estresse abiótico. 4. Fotossíntese. 5. Bioquimica. I. Castro, Caroline Marques, orient. II. Oliveira, Antônio Costa de, coorient. III. Maia, Luciano Carlos da, coorient. IV. Título.

CDD : 633.491912

Elaborada por Ubirajara Buddin Cruz CRB: 10/901

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Thesis approved, as a partial requirement, to obtain the degree of Doctor of Science, Graduate Program in Agronomy, Faculty of Agronomy Eliseu Maciel, Federal University of Pelotas

Defense date: August 30th, 2023

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To God, the Lord of my life

To my godson, Mario José

To my “*papito* Ricardo” †

Acknowledgements

To God, for giving up of me never, for his Eternal love, my Shepherd, the potter's Hands of this stubborn poor clay.

To my parents, Lucho and Sonia, for supporting me with loving hughs, teachings and prayers.

To my siblings, Rosie, Juanjo† and Lijo, without your life in my life, surely I would have been a different boring person. I am happy God thought so well on putting us together and I am proud of calling you sister and brothers.

To my brother and sister in-law, Simon and Rossemery, for the joy that means to me seeing you growing in spirit and truth on the vocation each of you had been called to.

To my dearest nephews and nieces, for the ones that are on heaven and the ones I am glad to see growing up even through distance. Such a great angels God gave us to get more of His presence. For the intercession of my heavenly ones and for the opportunity of sharing love with my earthly ones.

To Professor Antônio Costa de Oliveira, for his comprehension and support during the difficult moments I had to live, for the time he made on his busy schedule to correct and improve my first published article.

To Carol Castro, the mentor God had saved for me, for her guidance, patience and commitment, which made this difficult path a captivating one.

To my teachers of the CGF, Luciano da Maia and Camila Pegoraro, for the transmission of their knowledge and the kindness that accompanies it.

To the doctors that participated of the examining committee of my qualification: Dra. Camila Pegoraro, Dr. Giovanni Olegario da Silva and Dr. Arione da Silva Pereira, for the valuable contribution to the first article.

To the doctors that participated of the examining committee of the thesis: Dr. Gustavo Maia Souza, Dra. Camila Pegoraro, Dra. Beatriz Marti Emygdio, Dra. Daiana Doring Wolter, for the time they took to read and analyze my work in order to improve it. Besides, the availability to solve my questions before the evaluation day. I have learned a lot of each of you and I am very grateful.

To all my colleagues of PPGA, for the shared moments during classes, lunches and relaxation moments.

To the interns, employees and researchers of Embrapa Clima Temperado – sede, for all the support I received during experiments.

To the professor Luciano do Amarante, for his helpful way of being and the confidence to use the Vegetal Biochemestry Laboratory, for the analysis of the second experiment. To Douglas and Eduardo, for the recommendations and for solving my doubts during the process.

To the people I met on INIA-Uruguay during the first doctoral project, especially to Dr. Danilo Cabrera, for the effort he put into ensuring that I make the most of the knowledge they had gained as a country.

To Professor Flavio Herter, PhD, for the suggestions and preoccupation of my academic process.

To my sisters of heart, Amanda and Jennifer, for the daily living, for letting me grow up in a continuous learning of everyday life.

To the friends I made during this time: Alice, Diana H. Diana Z., Giovanna, Kellyn, Júlia, Ikram, Rodrigo, Vitor Hugo, Henrique, Liane, Aline, Octávio and Izabela for the many moments we shared together, for the good conversation and, in many cases, for the help on my academic work, through suggestions, teachings and more.

To Maleja, my little Colombian niece, for being such a special girl.

To my spiritual directors and intercessors, thanks for the yes given to God. He knows this soul of mine is a difficult one.

To the women of the Saturday´s “Circulo”, for the supportive group it became in order to live in this world without belonging to it. To the *Opus Dei* spirituality, through where God helps me see my work with supernatural sense.

“O Senhor desfaz os planos das nações
e os projetos que os povos se propõem.
Mas os desígnios do Senhor são para sempre,
e os pensamentos que ele traz no coração,
de geração em geração, vão perdurar.“
(Salmo 32:10-11)

Resumo

GUZMÁN-ARDILES, Ruth Elena**. Identificação de parâmetros morfofisiológicos para seleção de genótipos de batata para tolerância ao calor.** 2023. 122 f. Tese (Doutorado em Agronomia - Fitomelhoramento) - Programa de Pós-Graduação em Agronomia, Faculdade de Agronomia Eliseu Maciel, Universidade Federal de Pelotas, Pelotas.

A batata (*Solanum tuberosum*) é uma espécie com origem e domesticação nos Andes peruano-boliviano, sendo por isso, conhecida como cultura de clima frio. Com a expansão da área de cultivo para os trópicos e os prognósticos das mudanças climáticas, o efeito do estresse térmico no cultivo de batata é uma das maiores preocupações dos programas de melhoramento genético de batata. A eficácia na obtenção de genótipos tolerantes ao calor pode ser melhorada através de estudos multidisciplinares, envolvendo, além da genética, a fisiologia vegetal, assim como outras áreas do conhecimento. Com isso, o objetivo deste trabalho foi identificar parâmetros morfofisiológicos responsáveis pela maior adaptação da batata às condições de alta temperatura. Para tal, dois estudos foram conduzidos. O objetivo do primeiro estudo foi determinar a possibilidade de selecionar genótipos tolerantes ao calor usando métodos de avaliação não destrutivos, tendo como base as duas fases da fotossíntese da batata. Para tanto, oito genótipos de batata foram caracterizados de acordo com sua resposta à diferentes regimes térmicos. Foram analisadas a fluorescência da clorofila a e as variáveis de trocas gasosas, além da medição de variáveis morfoagronômicas. O segundo estudo teve como objetivo identificar a melhor época para realizar o screening de germoplasma para avaliação de tolerância ao calor, assim como as principais características morfológicas, bioquímicas e fisiológicas associadas à essa resposta. Para tal, quatro genótipos de batata foram submetidos a dois regimes de temperatura, controle e estresse. Foram realizadas avaliações em três épocas, início do período de tuberização, início de estágio de enchimento de tubérculo e final de fase de enchimento de tubérculos. O estresse por temperatura supraótima causou prejuízo na produção de energia e glicose devido ao fechamento dos estômatos, afetando negativamente o rendimento e a qualidade dos tubérculos. Os parâmetros fotossintéticos mostram-se como bons indicadores de tolerância ao calor, especialmente quando a avaliação é realizada no início da fase de tuberização sendo, dessa forma, as variáveis fotossintéticas as que melhor indicam a tolerância.

Palavras-chave: *Solanum tuberosum*. Temperatura supraótima. Estresse abiótico. Fitomelhoramento. Fotossíntese. Bioquimica. Qualidade de tubérculo.

Abstract

GUZMÁN-ARDILES, Ruth Elena. **Identification of morpho-physiological parameters for selection of heat tolerant potato genotypes.** 2023. 122 p. Thesis (Doctorate degree in Agronomy – Plant breeding) - Postgraduate Program in Agronomy, Faculty of Agronomy Eliseu Maciel, Federal University of Pelotas, Pelotas.

Potato (Solanum tuberosum) is a species with origin and domestication in the Peruvian-Bolivian Andes, and is therefore known as a cold climate crop. With the expansion of the cultivation area to the tropics and climate change forecasts, the effect of heat stress on potato crop is one of the biggest concerns in potato breeding programs. The effectiveness in obtaining heat-tolerant genotypes can be improved through multidisciplinary studies, involving, in addition to genetics, plant physiology, as well as other areas of knowledge. Therefore, the objective of this work was to identify morphophysiological parameters responsible for the greater adaptation of potatoes to high temperature conditions. To this end, two studies were conducted. The objective of the first study was to determine the possibility of selecting heat-tolerant genotypes using non-destructive evaluation methods, based on the two phases of potato photosynthesis. To this end, eight potato genotypes were characterized according to their response to different thermal regimes. Chlorophyll a fluorescence and gas exchange variables were analyzed, in addition to measuring morphoagronomic variables. The second study aimed to identify the best time to carry out germplasm screening to evaluate heat tolerance, as well as the main morphological, biochemical or physiological traits associated with this response. To this end, four potato genotypes were subjected to two temperature regimes, control and stress. Assessments were carried out at three times, in the beginning of the tuberization period, in the beginning of the tuber bulk stage and the end of the tuber bulk phase. Supraoptimal temperature stress caused losses in energy and glucose production due to the closure of stomata, affecting negatively the yield and quality of tubers. Photosynthetic parameters appear to be good indicators of heat tolerance, especially when the evaluation is carried out at the beginning of the tuberization phase, with photosynthetic variables being those that best indicate tolerance.

Keywords: *Solanum tuberosum*. supraoptimal temperatures. Abiotic stress. Plant breeding. Photosynthesis. Biochemestry. Tuber quality

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1 GENERAL INTRODUCTION

Potato (*Solanum tuberosum*) is a species original from the Peruvian-Bolivian altiplano, close to Lake Titicaca, which is currently cultivated throughout the world, ranking third among the most important crops in the world. Due to its place of origin, potatoes are considered a cold climate crop and, to achieve good quality production, the environment in which they grow has been a matter of care (HAVERKORT, 1990). However, the need for more cultivation area, in addition to years with atypical climates, different types of stress have been identified in potato plants over time, such as frost, drought, salinity and heat stress (CANET *et al.*, 2005; IBGE, 2023a).

From all South America, Brazil is the fourth country with the largest cultivated area and the second country with the largest production in 2021. Worldwide, it is considered among the first 30 potato producing countries (FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS, 2022). On 2022, the country had a total production of 3.89 million tons in 117845 hectares (IBGE, 2023b). Brazilian potato production is consumed either *in natura* or as a processed food, being the main potato processing industry, the frozen pre-fried french fries and the potato chips.

The production is the result of three harvest times, the first one, with the highest contribution, occurs on summer (warm season), the second one, on autumn (dry season) and the third one, on winter (cool season) (GODOY, 2001). Minas Gerais, Paraná, São Paulo, Rio Grande do Sul, Santa Catarina, Goiás and Bahia are the main potato producing states. The three first states contributed with 70% of the annual production in Brazil (IBGE, 2023b; SILVEIRA WREGE *et al.*, 2004). These states are predominantly of temperate or tropical climate and eventhough plantation is programmed for milder temperatures seasons (SILVEIRA WREGE *et al.*, 2004), eventual elevated temperatures on tropical regions produce smaller and more ephemeral leaves (SOUZA, 2003), affecting around 25% of the production and tuber quality (GANDOLFI BENITES, 2007; MENEZES; PINTO; LAMBERT, 2001).

In addition, many authors have warned about global warming (MCCARTHY *et al.*, 2001), which could result in a temperature increase of about 0.9°C-1.7°C to 4.9-5.8°C on the coming 100 years (MCCARTHY *et al.*, 2001; WEBSTER *et al.*, 2001; WIGLEY; RAPER, 2001). This temperature increment will lead to a production decrease of about 23% on between 2040 and 2069 on tropical states (HIJMANS, 2003). Nevertheless, on greater altitudes and latitudes, or very cold places, temperature increment would allow the cultivation season to be extended (LOPES *et al.*, 2011).

At the beginning, heat tolerance was not between the main topics on potato breading programs around the world. However, due to the growing importance of this crop, the need for more area of cultivation and the climate change, gave another direction to potato breeding (BONNEL, 2008). Turning that Brazilian potato breeding programs has as a priority the development of heat tolerant clones (BENITES; PINTO, 2011). At this respect, genotype selection should be adapted to each Brazilian environment (MENEZES; PINTO; LAMBERT, 2001).

However, due to the complexity of potato breeding, its progress is slow, becoming uninteresting for scientists. Thus, efforts to make this process more dynamic are being developed, discovering that a multidisciplinary work leads to more accurate choices in breeding process (BONNEL, 2008). In this way, plant physiology is an important tool, which can show us the plant response to high temperatures and its expression in terms of productivity permitting the identification of tolerant genotypes and the increment of genetic pool in a breeding program (BITA; GERATS, 2013)

Until now, many morphologic and physiological variables has shown a behavior pattern as a response to high temperature environment (HASANUZZAMAN et al., 2013; KALAJI et al., 2016; TEIXEIRA et al., 2015; WOLF; MARANI; RUDICH, 1990). Yet, it is still essential to know which traits in the potato are involved in the process of adaptation and tolerance to higher temperatures, in order to a faster heat tolerance screening for the development of cultivars that can be grown in tropical regions.

1.1 General objective

Identify morpho-physiological parameters of potato (*Solanum tuberosum*) that will help on the screening for heat tolerance.

1.2 Specific objectives

- To determine whether it is possible to select heat tolerant genotypes for plant breeding using non-destructive evaluation methods.
- To find characters and phenological stage for heat tolerance screening on potato.

2 LITERATURE REVISION

2.1 Introduction

Potato (*Solanum tuberosum*) is an herbaceous plant that belongs to the Solanaceae family. The edible organ of this crop is a tuber, which because of the easy way of growing and the versatility in consumption, is the most eaten vegetable around the world (NAVARRE; GOYER; SHAKYA, 2009).

As a storage organ, potato tubers have a high carbohydrate - mainly starch - and protein content of quality (TOLESSA, 2018). Though has been found to have a high vitamin C content (LOVE *et al.*, 2004) , in some cases can´t be considered as an important source of it, as is diminished by storage and cooking methods (PELLETIER *et al.*, 1977; TUDELA; ESPÍN; GIL, 2002). B9 (folate) and B6 vitamins were also found on potato tubers in a range of 11 to 35 g/ 100 g fresh weight (FW) for folate (GOYER; NAVARRE, 2007) and 0.26 to 0.82 mg/200 g FW for B6 (ROGAN *et al.*, 2000), both are barely modified when cooked (AUGUSTIN *et al.*, 1980; KONINGS *et al.*, 2001). In addition, potato have been found to be rich of minerals, phenolic compounds and ascorbic acid important for human nutrition (GRUDZIŃSKA *et al.*, 2016; NAVARRE *et al.*, 2011; NAVARRE; GOYER; SHAKYA, 2009).

All of this properties depends, in a good manner, on genotype (ABBAS *et al.*, 2011; ANDRÉ *et al.*, 2009; DALE; GRIFFITHS; TODD, 2003) and is in this way that the wide range of genotypes, in the Andes, sustain local food security (DE HAAN *et al.*, 2019). At the same time, the extensive potato variety in the Andes, gives to this crop a social and cultural importance, based on a highly advanced traditional knowledge of plant diversity, breeding and culinary characteristics accumulated since the domestication of potato (DE HAAN, 2009).

For what was described above, potato has been accepted for many market sectors in every place of the world and now, with 18 million hectares worldwide, potato (*Solanum tuberosum*) is the third most important food crop in the earth (FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS, 2022) suggesting it has expanded to unusual places.

The process of domestication of a crop gives the idea of the environmental conditions it became productive, in such manner; this understanding can give tools not only for its management but also on the development of new cultivars. In such manner, this review shows the place where potato was originated, followed by the diversification and expansion of the culture, in every case the environmental situation is related. Subsequently, the ideal environment for potato cultivation is presented, highlighting temperature as one of the main environmental factors to be considered for a success in potato production.

Nevertheless, where is potato being grown now? Do these places have the ideal temperature for the crop?. If not, what are the consequences of this? All of these is discussed and, at the end, some important advances of potato breeding for heat tolerance are described.

2.2 Origin and domestication of the potato

The distribution of potato wild relatives include from central Chile and Argentina to the southern United States (SPOONER; SALAS, 2006), getting to 150 species in the Petota section (HAWKES, 1992). Thus, some nationalist researchers have suggested Mexico, Uruguay, Chile, Ecuador, Colombia and Venezuela as the place of potato origin (BRÜCHER, 1975).

Phyllogenetic studies lead to two hypothesis about where cultivated potato was originated: (1) Multiple origins: cultivated potato originated from different wild gene pools on different places through South America. Hosaka (1995) suggested that every cultivated and wild species became from a complex of ancestral species and for this reason, besides occurring along time, occurred on different south-american places. Later, the area of origin was reduced to different places in Peru, from where it later was spread to Bolivia (SUKHOTU; HOSAKA, 2006). To the latest was added that besides *S. tuberosum* subsp. andigena (or Andigenum group) originated in Peru, the Chilotanum group descended from *Solanum maglia* Schltdl and was originated in Chile (SPOONER *et al.*, 2012; UGENT; DILLEHAY; RAMIREZ, 1987). (2) Single origin: refers of *S. tuberosum* subsp. andigena (or Andigenum group) being originated from a single ancestor, *S. brevicaule* complex (UGENT, 1970), which later was described as composed by a unique species, *S. bukasovii* (SPOONER *et al.*, 2005) at the region of South Peru and North Bolivia (SPOONER, 1990) from where was later spread to the

rest of the Andes and Chile (SPOONER *et al.*, 2005). In this hypothesis, *S. tuberosum* subsp. tuberosum (or Chilotanum group) was originated through the selection of the Andigenum group potato (HOSAKA, 1995) by adapting to other conditions, as highland equatorial climates (current Colombia and Venezuela) and longer summer days in Argentina and Chile's southern latitudes (HOSAKA, 2004). The possibility of an introgression or hybridization with *S. maglia* was also related (RODRÍGUEZ *et al.*, 2010), however, this last assessment needs more documentation (SPOONER *et al.*, 2012).

On the other side, many archeological studies were developed in order to have a better knowledge at this respect. Was found that along the area where wild potato species are found, only some of them were consumed as staple food (JOHNS; ALONSO, 1990). For example, there are indications that mexican and chilean indigenous communities used tubers of Solanum species for human consumption either boiled, as chuño or accompanied with edible clays (GUTAKER *et al.*, 2019). However, literature, a high number of wild relatives, sculptures and other kind of art work points out Peru as the center of origin (BRÜCHER, 1975; JANICK, 2013; SOTOMAYOR *et al.*, 2023).

Lately, an study pointed out that the arrival of human being to South America took place between 14600 and 13100 BC, throughout Pleistocene epoch (PRATES; POLITIS; PEREZ, 2020). Coherently, there are signs that 13000 years ago of Peruvian and Chilean coastal gatherers used wild potato tubers for consumption (UGENT; DILLEHAY; RAMIREZ, 1987; UGENT; PETERSON, 1988). During this epoch, glaciation processes occurred, modifying the sea level and the coastal Peruvian environment, since it was more inland, it was not as warmer as it is now (TATUR *et al.*, 2002; UGENT; PETERSON, 1988). At the end of terminal Pleistocene there was a limitation of water at the south coast of Peru, leading people to their first contact with the highlands for gathering and hunting, going back to the coast for fishing (SANDWEISS, 2003; SANDWEISS *et al.*, 1998).

The characteristics of potatoes found at the Chilca Canyon, dated of approximately 8000 BC (ENGEL, 1970), suggest potatoes were cultivated since then (UGENT; POZORSKI; POZORSKI, 1982). However, at that time (the beginning of Holocene), first signals of ENSO-like phenomena appeared (ANDRUS; SANDWEISS; REITZ, 2008; FONTUGNE *et al.*, 1999), making

agriculture somehow impossible. In this way, some authors suggested these potatoes got there through trade from the highlands (GRAVES, 2001). Unfortunately, the tendency to wet and freeze condition of the Peruvian Andes prevent organic matter conservation and not tuber remains from this period of time were found (PERRY, 2016).

At the same time, has been related that on the early to mid-Holocene epoch, a late glacial ice seems to have covered from around 9°S to as far south as 40°S, except for the mountains that border the Altiplano, between Peru and Bolivia (RODBELL; SMITH; MARK, 2009). In this way, there are evidences that Asana, a site that sits 3350 masl at the south of Peru, was first occupied in 9830 ± 160 cal BP (ALDENDERFER, Mark S., 1998), however, was very limited as the acclimation of human being to hypoxia took more time than to other environmental conditions (CAPRILES *et al.*, 2016).

Later, the occurrence of the last deglaciation, the shrinking of the massive glacial lakes and the availability of more water would have also revealed new Andean land for animal and plant species to expand (ALDENDERFER, Mark, 1999). At the same time, on the peruvian coast the consequent stabilization of eustatic sea level, gave good conditions for the establishment of human being, opening the late pre-ceramic period (SANDWEISS *et al.*, 2009). At this time (8000 - 3600 years ago) the sea surface temperature was cooler in the whole Peruvian littoral and El Niño Southern Oscillation (ENSO) started to appear in a low frequency, besides the diminishing of water supply from the highlands, which limited human occupation around some rivers (SANDWEISS, 2003; SANDWEISS; QUILTER, 2012). This is how potato remains were found in the Casma Valley, belonging to the Andean pre-ceramic period (2000 BC) and initial ceramic period (1200 BC) (UGENT; POZORSKI; POZORSKI, 1982). In addition, starch remains of potatoes were recently found from 3600 to 4000 years ago in the Cotahuasy Valley, in Arequipa (PERRY, 2016).

At this point, Ugent and Peterson (1988), suggested that the wild potato species which had previously been gathered from coastal Peru's higher river valleys and prehistoric savanna areas were now domesticated at highlands. The topography of Andes permitted the growth of many vegetal species, including potato, on different climatic conditions, thus creating a great genetic diversity of this species (GRAVES, 2001). Moreover, because of their subsequent

intermixing, intercrossing, and polyploidization, these ancestors merged at various chromosomal levels to create our modern cultigens. So, through the collected information seems like potato was first cultivated around 8000 BC and wild relative species distribution points out that the first place where this happened was in the northern Bolivian, southern Peru, at the region of Lake Titicaca/Lake Poopó (HAWKES, 1992; SPOONER *et al.*, 2005). Here, there are not more tuber remains that those found on the archeological sites at Chiripa, around the Lake Titicaca shore belonging to the initial formative period (1800 – 900 BC) (TOWLE, 1961).

Evidences proposed that after 1800 BC, the potato cultivation region stretched from the Casma Valley in the Department of Ancash to the city of Pisco in the Department of Ica, located to the south of Lima (UGENT; PETERSON, 1988). Ceramics found in Peru belonging to the Moche (100 BC – 800 AD), Chimu (1101-1500 AD) (Salaman, 1946) and Inca cultures (1438-1533 AD), as well as in the ceremonial vessels of the pre-Inca culture Tiahuanaco-Huari in 900 AD (Hawkes, 1992), provide insights of the use of potato in agriculture. For the places were potato was found to be domesticated can be seen the preference of this species for milder temperature conditions.

Many authors coincide on the fact that domestication started with the *S. brevicaule* complex, resulting in *S. stenotonum* (BRADSHAW; BRYAN; RAMSAY, 2006). From this last species three cultivated species were obtained: (a) *S. phureja* (2x) adapted to lower, warmer easter valleys of the Andes; (b) *S. tuberosum* subsp. andigena (or *S. tuberosum* group Andigenum, 2n = 4x = 48), the most cultivated in south America; (3) *S. tuberosum* subsp. tuberosum (or *S. tuberosum* group Chilotanum, 2n = 4x = 48), obtained from the andigena group, adapted to long days (BRADSHAW; BRYAN; RAMSAY, 2006; HARDIGAN *et al.*, 2017).

Potato's domestication reduced glycoalkaloid content (JOHNS; ALONSO, 1990) and modified the carbohydrate metabolism (JANSEN *et al.*, 2001), making it edible, permitting, in this way, the emergence of Highland cultures (La Barre cited by Hawkes, 1992).

2.3 Expansion of the crop

By 1524, Francisco Pizarro, Diego de Almagro and Hernando de Luque decided to conquer the Inca Empire, but it was not until 1532 that they actually managed to do so, subsequent to the capture and death of the Inca Atahualpa (PORTUGAL; MORAIS, 2012). Was just in this way that they got to conquer the empire, realizing, among other things, on the wealth of its agriculture, for what they sent some samples of agricultural products to the king of Spain, including potato tubers, by 1533 (CIEZA DE LEÓN, 1554).

Considering that potato was already a crop, samples taken to Europe during XVI and XVII centuries, were polyploidy cultigens and not wild species. Was from this reduced genetic diversity that European botanists reproduced the crop from sexual and asexual seeds (BRÜCHER, 1975; DAYDON JACKSON, 1896). Hawkes (1992) describes in detail the ways potato got to other countries inside and outside Europe from Spain, and suggests that the *S. tuberosum* group that arrived to Spain was Andigenum and there went through an adaptation process, changing to the group Chilotanum. In fact, *Solanum tuberosum* subsp. tuberosum (or group Chilotanum) supplied much of the genetic background in commercial cultivars worldwide (HARDIGAN *et al.*, 2017). On the other hand, there is an hypothesis that declare Europe as a “melting pot of multiple potato varieties” coming from different places of South America (GUTAKER *et al.*, 2019).

At the beginning, the tuber crop was not well accepted due to its aspect, but as it became known on taste and nutritional quality, was quickly spread (BRÜCHER, 1975). In this way, *S. tuberosum* has adapted to not too hot nor too cold weathers with short summer days in highland tropics and sub-tropics, long summer days in lowland temperate zones, and lastly short winter days in lowland sub-tropics and tropics (BRADSHAW; BRYAN; RAMSAY, 2006).

2.4 Ideal environment for potato

The first appearance of tuber-bearing Solanum occurred 1.5 million year after the divergence of potato and tomato (KAWAGOE; KIKUTA, 1991) through an evolutionary adaptation to the environment it developed. Along with serving as a mode of asexual reproduction, tubers emerged as a species' evolutionary adaptation to help it endure lengthy periods of abiotic stress and winter (VALENCIA-LOZANO *et al.*, 2022).

In potato, the storage organ is the edible one, so yield is measured in terms of tuber production and, for this reason, environmental conditions in which the plant produces more tubers are desired, which are cold but not freez temperatures. Many researchers have tried to determine the temperature this crop develops better, stablishing different ranges according to the development stage of the plant.

After harvest, tubers enter into dormancy which is broken through a change of hormonal balance, being the cytokinin the main hormone responsible for budbreak and giberellin the responsible for sprouting (HARTMANN *et al.*, 2011). At this moment, optimal temperature is of 20°C (KLEMKE; MOLL, 1990), to less than 25°C (FIRMAN; O'BRIEN; ALLEN, 1992). For stolons' growth and branching, temperatures around 25°C are beneficial (STRUIK, 2007), but extremely high temperature becomes detrimental, specially when acompanied with high soil temperature (STRUIK; GEERTSEMA; CUSTERS, 1989).

Tuber initiation is the most heat-sensitive stage of potato growth and development (KIM; LEE, 2019; STRUIK, 2007) and consists on the change of growth direction, from longitudinal to radial via hormonal regulation (VREUGDENHIL, 2004), which has been proved to be suppressed under temperature above 20°C (HANCOCK *et al.*, 2014). So, although high temperatures don't repress stolon growth, it can repress tuber initiation (EWING; STRUIK, 1992). Some authors declare tuberization is reliant on the time high temperatures occur, being adverse during night (MINHAS *et al.*, 2001; WOLF; MARANI; RUDICH, 1990).

Once tubers are formed, they act as organs that store photosynthates as starch, therefore any environmental change that speeds up respiration more than photosynthesis, could have an impact on the yield outcome (Souza, 2003). In this way, Hancock et al. (2014) found that temperatures of 30/20 °C day/night negativey affected tuber dry matter and harvest index, being ideal temperatures in the 15-20 °C range (MOMČILOVIĆ *et al.*, 2016). However, the rate at which assimilate partitioning from shoot to tuber happens is affected also by photoperiod (KOOMAN; HAVERKORT, 1995).

Although the influence temperature has on each stage depends in a good size on the genetic factor (EWING; STRUIK, 1992; STRUIK, 2007), in every case, elevated soil and air temperature was observed to decrease tuber yield

(RANDENI; CAESAR, 1986; REYNOLDS, M. P.; EWING, 1989; STRUIK; GEERTSEMA; CUSTERS, 1989)

2.5 Potato around the world

Potato, the third most important crop in the world is cultivated in every continent, in 149 countries. However, the world cultivation area of potato have diminished, because of a decline of cultivation area on developed countries, while on developing countries this tuber crop takes more importance as a staple food (HIJMANS, 2001).

Fifty percent of the total area is cultivated in Asia (FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS, 2022). In this continent, potato is grown as a winter crop on hot places, while on warm places, they are cultivated in all seasons (HIJMANS, 2001)

Europe, with four million hectares, is the second continent with more potato-harvested area (FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS, 2022). Besides, the relative potato area over total land area (RPA) in the areas where potato is traditionally grown is very high (HIJMANS, 2001).

Africa and America have almost the same potato cultivated area (FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS, 2022). However, in America the Bolivian, Colombian and Peruvian Andes have the highest RPA, while in Africa, North Africa, Ethiopia, East African Highlands and in South Africa have the highest RPA (HIJMANS, 2001)

Talking about latitudes, the main potato cultivated area is in the northern hemisphere's temperate zone, during summer when there are no frosts. In tropics, it is grown on high altitudes. In the subtropic zone, depending on the system and altitude, potato is grown during summer, spring, autumn or winter, during heat-free period (DEVAUX, André *et al.*, 2021; WEI, 1997).

In summary, has been observed that either by location, either by time of plantation, farmers have looked for cold in order to have a good production. However, since 1950 the expansion of this crop to lower latitudes has exposed it to high temperatures (THIELE *et al.*, 2008), even above 30°C, as in Nigeria, India, and coast of Peru (HAVERKORT *et al.*, 2013) facing heat stress (MONNEVEUX *et al.*, 2014) and high rate of pests appearance (VAN DER WAALS *et al.*, 2013).

Also, some places like in temperate north America, there is an increase of production areas and seasonality (WALKER; SCHMIEDICHE; HIJMANS, 1999), demonstrating a migration or expansion of this crop, therefore expanding the need of other kind of technologies.

2.6 Heat effect on potato

It´s known that high temperature affects plant cells metabolically, physiologically and morphologically. Beginning with protein and membrane destabilization, continuing with photosynthesis inhibition, high production of oxygen reactive species, negative modulation of the levels of hormones, primary and secondary metabolites, and if the condition continues, cellular death may occur (HEMANTARANJAN, 2014).

Potato plants showed to be more sensitive to high temperature during tuber bulking than during tuber formation as the photosynthetic rate decreased faster (AIEN; KHETARPAL; SINGH, 2011). Although it may also depends on the species (Havaux, 1995), cultivar (AIEN; KHETARPAL; SINGH, 2011; NAGARAJAN; SINGH MINHAS, 1995; PRANGE *et al.*, 1990) and on the interaction with other environmental factors (LIZANA *et al.*, 2017; REYNOLDS, Matthew E; EWING, 1989; WOLF; MARANI; RUDICH, 1990).

2.6.1 Physiology

The edible organ of potato is a tuber, a subterranean stem that serves as carbohydrate reservoir for the plant. In this way, tuber production depends, basically, on the energy and carbohyrates production through photosynthesis. Photosynthesis occurs in the chloroplasts of the mesophyll cells and is composed of two phases: photochemical phase and biochemical phase. The first one takes place on the thylakoid membrane of the chloroplasts and is responsible for converting light energy into chemical energy, generating energy molecules (ATP and NADPH) (MARDER; BARBER, 1989), that will be used in many metabolic process, including the second phase of photosynthesis. The biochemical phases takes place in the estroma and consists on the fixation and reduction of CO2 in organic compounds, having as the first product the glucose (LEVINE, 1969).

Havaux (1993) found that high temperature affect differently to the thylakoid proteins, being water splitting inhibited at around 32°C, followed by

inactivation of PSII, electron transport modification at around 42°C and PSI appeared to be the most tolerant thylakoid protein to heat. On the contrary, Kaur et al. (2023) observed a highest heat tolerance on PSII and PSI than on the intersystem electron transport, however this is dependent on genotypes and other environmental factors.

Either way, in general, heat stress has been observed to induce hyperfluidization of thylakoid membranes, which in long periods of time could lead to a loss of PSII function (HAVAUX, 1995; RISTIC; BUKOVNIK; PRASAD, 2007), expressed in high chlorophyll fluorescence (SCHREIBER; BERRY, 1977). This suggests a less re-oxidation of the electron acceptors in PSII, resulting in decreased photosynthesis (Sipos and Prange, 1986). In addition, the non-photochemical quenching (NPQ) mechanism is activated as a protection of the PSII (ÖGREN, 1991).

The effect on the biochemical phase (Calvin cycle) will depend on the period of time plants are exposed to this condition. First, an increase of stomatal conductance and transpiration rate was observed (DEMIREL *et al.*, 2017). However, over time, temperature affects the mechanism of ABA action on guard cells or the distribution of ABA within the leaf, leading to a closure of the stomata and, thus, limited CO_2 entrance (CORNIC; GHASHGHAIE, 1991). At last, carbon fixation gets inhibited due to the inactivation of Rubisco (BERRY; BJORKMAN, 1980).

As other biotic or abiotic stresses, heat also cause an elevated production of reactive oxygen species (ROS) and malondialdehyde (MDA) (MITTLER, 2002). In order to maintain the cellular homeostasis, a defense mechanism is activated, which consists antioxidative enzymes, such as catalase (CAT), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR), besides the non-enzymatic antioxidants, such as ascorbate (AsA), glutathione (GSH), anthocyanin, phenolics, flavonoids, soluble sugars content (ALLAKHVERDIEV *et al.*, 2008)

Furthermore, molecular analysis revealed higher expression of transcripts that encodes polypeptides associated with PSII, ferredoxins, subunits of RuBisCo, RuBisCo activase and some Calvin cycle enzymes on plants grown under moderate high temperature (USADEL *et al.*, 2005)

2.6.2 Morpho-agronomic

In potato, earlier studies showed higher plants, with heavier haulm, thinner stems, higher leaf area index, longer internodes, more acute leaf angle and more axillary branching when submitted to high temperatures (DEMIREL *et al.*, 2017; NAGARAJAN; SINGH MINHAS, 1995). Aerial enhancement seems to occur in detriment of tuber dry matter as a result of C partitioning and starch accumulation impairment (HANCOCK *et al.*, 2014). Thus, in some cases, a decrease or even the inhibition of tuber formation (DEMIREL *et al.*, 2017; LEVY; VEILLEUX, 2007; REYNOLDS, Matthew E; EWING, 1989).

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2.6.3 Tuber quality

High temperatures during tuber bulking affect chipping potato quality, as enhances amino acid and reducing sugar content, because tuber growth outstrip starch deposition rate (BUSSE; WIBERLEY-BRADFORD; BETHKE, 2019; ZOMMICK *et al.*, 2014).

Has been described that both molecules participate in the Maillard reaction, and elevated concentration will negatively interfere on acrylamide content, color, aroma and flavor of potato chips (BUSSE; WIBERLEY-BRADFORD; BETHKE, 2019; HALFORD *et al.*, 2012; HANCOCK *et al.*, 2014; RODRIGUEZ-SAONA; WROLSTAD, 1997)

Tubers can also present mottling and translucent tissue due to high sugar content in tubers, making them undesirable for fresh market (ZOMMICK *et al.*, 2013). Also, high incidence of internal heat necrosis of potato was observed under high minimum temperatures, although other environmental factors might influence as well (YENCHO *et al.*, 2008)

Genetic factor is decisive in the affection of high temperature over any of the above itens, as observed by many authors (HERMAN; KNOWLES; KNOWLES, 2017; KIM; LEE, 2019)

2.6.4 Plant breeding for heat tolerance

Potato species and cultivars that are less affected by heat stress are the ones that either scape from stress through early initiation of tuberization ( ) or the tolerant ones. Have been observed that heat tolerant cultivars had a better

antioxidative protection by the inducibility of SOD isoforms (Rudic et al., 2022), as well as a higher stomatal conductance (Reynolds et al., 1990) which may cause a faster evaporative cooling (Aien et al, 2011) and an increment in CO_2 assimilation (Lizana et al, 2017). All of this results in a higher rate of photosynthesis and better plant growth (Aien et al., 2011).

Heat tolerance is known as a multigenic treat involving maintenance of homeostasis for proper survival under high temperature environment. Thus the knowledge of physiological plant response to high temperatures and its expression in terms of productivity is important to identify tolerant genotypes in a breeding program.

For instance, Reynolds e Ewing (1989) identified six heat tolerant accessions by evaluating their ability to have a good tuber and shoot growth under high temperature conditions. Other studies suggested high stomatal conductance, CO_2 fixation rate (Reynolds et al, 1990), the increase in internode length (Nagajaran e Minhas, 1995), higher root length and higher stomatal density (Sabina and Sameena, 2022) as selection criterion for screening heat-tolerant potato clones.

Furthermore, Demirel et al (2017) found that some traits of not-stressed plants, like haulm dry weight, leaf area index, photosynthetic rate, stomatal conductance, transpiration rate, canopy temperature, and chlorophyll index could be used for heat-tolerant genotypes selection with no need of growing them at high temperature conditions. Additionally, Gangadhar et al (2013) identified potato genes with potentials to transmit heat tolerance using a yeast-based functional screening method, some of which are also responsive to other abiotic stresses.

3 CHAPTER I: Photosynthetic and morpho-agronomic response of potato genotypes submitted to different thermal regime

3.1 Introduction

Potato (*Solanum tuberosum*) belongs to the Solanaceae family and is classified in two subspecies: andigena and tuberosum, the latest being cultivated around the world. Additionally, the edible organ of this crop is a tuber, a modified underground stem, grown at the distal tip of the stolons. Potato is native from the high Altiplano region (around 3750 masl) near Lake Titicaca (LOVE et al., 2020), a region with cold environment. Thus, the mentioned storage organ appeared as an evolutionary adaptation of the species in order to survive over winter and prolonged periods of abiotic stress, besides being a form of asexual reproduction (VALENCIA-LOZANO et al., 2022).

As most of the species of the kingdom plantae, potato is a photoautotroph organism, which means that produces its own energy via photosynthesis. Photosynthesis is a metabolic process performed by chloroplasts, and consists on the capture of light to convert water taken from the soil and carbon dioxide from the air into biochemical energy used for the production of carbohydrates (ALBERTS et al., 2002). On tuberous species during tuber induction, the first product of photosynthesis, a low-molecular-weight sugar, is used for stolon growth, which through hormonal regulation, changes its growth direction from longitudinal to radial (VREUGDENHIL, 2004). Once tuber are formed, they become the sink organs for photosynthates and are storaged as starch, thus, any change on the environment that accelerates respiration rate in a higher degree than photosynthesis will compromise the final yield result (SOUZA, 2003).

In this regard, high temperatures have been reported as disadvantageous either for photosynthesis and for photosynthates translocation (BUSSE; WIBERLEY-BRADFORD; BETHKE, 2019; HERMAN; KNOWLES; KNOWLES, 2017; REYNOLDS, Matthew P; EWING; OWENS, 1990; SINGH, Anupama *et al.*, 2015; SINGH, Baljeet; KUKREJA; GOUTAM, 2020; WANG, Huiqun *et al.*, 2009). Therefore, potato selection for heat tolerance has been, for many years, a concern of potato breeding programs around the world (TEIXEIRA et al., 2015), using, for this purpouse, phenotyping methods. Chlorophyl a fluorescence and

gas interchange measures are the most used tools for photosynthesis phenotyping, from where fluorescence gives an idea of the photochemical phase function (KOCH; NOGA; STRITTMATTER, 1994) and gas interchange with the infrared gas analyzer (IRGA), of the biochemical phase performance (PANDEY; PAUL; SINGH, 2017).

In order to understand the effect of high temperature on photosynthesis, many authors have used one of these two methos of evaluation on potato plants (AIEN et al., 2013; IERNA, 2007; KAMINSKI et al., 2014; MIENIE; DE RONDE, 2008; OBIERO; MILROY; BELL, 2020). However, few works combine both methods (LAZAREVIĆ et al., 2022; MIDMORE; PRANGE, 1991), but the first was made in a very short period of time (five days) and the second, in young plants. In this way, more studies that help to deepen the knowledge of photosynthesis process affected by high temperature are needed in order to make of these nondestructive methods reliable for plant breeding.

Therefore, the goal of this study was to determine whether it is possible to select heat tolerant genotypes for plant breeding using non-destructive evaluation methods, based on the effect different temperature regime has on the two phases of photosynthesis in potato.

3.2 Materials and methods

Plant material

The experiment took place in growth chambers at Embrapa Clima Temperado, Pelotas, Rio Grande do Sul state, Brazil, from October 2021 to January 2022. Five advanced clones from Embrapa's potato breeding program suitable for the frozen pre-fried French fries industry (Od80-02, C41, F53, O14 and F88) and three cultivars (Asterix, Markies and Innovator) (Table 1) were characterized according to their response to different thermal regimes.

Table 1. Potato cultivars used on the experiment

Cultivar	Main characteristic
Asterix	Main cultivar used for frozen pre-fried French fries in Brazil.
Markies	Main cultivar used for frozen pre-fried French fries in Brazil from a quality point of view.
Innovator	It first was used for frozen pre-fried French fries unstable in production with field problems.

The experimental design was a randomized complete block under factorial arrangement (eight genotypes and three thermal regimes) with three replicates.

Growth conditions

Potato tuber seeds (2.0 to 3.0 cm of length) were planted on October 4th, 2021 in phenolic foam moistened with nutrient solution. The tubers stayed in greenhouse (average temperature of 20oC) for fifteen days, when uniform tubers (sprouting length of 0.5 to 1.0 cm) were transplanted into 5-liter pots with organo-mineral substrate. The pots were then distributed in three growth chambers (T), each one with a distinct thermal regime (Figure 1), as follows:

- T1: control treatment, with thermal amplitude from 14°C to 27°C. Which refers to the best growing season temperatures of Cerrado biome, during winter.
- T2: heat treatment, with thermal amplitude from 24°C to 34oC. According to literature, liquid potato photosynthesis becomes negative on temperatures above 24°C (TIMLIN et al., 2006; WOLF et al., 1990)
- T3: mild heat treatment, with thermal amplitude from 17°C to 29oC. Treatment that emulate the growing season of spring-summer at Cerrado biome, considered of high risk, as temperatures become higher.

Apart from the temperature, the other environmental parameters were the same in the three chambers, photoperiod of 12 hours with 400 µmol m-2 s-1 of luminous intensity. The pots were irrigated two times in the day, until field capacity. Plants were maintained in the chambers for 87 days, when they were harvested (102 days after planting).

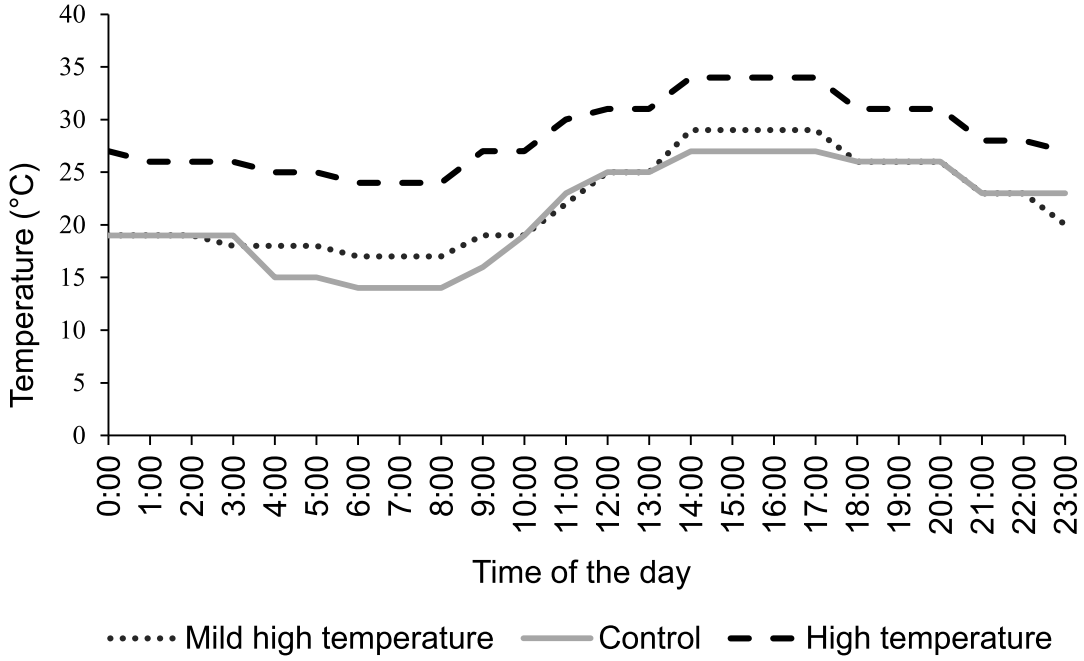

Figure 1. Daily temperatures programmed in growth chambers for three different temperature conditions: control temperature treatment (T1), high temperature treatment (T2) and mild high temperature treatment (T3). Pelotas, 2021.

Physiological analysis

Physiological traits were assessed by three measures of chlorophyll fluorescence at the 35th, 49th and 62nd day after planting (DAP) and two measures of gas exchange (54 and 69 days after planting) on the third expanded leaf counting from the top. For chlorophyll fluorescence measurement, potato leaves were dark adapted for 30 minutes in a temperature according to its treatment (T1: 27°C, T2: 34°C and T3: 29°C). Fluorescence was induced by application of saturation pulses of 7000 µmol fótons m-2 s-1 using IMAGING-PAM chlorophyll fluorometer (model PAM-2500 da Walz Heinz GmbH, Effeltrich, Germany). Obtained data was processed in a excel sheet, where maximal PS II quantum yield (Fv/Fm) was calculated according to the equation: Fv/Fm = (Fm - Fo)/Fm, considering the data generated after the first light pulse. Apparent rate of photosynthetic electron transport (ETR), non-photochemical quenching (NPQ/4), effective photosystem II quantum yield (Y(II)) and quantum yield of non-

regulated energy dissipation (Y(NO)) parameters were calculated as the average of the data obtained on light pulse of 461 and 531 PAR.

For the gas exchange analysis, values of photosynthetic rate (A), transpiratory rate (E), stomatal conductance (gs), internal CO2 concentration (Ci) were determined using infra-red gas analyser IRGA (LI- 6400XT LI-COR, Inc., Lincoln, NE, USA). Before measuring, reference CO2 and flow rate to the sample cell was set at chamber's light intensity. and temperature was set at 34°C (for T2), 29°C (for T3) and 27°C (for T1). Using the lamp annexed to the equipment, the output of quantum sensor was established at 600 µmol of photon m-2 s-1. From these results, water use efficiency (WUE) was calculated dividing A by E for each of the measure dates (54 and 69 dap).

The evaluation dates were chosen so that they begin a little before the beginning of tuberization, considering that the earliest cultivars begins tuberization, 45 DAP.

Morpho-agronomic measurements

At harvest time, 102 DAP, the number of stems per plant were counted (SN) and aerial part (leaves and stems) and tubers were separated. All the aerial part of each plant was put in paper bags and kept into a forced-air-drying oven for 72 hours at 70° C, after this time dry weight of aerial part (ADW) was obtained. The total tuber number produced per plant (TTN) was counted and weighted the tubers to obtain the total tuber weight produced per plant (TTW) and from the relation TTW/TTN, was calculated the average tuber weight (ATW). Five commercial tubers without peeling were cutted into cubes and a sample of 250 g was weighed and put into a forced-air-drying oven for 72 hours at 80°C, after this time, each sample was weighted and the percentage of dry matter (%DM) was calculated (CENTRO INTERNACIONAL DE LA PAPA (CIP), 2010).

Flesh color (Pulp col) of the tubers was evaluated based on established grades, where (1) means white flesh color, (2) was assigned for cream, (3) for light yellow, (4) for mid yellow, (5) for dark yellow, (6) was red, (7) partially red, (8) blue and (9) partially blue. Slices of 1-2 mm thick were obtained from tubers and three alike slices of each tuber were selected, rinsed, dried and fried in vegetal oil at an initial temperature of 180 degrees until it stops bubbling (2-3 minutes). Fried potatoes color of the chips (Chips col) were evaluated with grades

being assigned according to the color of the chips: dark chips identified as 1 and bright ones as 9 (TIEMENS-HULSCHER et al., 2013).

Statistical analysis

The data obtained was analyzed using Genes statistical program and mean values were grouped using Scott-Knott multiple range test at 5% probability level. Principal Component analysis was also performed using the Genes statistical program (CRUZ, 2013).

3.3 Results

Analysis of variance showed that the genotype x temperature (GxT) interaction was significant for all fluorescence parameters evaluated at 35 DAP, for Fv/Fm, Y(II), NPQ and ETR evaluated at 49 DAP, while on the 62th day after planting, only NPQ showed a significant GxT interaction. Genotype main effect was significant on all fluorescence parameters, except for Y(NO) evaluated at 62 DAP. On the other hand, temperature main effect affected Fo evaluated at 49 DAP, Fv/Fm on the three measurements, Y(II) evaluated at 35 and 49 DAP, Y(NO) at 49 DAP, NPQ and ETR at 35 and 49 DAP. (Table 2)

Table 2. Analysis of variance for minimal fluorescence (Fo), maximum photochemical efficiency of PSII (Fv/Fm), effective quantum yield of PSII (Y(II)), quantum yield of nonregulated energy dissipation (Y(NO)), non-photochemical quenching (NPQ/4), apparent rate of photosynthetic electron transport (ETR) measured at 35, 49 and 62 days after planting, on eight potato genotypes grown under three temperature condition treatments. Pelotas, 2021.

Source of variance	dF	Fo 35	Fo 49	Fo 62	Fv/Fm 35	Fv/Fm 49	Fv/Fm 62	YII 35	YII 49	YII 62
Genotype (G)	7	0.0006**	0.0045**	0.0003**	0.003**	0.003**	0.0003*	0,02**	0,01**	0,003**
Temperature (T)	2	0.0001^{ns}	0.0045**	0.0001^{ns}	0.0004*	0.009**	0.0004*	0,03**	0,06**	0,001^{ns}
GxT	14	0.0002**	0.0001^{ns}	0.0002^{ns}	0.0002*	0.0008*	0.0002^{ns}	0,01**	0,004**	0,001^{ns}
CV (%)		10.09	13.34	11.48	1.24	1.94	1.35	50.06	26.80	25.69
Source of variance	**dF**	**YNO 35**	**YNO 49**	**YNO 62**	**NPQ 35**	**NPQ 49**	**NPQ 62**	**ETR 35**	**ETR 49**	**ETR 62**
Genotype (G)	7	0.004**	0.001**	0.0002^{ns}	0.03**	0.05**	0.016**	715.08**	533.73**	150.29**
Temperature (T)	2	0.000^{ns}	0.006**	0.0004^{ns}	0.05**	0.04**	0.003^{ns}	1168.64**	1891.02**	45.68^{ns}
GxT	14	0.001**	0.000^{ns}	0.0003^{ns}	0.006*	0.006*	0.006**	217.42**	152.65**	35.45^{ns}
CV (%)		8.46	8.75	5.83	7.79	7.41	6.07	50.58	15.36	25.69

*: significant at 5% probability level, **: significant at 1% probability level, ns: not significant

In addition, for the gas exchange analysis, the analysis of variance indicated significant difference among the genotypes for A and gs at both days of evaluation, and E at 54 DAP. Temperature affected significantly all the gas exchange parameters, with exception of E evaluated at 54 DAP. On the other hand, the GxT interaction didn´t affect any of these parameters, showing that the behavior patterns of each cultivar were consistent over temperature treatments parameters (Table 3).

Table 3. Analysis of variance for net CO_2 assimilation (A), stomatal conductance (gs), intercellular CO_2 concentration (Ci), transpiration (E), ratio between internal and external CO_2 concentration (Ci/Ca) and water use efficiency (WUE) measured at 54 and 69 days after planting, on eight potato genotypes grown under three temperature condition treatments. Pelotas, 2021.

Source of variance	dF	A54	A69	gs54	gs69	Ci54	Ci69
Genotype (G)	7	18.81*	49.61**	0.09*	0.07**	2047.80^{ns}	10033.62^{ns}
Temperature (T)	2	44.69**	73.59**	1.24**	0.08*	15103.12**	53010.04**
GxT	14	10.96^{ns}	5.79^{ns}	0.06^{ns}	0.01^{ns}	1536.30^{ns}	7129.39^{ns}
CV (%)		20.22	27.54	45.12	73.07	15.99	44.06
Source of variance	**dF**	**E54**	**E69**	**Ci/Ca54**	**Ci/Ca69**	**WUE54**	**WUE69**
Genotype (G)	7	3.69^{ns}	9.30**	0.02^{ns}	0.12^{ns}	1.20^{ns}	4.91^{ns}
Temperature (T)	2	141.45**	7.42^{ns}	0.13**	0.37**	31.77**	11.78*
GxT	14	2.58^{ns}	1.94^{ns}	0.012^{ns}	0.05^{ns}	0.58^{ns}	2.06^{ns}
CV (%)		28.81	54.75	18.02	45.42	3.16	4.82

*: significant at 5% probability level, **: significant at 1% probability level, ns: not significant

For all agronomic parameters, genotype main effect was significant. The same behavior was observed for temperature main effect, except for ADW. On the other hand, the GxT interaction was significant only for C2, SN, ADW and CC. (Table 4).

Table 4. Analysis of variance for number of stems (SN), aerial dry weight (ADW), percentage of tuber dry matter (%DM), chips color (Chips col), total tuber number per plant (TTN), total tuber weight per plant (TTW) and tuber average weight (TAW) on eight potato genotypes grown under three temperature condition treatments. Pelotas, 2021.

Source of variance	dF	SN	ADW	%DM	Chips col	TTN	TTW	ATW
Genotype (G)	7	3.87**	259.79**	65.71**	4.21**	70.24**	9461.69**	209.39**
Temperature (T)	2	1.93*	7.35ns	46.13**	2.23*	124.35**	133254.43**	263.76**
GxT	21	1.26*	37.42**	4.53ns	2.09**	12.19ns	1643.45ns	53.28ns
CV (%)		25.52	17.28	7.63	16.11	24.07	20.66	30.53

*: significant at 5% probability level, **: significant at 1% probability level, ns: not significant.

On Table 5 is shown the means grouping for fluorescence parameters. At 35 days after planting, the Fo of most of the genotypes were not affected by the increment of temperature, except for Od80-02, C41 and Asterix, which responded in different ways. Od80-02 had its Fo incremented by 28% either under high and mild high temperatures. C41 showed a higher Fo under high temperature by 24% when compared to control and 22% when compared to mild high temperature. Asterix had its Fo reduced by 23% when high temperature treatments were applied. Over the three dates of evaluation, Fo stayed low on F53, O14, C41 and Asterix, when compared to the other genotypes. Only on the second date of evaluation, Fo had significant differences between treatments, where high temperatures produced a reduction of 22 to 25% of Fo when compared to the control treatment.

On average, the Fv/Fm was always higher on C41, while F53, O14, Asterix and Markies, were higher only on the last two dates of evaluation. At 35 days after planting, T2 decreased Fv/Fm by 1%, while T3 didn't have any effect on this parameter. The same pattern was observed on Innovator, with a lower Fv/Fm (-2%) when growth under T2, and at this time, F88 and Markies had its Fv/Fm reduced by T2 (-1.4% and -2.7%) and T3 (-3.2% and -1.7%). When plants were 49 days, Fv/Fm reached values ranging from 0.68 to 0.8 and was higher for T2 and T3 than for T1. Both, T2 and T3, induced higher Fv/Fm on Od80-02 (+12%, +13%), T2 on Innovator (+8%) and T3 on O14 (+5%). 62 days after planting, on average, temperature had the same effect on Fv/Fm that had on the first day of

evaluation: T2 induced a reduction of 1% of Fv/Fm, while T3 didn´t have any effect.

When plants were 35 days old, Y(II) was higher in those that grew under T2, but eventhough T1 had the lowest Y(II) values, it was similar for all the genotypes. At this time, the highest Y(II) under T2 was observed on O14 (0.22) and Markies (0.18), while at T3, O14 has de highest Y(II). 49 DAP, this parameter increased approximately twice on average, with the biggest alteration at T1 on Asterix (+604%), Innovator (+384%) and C41 (+307%) and on Asterix (+378%) and Innovator (+342%), at T2. Two groups of genotypes were formed according to Y(II) on the 62nd DAP, being F53 and Od80-02 those with lowest Y(II).

The effect of temperature over Y(NO) was different for each genotype when plants were 35 days old, no effect of T2 and T3 was observed on F53, Od80-02, F88 and a negative effect was observed on O14 (-13% for T2, -19% for T3) and Asterix (-11.7% for T2, -19.6% for T3). On average, at this time, the highest Y(NO) value was observed on Innovator (0.30) and the lowest, on F53 (0.24) and O14 (0.22). At 49 DAP, high temperatures induced less Y(NO) in most of the tested genotypes, under high mild temperature the decrease of Y(NO) was greater (-12%).

At 35 DAP, the average for NPQ on T1 was 0.72, on T2 was 0.63 and on T3, 0.67, with F53 and Od80-02 as the genotypes with the highest value and Innovator with the lowest, on the three temperature conditions. On most of the genotypes, T2 induced a decrease in NPQ, with -19% on F53, -11% on Od80-02, -10% on O14, -18% on C41 and -16% on Markies, while T1 did it to F53 (-13%), Od80-02 (-10%), C41 (-20%) and Markies (-11.5%). At 49 DAP, NPQ was on average 6.5% lower at T2 and 5.2% higher at T3 compared to T1. In addition to F53 and Od80-02, O14 also had the highest NPQ. F88, O14 and Innovator´s NPQ were not affected by temperature treatments, while NPQ of C41 (-11%), Asterix (-18.6%) and Markies (-22.5%) were negatively affected by T2. At 62 DAP, only on F53 and Innovator, T2 and T3 induced a decrease in NPQ, by -8.5% and -9.6% for F53 and -15.5% and -12.3% for Innovator. At this time, F53, Od80-02 and C41 showed, in average, the highest NPQ values.

Under T1, average for ETR at 35 DAP was 9.18, under T2 was 23.02 and under T3, 14.59. Highest values were always observed on O14, with an average of 31.84. In most of the genotypes high temperatures positively affected ETR, T2

caused a three time increment on F88, O14 and Markies, a six time increment on C41, a 14 time increment on Asterix, while T3 caused a three time increment on O14 and a 15 time increment on Asterix. At 49 DAP, ETR on T2 and T3 was on average 125% higher than T1, Od80-02 and C41 had the largest difference in both treatments, and between genotypes, Innovator and Markies showed the highest ETR values. At 62 DAP, no significant differences were observed between treatments and in average, F53 and Od80-02 had the lowest ETR values.

Over time (Figure 2) were observed significant differences for almost all the parameters and temperature treatments, except for Fo under the control temperature treatment. This parameter had the same dynamic pattern when plants grew under T2 and T3, high Fo value at 35 DAP, decreasing at 49 DAP and increasing at 62 DAP. Fv/Fm changes in all treatments in the course of time, but in an opposite way, while plants grown under control temperature conditions, had its lower value at 49 DAP, those that grew under T2 and T3 had its higher value at 49 DAP. Y(II) had an increasing dynamic over time under control temperatures, while T2 incremented a third part of the initial value and T3 doubled its value at 49 DAP to decrease by 4% at 62 DAP on both heat treatments. On the three treatments, the highest value of Y(NO) was observed at the first evaluation, then, T2 and T3 caused a reduction of Y(NO) at 49 DAP and stayed without significantly changes until 62 DAP, while T1 caused this reduction at 49 DAP. Significant changes over time were also observed on NPQ, where the highest value was observed on the last day of evaluation independent of the treatment. At last, ETR showed a significant increment from 35 to 49 DAP on plants grown under the three temperature conditions, in a different intensity, obtaining the highest value at 49 DAP.

Table 5. Means grouping for fluorescence parameters: minimal fluorescence (Fo), maximum photochemical efficiency of PSII (Fv/Fm), effective quantum yield of PSII (Y(II)), quantum yield of nonregulated energy dissipation (Y(NO)), non-photochemical quenching (NPQ/4), apparent rate of photosynthetic electron transport (ETR) measured at 35, 49 and 62 days after planting, on eight potato genotypes grown under three temperature condition treatments (T1: control temp, 14°C-27°C; T2: high temp, 24°C-34°C; T3: mild high temp, 17°C-29°C). Pelotas, 2021

	Fo 35				**Fo 49**				**Fo 62**	**Fv/Fm 35**				**Fv/Fm 49**				**Fv/Fm 62**			
	T1	T2	T3	Avg.	T1	T2	T3	Avg.	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.
F53	0.09 Ab	0.09 Ab	0.09 Aa	0.09 c	0.09	0.07	0.08	0.08 b	0.08 b	0.77 Aa	0.76 Ab	0.76 Aa	0.76 b	0.76 Aa	0.78 Aa	0.78 Aa	0.77 a	0.77	0.75	0.77	0.76 a
Od80-02	0.08 Bb	0.10 Aa	0.10 Aa	0.09 c	0.12	0.09	0.07	0.09 a	0.09 a	0.71 Ac	0.71 Ac	0.72 Ab	0.71 d	0.68 Bc	0.76 Ab	0.77 Ab	0.74 c	0.74	0.75	0.75	0.75 b
F88	0.11 Aa	0.10 Aa	0.12 Aa	0.11 a	0.11	0.08	0.08	0.09 a	0.09 a	0.76 Ab	0.74 Bb	0.73 Bb	0.74 c	0.74 Bb	0.77 Ab	0.77 Ab	0.76 b	0.75	0.75	0.75	0.75 b
O14	0.09 Ab	0.09 Ab	0.08 Ab	0.09 c	0.09	0.08	0.07	0.08 b	0.08 b	0.76 Ab	0.75 Ab	0.76 Aa	0.76 b	0.75 Ba	0.76 Bb	0.79 Aa	0.77 a	0.77	0.76	0.77	0.77 a
C41	0.08 Bb	0.10 Aa	0.08 Bb	0.09 c	0.09	0.08	0.06	0.08 b	0.08 b	0.77 Aa	0.76 Aa	0.78 Aa	0.77 a	0.77 Ba	0.79 Aa	0.8 Aa	0.79 a	0.76	0.76	0.77	0.76 a
Asterix	0.10 Aa	0.08 Bb	0.09 Bb	0.09 c	0.09	0.07	0.07	0.08 b	0.09 b	0.76 Ab	0.77 Aa	0.77 Aa	0.76 b	0.76 Ba	0.78 Aa	0.79 Aa	0.78 a	0.77	0.76	0.75	0.76 a
Innovator	0.10 Aa	0.11 Aa	0.10 Aa	0.10 b	0.11	0.09	0.09	0.09 a	0.09 a	0.76 Ab	0.74 Bb	0.77 Aa	0.76 b	0.73 Bb	0.79 Aa	0.74 Bc	0.75 b	0.77	0.75	0.76	0.76 a
Markies	0.09 Ab	0.11 Aa	0.10 Aa	0.09 b	0.09	0.08	0.07	0.08 b	0.09 a	0.77 Aa	0.75 Bb	0.76 Ba	0.76 b	0.77 Aa	0.78 Aa	0.79 Aa	0.78 a	0.76	0.75	0.76	0.76 a
Average	0.094	0.097	0.097		0.099 A	0.078 B	0.075 B			0.76 A	0.75 B	0.76 A		0.75 B	0.78 A	0.78 A		0.76 A	0.75 B	0.76 A	
CV(%)		10.09				13.34			11.48		1.24				1.94				1.35		
	YII 35				**YII 49**				**YII62**	**YNO 35**				**YNO 49**				**NPQ 35**			
	T1	T2	T3	Avg.	T1	T2	T3	Avg.	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.
F53	0.08 Aa	0.10 Ab	0.10 Ab	0.09 b	0.08 Ab	0.11 Ab	0.12 Ab	0.1 c	0.10 b	0.22 Ab	0.25 Ab	0.24 Ac	0.24 c	0.24	0.23	0.20	0.22 b	0.83 Aa	0.67 Ba	0.72 Ba	0.74 a
Od80-02	0.03 Aa	0.01 Ac	0.00 Ac	0.01 d	0.02 Bb	0.06 Ac	0.10 Ab	0.06 d	0.09 b	0.23 Ab	0.26 Ab	0.26 Ab	0.25 b	0.25	0.23	0.20	0.23 b	0.80 Aa	0.71 Ba	0.72 Ba	0.75 a
F88	0.03 Ba	0.11 Ab	0.05 Bc	0.06 c	0.15 Aa	0.13 Ab	0.16 Aa	0.15 a	0.11 a	0.27 Aa	0.25 Ab	0.27 Ab	0.26 b	0.26	0.25	0.22	0.25 a	0.69 Ab	0.64 Aa	0.65 Ab	0.66 b

O14	0.06 Ba	0.22 Aa	0.18 Aa	0.15 a	0.06 Bb	0.16 Aa	0.16 Aa	0.13 b	0.14 a	0.25 Ab	0.22 Bb	0.20 Bc	0.22 c	0.25	0.23	0.20	0.22 b	0.70 Ab	0.63 Ba	0.76 Aa	0.70 b
C41	0.02 Ba	0.13 Ab	0.02 Bc	0.06 c	0.04 Bb	0.18 Aa	0.15 Aa	0.13 b	0.12 a	0.24 Bb	0.25 Bb	0.29 Aa	0.26 b	0.25	0.23	0.22	0.23 b	0.77 Aa	0.63 Ba	0.62 Bb	0.67 b
Asterix	0.01 Ba	0.11 Ab	0.12 Ab	0.08 c	0.03 Cb	0.19 Aa	0.13 Bb	0.12 b	0.13 a	0.28 Aa	0.25 Bb	0.22 Bc	0.25 b	0.24	0.23	0.23	0.23 b	0.65 Bb	0.65 Ba	0.74 Aa	0.68 b
Innovator	0.07 Aa	0.04 Ac	0.03 Ac	0.04 c	0.05 Bb	0.21 Aa	0.19 Aa	0.15 a	0.13 a	0.27 Ba	0.31 Aa	0.31 Aa	0.30 a	0.28	0.24	0.25	0.26 a	0.61 Ab	0.53 Ab	0.55 Ab	0.57 c
Markies	0.06 Ba	0.18 Aa	0.08 Bc	0.11 b	0.12 Ba	0.22 Aa	0.20 Aa	0.18 a	0.14 a	0.25 Ab	0.24 Ab	0.27 Ab	0.25 b	0.22	0.24	0.22	0.23 b	0.71 Ab	0.59 Bb	0.63 Bb	0.65 b
Average	0.05 C	0.11 A	0.07 B		0.07 B	0.16 A	0.15 A			0.25	0.25	0.26		0.25 A	0.23 B	0.22 C		0.72 A	0.63 C	0.67 B	
CV(%)		50.06				26.80			25.69		8.46				8.75				7.79		

	NPQ 49				**NPQ 62**				**ETR 35**				**ETR 49**				**ETR 62**			
	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg
F53	0.72 Ba	0.74 Ba	0.82 Aa	0.76 a	0.83 Aa	0.76 Bb	0.75 Ba	0.78 a	15.95 Aa	21.86 Ab	20.65 Ab	19.49 b	15.30 Bc	18.44 Bc	24.25 Ac	19.33 d	20.96	16.15	22.21	19.77 b
Od80-02	0.74 Ba	0.75 Ba	0.88 Aa	0.79 a	0.80 Aa	0.84 Aa	0.78 Aa	0.81 a	5.52 Aa	1.24 Ac	0.20 Ac	2.32 d	5.45 Bd	25.84 Ac	19.81 Ac	17.03 d	20.33	17.67	16.92	18.31 b
F88	0.59 Ab	0.63 Ab	0.68 Ab	0.64 c	0.73 Ab	0.73 Ac	0.72 Ab	0.73 b	6.47 Ba	22.06 Ab	9.89 Bc	12.81 c	33.46 Ba	19.89 Cc	42.28 Aa	31.88 b	22.08	23.63	26.05	23.92 a
O14	0.75 Aa	0.69 Aa	0.79 Aa	0.74 a	0.65 Bb	0.76 Ab	0.81 Aa	0.74 b	12.74 Ba	45.02 Aa	37.77 Aa	31.84 a	16.98 Bc	33.00 Ab	33.63 Ab	27.87 c	32.17	27.45	28.30	29.31 a
C41	0.73 Aa	0.64 Bb	0.73 Ab	0.70 b	0.78 Aa	0.72 Ac	0.78 Aa	0.76 a	4.36 Ba	27.29 Ab	3.73 Bc	11.79 c	9.29 Bd	38.04 Ab	32.08 Ab	26.47 c	21.54	23.09	29.14	24.59 a
Asterix	0.75 Aa	0.61 Bb	0.72 Ab	0.70 b	0.75 Aa	0.70 Ac	0.71 Ab	0.72 b	1.58 Ba	22.44 Ab	23.77 Ab	15.93 c	17.41 Bc	40.38 Aa	35.18 Ab	30.99 b	27.56	29.24	26.30	27.70 a
Innovator	0.57 Ab	0.56 Ab	0.57 Ac	0.57 d	0.75 Aa	0.64 Bc	0.66 Bb	0.68 c	14.29 Aa	7.92 Ac	4.90 Ac	9.04 c	25.14 Bb	43.93 Aa	40.27 Aa	36.45 a	22.41	31.43	28.97	27.60 a
Markies	0.74 Aa	0.57 Bb	0.67 Ab	0.66 c	0.71 Ab	0.67 Ac	0.70 Ab	0.69 c	12.50 Ba	36.36 Aa	15.79 Bc	21.55 b	24.41 Bb	45.40 Aa	47.79 Aa	39.2 a	28.39	22.41	34.09	28.30 a
Average	0.69 B	0.65 C	0.73 A		0.75	0.73	0.74		9.18 C	23.02 A	14.59 B		18.43 B	33.12 A	34.41 A		24.43	23.88	26.50	
CV(%)		7.41				6.07				50.58				15.36				25.69		

Within the same row, values followed by the same capital letter are not significantly different. Within the same column, values followed by the same lowercase letter are not significantly different. P ≤ 0.05, through Scott-Knott test.

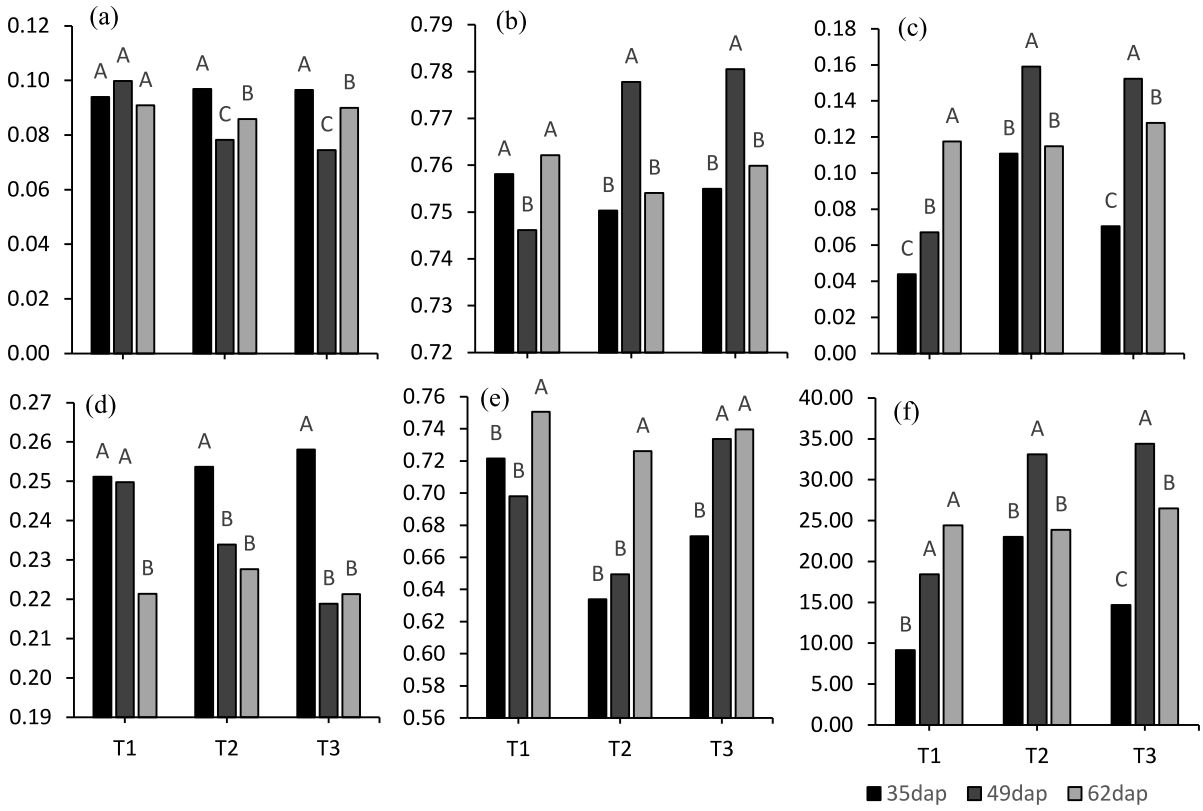

Figure 2. Mean values of fluorescence parameters grown under three temperature treatments: Control temperature treatment (T1, 14°C-27°C), high temperature treatment (T2, 24°C-34°C) and mild high temperature treatment (T3, 17°C-29°C). (a) Fo – minimal fluorescence (b) Fv/Fm – maximum quantum yield of photosystem II (PSII), (c) Y(II) – effective quantum yield of PSII, (d) Y(NO) – quantum yield of non-regulated energy dissipation, (e) NPQ/4 – non photochemical quenching, (f) ETR – apparent rate of photosynthetic electron transport. Same capital letters constitute a statistical homogeneous group between evaluation date of the same treatment.

On Table 6 is seen that none of the gas exchange parameters showed significant differences on interaction GxT, only some of them showed differences between genotypes, but all of them had its values significantly modified between temperature treatments. In this way, by the average comparison could be seen that these parameters were negatively modified over time on plants that were under high temperature conditions (Figure 3). Net CO2 assimilation (A) was on average 26.7% (T2) and 7.3% (T3) higher than T1 at 54 DAP and, at 69 DAP, decreased, respectively, to 19% and 26% in comparison to T1. From the tested genotypes, Od80-02 didn´t change with time under high temperatures in relation to control treatment and Asterix had a slightly reduction of about 85%. Stomatal

conductance (gs) relationship between heat and control treatment decreased from 241% (T2) and 114% (T3) at 54 DAP to 72% (T2) and 56% (T3) at 69 DAP. Again, this relationship on Od80-02 decreased less (55-65% aprox.) than the other genotypes, while Asterix was the only one that under mild high temperatures was observed an increment of gs. Ci at 54 DAP was on average 15,26% higher on T2 and 2.39% lesser on T3 and decreased to 28.25% on T2 and 35% on T3 lower when compared to the control treatment. At 69 DAP, the highest decrease of this relationship of Ci was observed on Markies and O14. E, in average, increased more under higher temperatures (173% for T2 and 48% for T3), this increment was poor or negative over time, with 15% higher for T2 and 23.6% less for T3. Exceptionally, Od80-02 has its E almost not modified with high temperatures over time. Ci/Ca from 54 DAP increased 15% on average at T2 with C41 (+36) and Markies (+34%) showing the greatest differences. T3 had an opposite effect, reducing Ci/Ca by 4% on average, with higher changes in Markies (-20%). 15 days later, high temperatures lowered Ci/Ca to -27.5% (T2) and -35% (T3) on average.

The WUE was lower on T2 on both evaluation dates, T3 caused a decrease on this parameter by 21% at 54 DAP, but had not significant differences with control treatment at 69 DAP. The change of WUE over time, was opposite to what was observed on the others gas exchange parameters of plants grown under high temperature conditions (T2, T3), what resulted in a increase in the efficiency of the use of water by this plants. (Figure 3)

Table 6. Means grouping for gas exchange parameters: net CO2 assimilation (A), stomatal conductance (gs), intercellular CO2 concentration (Ci), transpiration (E), ratio between internal and external CO2 concentration (Ci/Ca) and water use efficiency (WUE) measured at 54 and 69 days after planting, on eight potato genotypes grown under three temperature condition treatments (T1: control temp, 14°C-27°C; T2: high temp, 24°C-34°C; T3: mild high temp, 17°C-29°C). Pelotas, 2021.

	A 54 (μmol CO_2 m^{-2} s^{-1})				**A 69 (μmol CO_2 m^{-2} s^{-1})**				**gs 54 (mol H_2O m^{-2} s^{-1})**				**gs 69 (mol H_2O m^{-2} s^{-1})**			
	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg
F53	12.02	14.63	15.82	14.16 a	13.44	9.72	11.22	11.46 b	0.26	0.54	0.33	0.38 b	0.22	0.06	0.11	0.13 b
Od80-02	15.73	15.17	13.34	14.75 a	16.13	16.03	15.53	15.90 a	0.41	0.69	0.52	0.54 a	0.39	0.36	0.33	0.36 a
F88	7.44	14.77	12.8	11.67 b	11.59	11.59	8.35	10.51 b	0.08	0.61	0.35	0.35 b	0.14	0.19	0.08	0.14 b
O14	12.9	14.38	13.18	13.49 a	14.08	10.24	7.1	10.47 b	0.38	0.53	0.29	0.40 b	0.3	0.17	0.04	0.17 b
C41	9.97	14.1	11.63	11.90 b	13.2	12.4	10.63	12.08 b	0.19	0.81	0.28	0.43 b	0.26	0.24	0.11	0.20 b
Asterix	15.1	15.27	13.5	14.62 a	14.23	12.41	11.35	12.66 b	0.47	1.12	0.33	0.64 a	0.26	0.3	0.33	0.29 a
Innovator	13.83	14.91	13.03	13.92 a	10.32	7.04	7.21	8.19 b	0.31	0.52	0.33	0.39 b	0.2	0.04	0.06	0.11 b
Markies	10.93	14.83	7.36	11.04 b	13.2	7.03	7.71	9.31 b	0.21	0.79	0.17	0.39 b	0.26	0.05	0.08	0.13 b
Average	12.24 B	14.76 A	12.58 B		13.27 A	10.81 B	9.89 B		0.29 B	0.70 A	0.33 B		0.25 A	0.18 B	0.14 B	
CV(%)	20.22				27.54				45.12				73.07			

	Ci 54 (μmol CO_2 mol^{-1})				**Ci 69 (μmol CO_2 mol^{-1})**				**E 54 (mmol H_2O m^{-2} s^{-1})**				**E 69 (mmol H_2O m^{-2} s^{-1})**			
	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg
F53	229.33	275.33	268.98	257.88	196.67	107.11	173.73	159.17	2.91	7.00	5.06	4.99	2.7	1.9	2.5	2.37 b
Od80-02	284.33	308	280	290.78	283	175.51	259	239.17	4.19	7.21	5.39	5.60	3.8	6.2	4.8	4.97 a
F88	235.67	273.33	273	260.67	257.48	256.61	156.9	223.66	1.45	7.62	4.34	4.47	2.1	3.7	1.9	2.58 b
O14	281.74	309	270.28	287.01	274.98	124.79	108.61	169.46	3.71	8.14	4.78	5.54	3.2	3.3	1.1	2.56 b

C41	248.67	321.33	250	273.33	183.25	214.11	197.67	198.34	2.48	8.19	3.96	4.88	3.1	3.6	2.5	3.07 b
Asterix	298.67	326	256.67	293.78	253	209.37	132.27	198.21	4.48	9.85	4.38	6.24	3	4.8	2.5	3.43 b
Innovator	283.33	289.5	240.28	271.04	210.33	165.61	88.46	154.8	3.69	6.63	4.21	4.84	2.3	1.8	1.1	1.76 b
Markies	248.67	317	204	256.56	262	89.59	78.79	150.04	2.69	8.10	2.16	4.32	2.8	1.5	1.6	1.97 b
Average	263.8 B	302.44 A	255.4 B		240.09 A	167.84 B	151.89 B		3.20 C	7.84 A	4.29 B		2.89	3.36	2.26	
CV(%)		15.99				44.06				28.81				54.75		

	Ci/Ca 54				**Ci/Ca 69**				**WUE 54 (μmol CO_2 mol^{-1} H_2O)**				**WUE 69 (μmol CO_2 mol^{-1} H_2O)**			
	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg	T1	T2	T3	Avg
F53	0.62	0.76	0.67	0.69	0.52	0.22	0.3	0.35	4.78	2.22	3.19	0.35	6.69	5.46	4.85	5.67
Od80-02	0.77	0.85	0.76	0.79	0.78	0.71	0.7	0.73	3.81	2.14	2.82	0.73	4.27	2.64	3.36	3.42
F88	0.69	0.77	0.73	0.73	0.65	0.64	0.49	0.59	5.28	1.96	3.76	0.59	5.57	4.33	5.36	5.09
O14	0.79	0.87	0.72	0.79	0.73	0.51	0.18	0.47	3.52	1.77	2.76	0.47	4.65	3.47	6.94	5.02
C41	0.65	0.88	0.73	0.75	0.74	0.52	0.53	0.60	4.71	1.73	3.34	0.60	4.3	3.77	4.27	4.11
Asterix	0.82	0.83	0.7	0.78	0.68	0.67	0.37	0.57	3.37	1.55	3.29	0.57	4.95	3.38	5.62	4.65
Innovator	0.76	0.78	0.65	0.73	0.56	0.33	0.62	0.50	3.75	2.27	3.28	0.50	4.67	4.25	6.54	5.15
Markies	0.65	0.87	0.52	0.68	0.71	0.38	0.27	0.45	4.52	1.85	4.27	0.45	4.81	5.1	6.43	5.45
Average	0.72 B	0.83 A	0.69 B		0.67 A	0.49 B	0.43 B		4.22 A	1.94 C	3.34 B		4.99 A	4.05 B	5.42 A	
CV(%)		18.02				45.42				3.16				4.82		

Within the same row, values followed by the same capital letter are not significantly different. Within the same column, values followed by the same lowercase letter are not significantly different. $P \leq 0.05$, through Scott-Knott test.

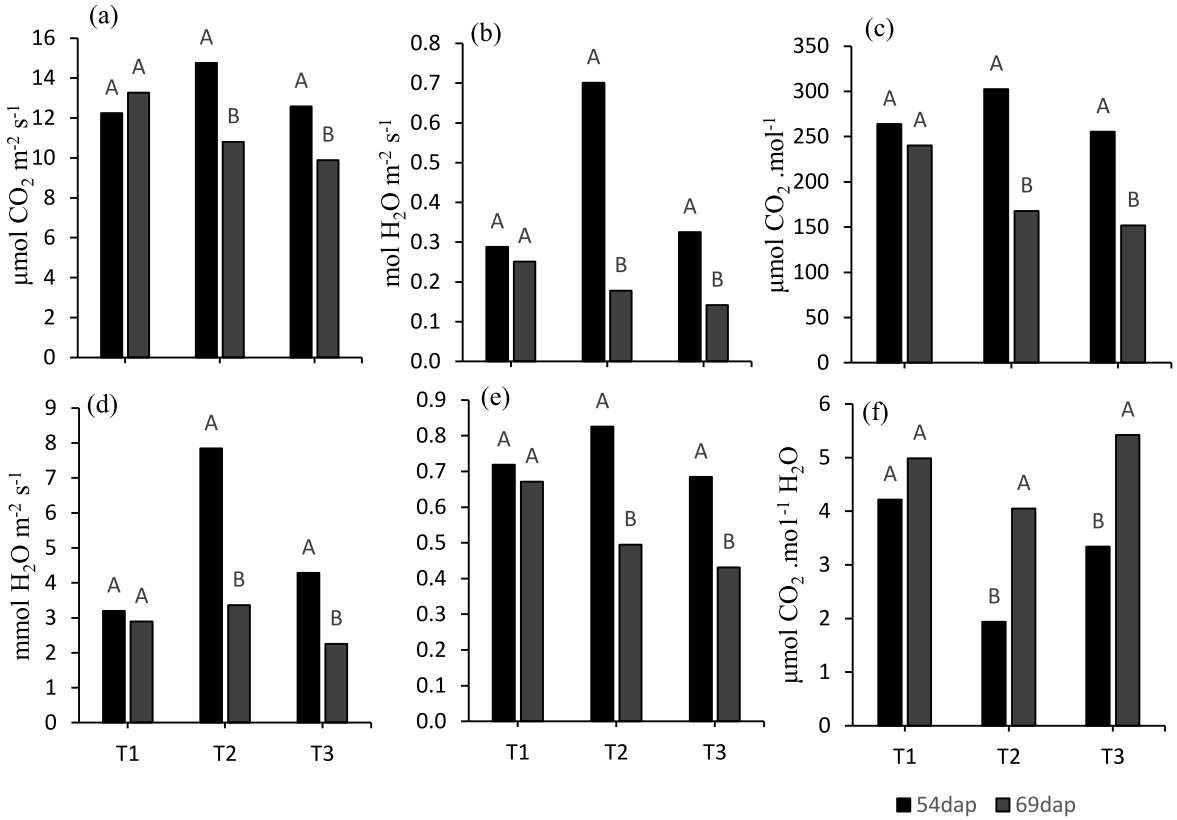

Figure 3. Mean values of fluorescence parameters grown under three temperature treatments: Control temperature treatment (T1, 14°C-27°C), high temperature treatment (T2, 24°C-34°C) and mild high temperature treatment (T3, 17°C-29°C). (a) A - Net photosynthetic CO_2 assimilation, (b) gs – Stomatal conductance, (c) Ci – Internal CO_2 concentration, (d) E - Transpiration, (e) Ci/Ca - Ratio of internal to atmospheric CO_2 concentration, (f) WUE – Water use efficiency. Same capital letters constitute a statistical homogeneous group between evaluation dates of the same treatment.

On Table 7 is shown the mean comparison for agronomical traits. Plants grown under mild high temperatures had more stems and, on average, significant differences were not observed between T1 and T2, but mean comparison considering the GxT interaction showed that O14 had less SN under T2, Innovator under T1 and Asterix under T1 and T2. No differences were observed between genotypes when grown under T1 and T3, yet Asterix and O14 produced less SN when grown under T2. On average, genotypes that produced more SN were C41, Innovator and Markies. By the other side, O14 had the highest aerial dry weight (ADW) on average (27.74 gr), on T1 (36.24 gr) and on T3 (27.74 gr). Even though not significant differences were observed between treatments for

ADW in general, differences were observed on F53 (23% higher on T2 than T1 and T3) and on O14 (around 40% higher on T1 than T2 and T3). High temperature condition (T2) caused, in general, plants to have less yield (TTW), less tubers (TTN), with less weight (ATW) and less dry matter content (%DM) as well as produced darker chips (Chips col). Between genotypes, C41 and Markies had the lowest %DM with 20.02 gr and 18.80 gr respectively, while F53 (23.47 gr), F88 (23.11 gr) and O14 (24.02 gr), the highest. Darker chips were observed on O14 under T1 and T3, on C41 under T2 and T3 and on Markies under T2, but in general, Innovator presented the darkest chips between the tested genotypes. O14 had a low productivity, with few tubers/plant and one of the cultivars with lower TTW, but, in turn, it was one of the genotypes with the highest average tuber weight.

Table 7. Mean comparison for morfoagronomic parameters: Number of stems (SN), aerial part dry weight (ADW), dry matter content (%DM), color of the tuber flesh (Pulp col), color of the chips (Chips col), total tuber number (TTN), total tuber weight (TTW), average tuber weight (ATW) on eight potato genotypes grown under three temperature condition treatments (T1: control temp, 14°C-27°C; T2: high temp, 24°C-34°C; T3: mild high temp, 17°C-29°C). Pelotas, 2021

	SN				ADW (gr)				%DM				Pulp col			
	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.
F53	2.33 Aa	1.67 Ac	3.00 Aa	2.33 b	16.94 Bb	22.14 Aa	16.86 Bb	18.64 b	24.78	22.25	23.38	23.47 a	2.00 Ac	2.00 Ac	2.00 Ab	2.00 c
Od80-02	2.33 Aa	2.67 Ab	2.33 Aa	2.44 b	17.54 Ab	20.12 Aa	15.84 Ab	17.83 b	22.05	19.26	24.14	21.81 b	4.00 Aa	3.67 Ab	3.67 Aa	3.78 a
F88	2.67 Aa	3.00 Ab	3.00 Aa	2.89 b	16.02 Ab	19.59 Aa	16.85 Ab	17.49 b	23.43	21.96	23.94	23.11 a	1.67 Ac	2.00 Ac	2.00 Ab	1.89 c
O14	2.67 Aa	1.00 Bc	3.00 Aa	2.22 b	36.24 Aa	21.34 Ba	25.64 Ba	27.74 a	26.13	23.85	22.09	24.02 a	2.00 Ac	1.89 Ac	2.00 Ab	1.96 c
C41	3.33 Aa	3.67 Aa	3.33 Aa	3.44 a	14.51 Ab	16.77 Ab	15.83 Ab	15.70 b	21.22	18.22	20.61	20.02 c	1.00 Bd	2.00 Ac	2.00 Ab	1.67 c
Asterix	2.67 Ba	2.00 Bc	3.67 Aa	2.78 b	14.46 Ab	9.91 Ac	14.35 Ab	12.91 c	22.78	21.50	22.90	22.39 b	3.00 Bb	4.33 Aa	3.33 Ba	3.56 a
Innovator	3.00 Ba	4.67 Aa	4.00 Aa	3.89 a	10.15 Ab	7.19 Ac	11.49 Ab	9.61 d	17.46	13.73	17.31	16.16 d	3.33 Bb	4.22 Aa	3.98 Aa	3.84 a
Markies	3.00 Aa	4.33 Aa	4.00 Aa	3.78 a	12.85 Ab	14.64 Ab	13.66 Ab	13.72 c	19.20	16.25	20.94	18.80 c	3.00 Ab	3.33 Ab	3.33 Aa	3.22 b
Average	2.75 B	2.88 B	3.29 A		17.34	16.46	16.31		22.13 A	19.63 B	21.91 A		2.5 B	2.93 A	2.79 A	
CV(%)	25.52				17.28				7.63				14.41			

	Chips col				TTN				TTW (gr)				ATW (gr)			
	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.	T1	T2	T3	Avg.
F53	5.67 Aa	4.67 Ab	5.33 Aa	5.22 b	12.33	11.67	13.67	12.56 a	271.66	127.55	269.03	222.75 a	23.65	11.11	20.64	18.47 b
Od80-02	6.33 Aa	5.33 Aa	6.00 Aa	5.89 a	8.67	7.33	10.00	8.67 b	180.22	95.84	174.88	150.31 b	22.02	12.99	16.31	17.11 b
F88	5.33 Aa	6.00 Aa	6.33 Aa	5.89 a	16.00	10.00	19.00	15.00 a	255.97	127.17	244.43	209.19 a	16.24	12.76	13.06	14.02 b
O14	4.45 Bb	6.06 Aa	4.33 Bb	4.95 b	8.33	3.67	7.00	6.33 c	186.31	109.17	181.91	159.13 b	23.06	31.52	29.34	27.97 a
C41	6.33 Aa	4.00 Bb	5.00 Ba	5.11 b	13.00	6.33	8.67	9.33 b	276.94	123.71	246.08	215.58 a	21.80	20.59	32.17	24.86 a
Asterix	4.67 Ab	4.67 Ab	5.00 Aa	4.78 b	14.33	7.00	12.67	11.33 a	300.65	125.17	285.30	237.04 a	20.95	18.56	23.06	20.86 a
Innovator	4.00 Ab	3.97 Ab	3.33 Ab	3.77 c	17.67	10.67	12.00	13.44 a	282.85	79.42	253.19	205.15 a	16.96	7.24	21.11	15.11 b
Markies	6.33 Aa	3.67 Bb	6.33 Aa	5.44 a	11.00	10.00	10.67	10.56 b	272.66	158.70	268.49	233.29 a	24.71	15.93	25.79	22.15 a
Average	5.39 A	4.79 B	5.21 A		12.67 A	8.33 B	11.71 A		253.41 A	118.34 B	240.41 A		21.18 A	16.34 B	22.69 A	
CV(%)	16.11				24.07				20.66				30.53			

Within the same row, values followed by the same capital letter are not significantly different. Within the same column, values followed by the same lowercase letter are not significantly different. $P \leq 0.05$

Pearson's correlation matrices are shown on Figures 4, 5 and 6. Under control temperature condition (Figure 4), TTN was strongly negative correlated with A69 (-0.83), E69 (-0.82), gs69 (-0.80), Ci/Ca69 (-0.61), NPQ49 (-0.79), ADW (-0.66), ATW (-0.79) and positively correlated with TTW (0.76), Y(NO)49 (0.60), of these correlations, those with A69, ADW, ATW, E69, NPQ49, gs69 and TTW were significant. ATW was correlated positively with A69 (0.66), E69 (0.62), NPQ49 (0.89) and negatively with Y(NO)49 (-0.84), Y(NO)35 (-0.60), Fo35 (-0.76), being significant the A69, Y(NO49), NPQ49 and Fo35. TTW had a positive correlation with TTN (0.76), Fv/Fm35 (0.68), Fv/Fm49 (0.62), and a negative correlation with ADW (-0.71), Ci69 (-0.62) and E69 (-0.62), from which the correlation of TTW with Fv/Fm35, Fv/Fm49, TTN, Fv/Fm35, ADW and E69 were significant. High positive correlation were also observed between %DM and ADW (0.76).

Under high temperature stress (Figure 5), there was a significant strong negative relationship between TTN and Ci/Ca54 (-0.72), Fv/Fm62 (-0.83), ATW (-0.89). The same parameter was positive correlated to WUE54 (0.65), WUE69 (0.73) and Y(NO)62 (0.63). Whereas, ATW was significant highly correlated to Ci/Ca54 (0.67), ETR35 (0.77), Fv/Fm62 (0.71), Y(II)35 (0.77), WUE54 (-0.71) and Y(NO)35 (-0.80). %DM had a significant strong correlation with ADW (0.68), Chips col (0.78), ETR49 (-0.65), Fo35 (-0.67), Fo62 (-0.85), Fv/Fm62 (0.64), SN (-0.93), Y(NO)35 (-0.78), Y(NO)62 (-0.65) and a not significant high correlation with Fo49 (-0.61), NPQ49 (0.62), SN(-0.93).

At mild high temperatures (Figure 6), plants showed a strong significant relationship between TTN and ATW (-0.78) and Fo35 (0.81), a high significant relationship between ATW and Fo35 (-0.88), Fo62 (-0.65), Fv/Fm35 (0.78), Fv/Fm49 (0.64) and Y(NO)62 (-0.65), a high significant relationship of TTW with SN (0.68), NPQ62 (-0.71) and WUE54 (0.63), a high not significant relationship of TTW with DWA (-0.61). Also, under this condition, %DM showed a significant high correlation with Chips col (0.71), Fv/Fm35 (-0.62), NPQ35 (0.77), NPQ49 (0.76), SN (-0.77), Y(II)49 (-0.72), Y(NO)49 (-0.72) and a non-significant high correlation with Ci54 (0.62), ETR62 (-0.62), Y(II)35 (-0.61) and Y(NO)35 (-0.60).

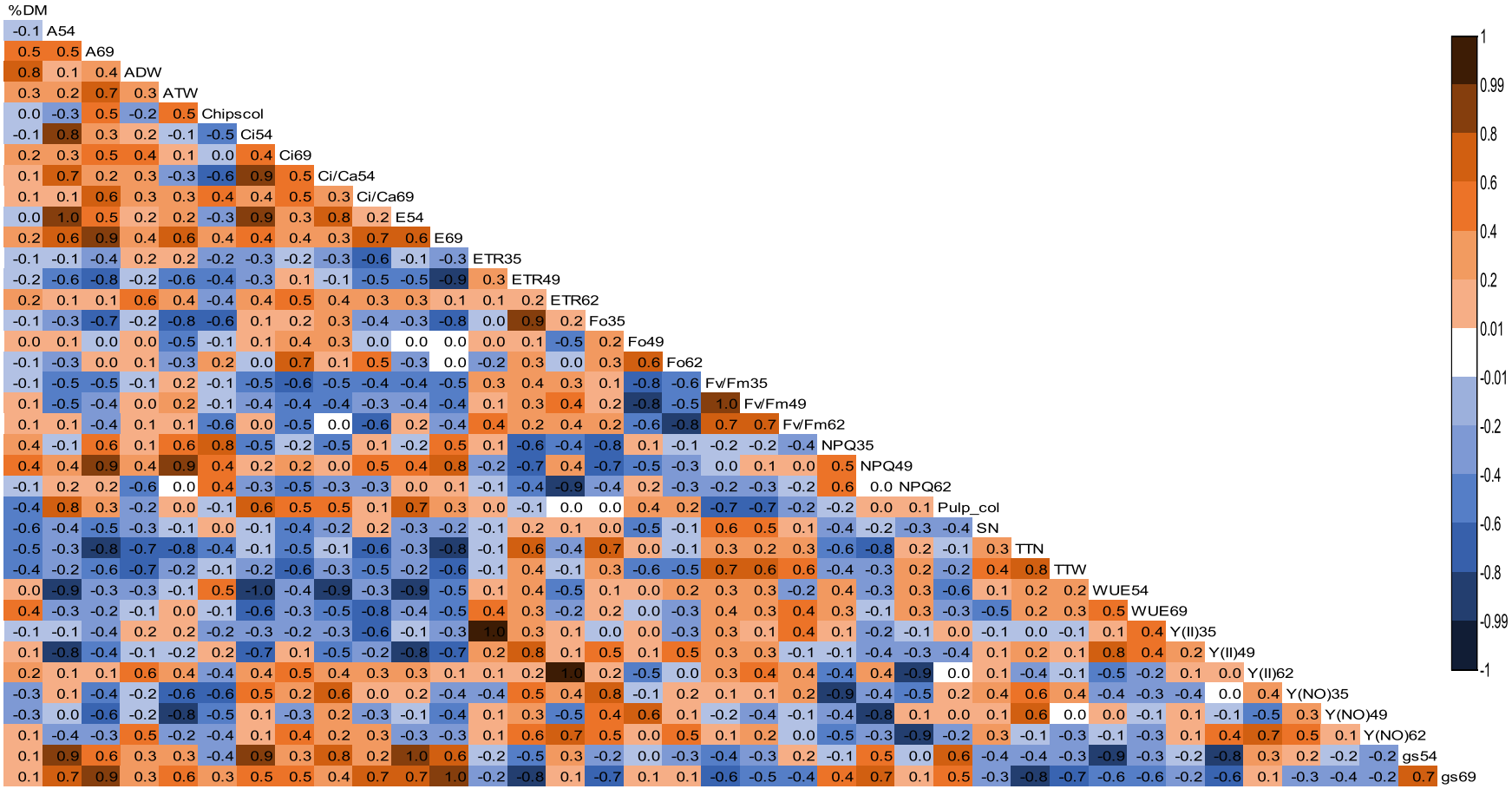

Figure 4. Pearson correlation matrix showing correlations among population means for physiological traits measured in eight genotypes grown under control temperature treatment (T1: control temp, 14°C-27°C). Number represents the magnitude of the correlation. and the color represents the positive and negative correlations. Significance levels of correlation: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. **** $p \leq 0.0001$

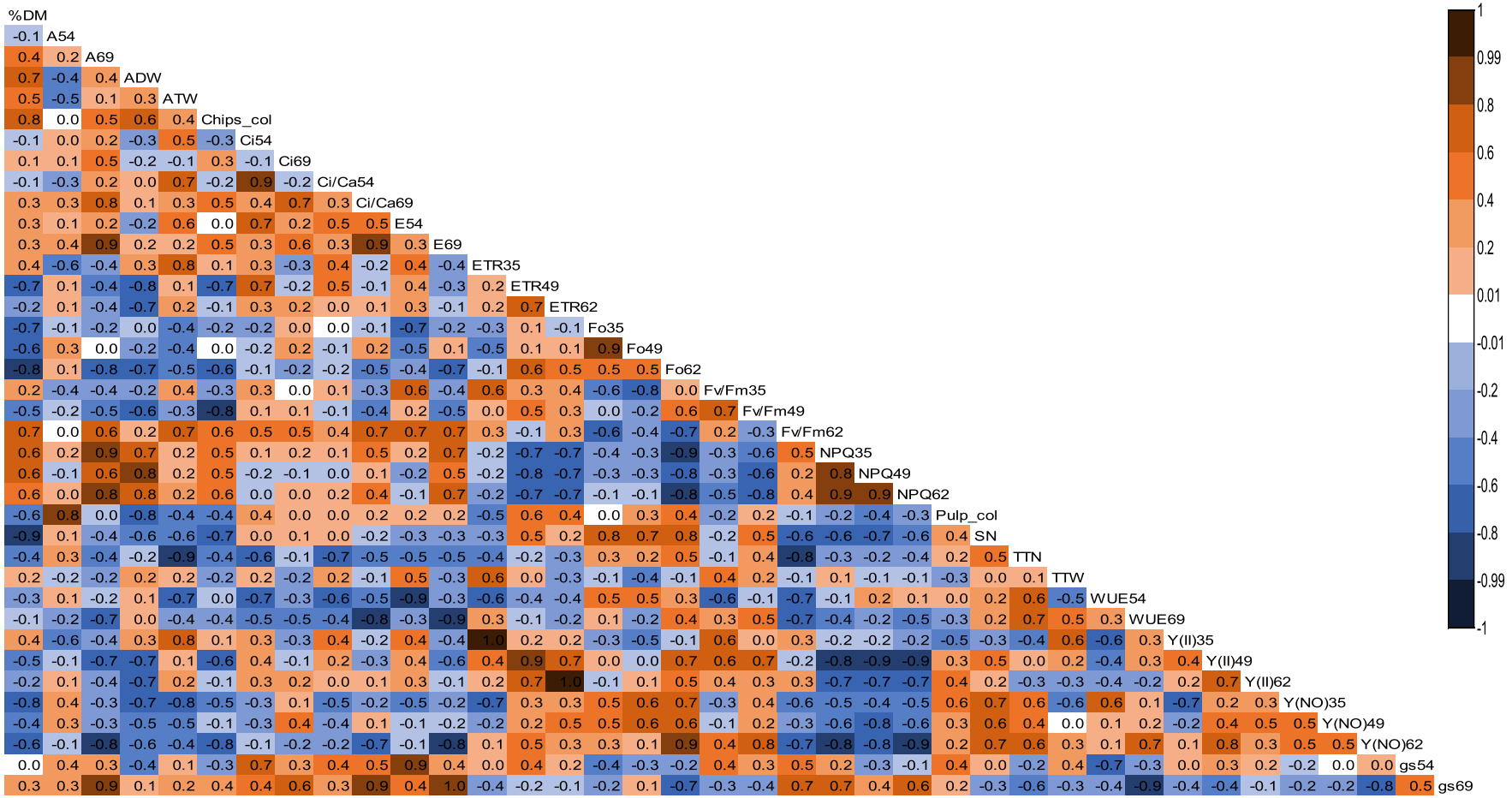

Figure 5. Pearson correlation matrix showing correlations among population means for physiological traits measured in eight genotypes grown under high temperature treatment (T2: high temp, 24°C-34°C). Number represents the magnitude of the correlation. and the color represents the positive and negative correlations. Significance levels of correlation: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. **** $p \leq 0.0001$

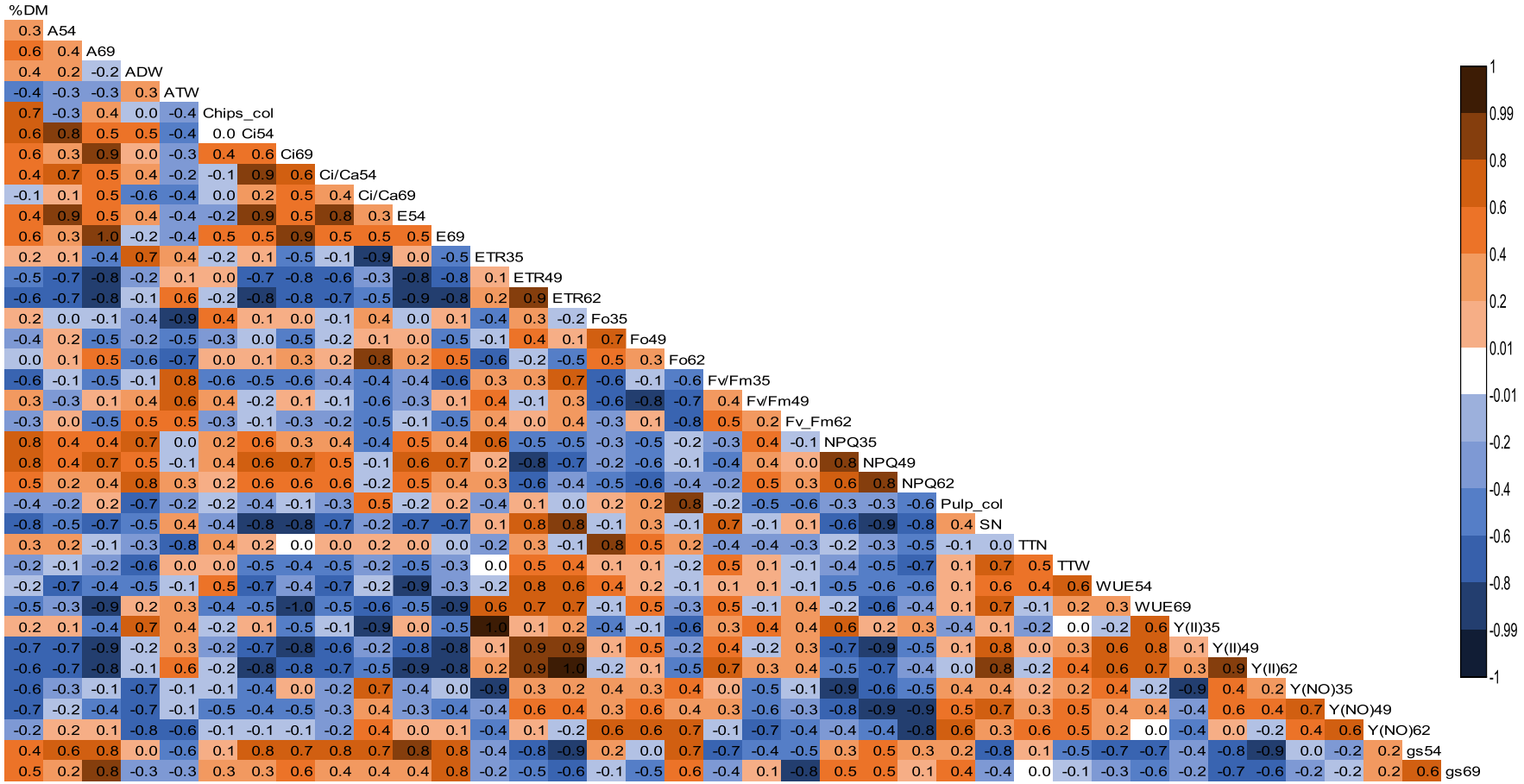

Figure 6. Pearson correlation matrix showing correlations among population means for physiological traits measured in eight genotypes grown under high mild temperature treatment (T3: mild high temp, 17°C-29°C). Number represents the magnitude of the correlation. and the color represents the positive and negative correlations. Significance levels of correlation: * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. **** $p \leq 0.000$

The principal component analysis of eight potato genotypes grown on the three thermal regime based on correlation matrix of 38 traits showed that 61.6% of the accumulated variation was explained by the three first components. The maximum variation of 24.38% was explained by first component followed by the second component with 21.14%. The first principal component variables that better contributed to genotypes distribution were related to photochemical phase of photosynthesis at 49 dap (ETR49, Y(II)49) opposed to photosynthesis process at later periods, with a high positive weight to ETR49 and Y(II)49 and high negative weight to A69, gs69 and NPQ62. The second principal component is related to gas exchange variables measured at 54 dap, having high positive weight to WUE54 and high negative weight to Ci54, Ci/Ca54, E54 and gs54. (Table 7)

In the PCA bi-plot (Figure 7), all the plants that grew under high temperature conditions were located on or close to the right inferior quadrant, while the ones under control treatment and mild-high temperature treatment were mixed on the other quadrants, but plants grown under mild-high temperature treatment were mostly on the right upper quadrant. Whereas Od80-02 is located on the left inferior quadrant, independent on the temperature treatment. Variables that contributed the most to the separation of T2 to the rest of the treatments were gas exchange variables evaluated at 54 dap, as A54, Ci54, Ci/Ca54, gs54, E54, even though Markies and Innovator grown on the same temperature condition was mostly influenced by ETR and Y(II) evaluated at 49 dap. Also mainly WUE54 and TTW contributed in an opposite way to this separation, being in agreement with the Scott Knott test where levels of gas exchange data evaluated at 54 dap were higher on T2, while WUE evaluated at the same time (Table 5) and yield data were lower at the same treatment (Table 6). F88 and Asterix grown under T3 were mostly influenced by Fv/Fm35 and Fo62, while Asterix and O14 grown under T1 were influenced by the color of the chips and F53, C41 grown under the same treatment was mostly influenced by Fo49.

Table 8. Latent vectors of 38 evaluated variables on eight genotypes grown under three different temperature conditions (T1: control temp, 14°C-27°C; T2: high temp, 24°C-34°C; T3: mild high temp, 17°C-29°C). PC1= first principal component, PC2= second principal component. Pelotas, 2019.

Variables	PC1	PC2
%DM	-0.20	0.03
A54	0.01	-0.27
A69	-0.29	-0.10
ADW	-0.11	-0.05
ATW	-0.05	0.10
Chips col	-0.19	0.06
Ci54	0.04	-0.32
Ci69	-0.21	-0.03
Ci/Ca54	0.03	-0.31
Ci/Ca69	-0.20	-0.04
E54	0.12	-0.32
E69	-0.19	-0.23
ETR35	0.14	-0.11
ETR49	0.28	0.01
ETR62	0.16	0.12
Fo35	0.11	0.04
Fo49	-0.14	0.10
Fo62	0.05	0.09
Fv/Fm35	0.10	0.15
Fv/Fm49	0.18	-0.01
Fv/Fm62	-0.03	0.12
NPQ35	-0.27	0.03
NPQ49	-0.21	-0.02
NPQ62	-0.23	-0.04
Pulp col	0.08	-0.09
SN	0.19	0.13
TTN	-0.02	0.21
TTW	-0.08	0.29
WUE54	-0.14	0.31
WUE69	0.08	0.26
Y(II)35	0.14	-0.11
Y(II)49	0.29	-0.01
Y(II)62	0.16	0.12
Y(NO)35	0.13	0.08
Y(NO)49	-0.02	0.06
Y(NO)62	0.19	-0.02
gs54	0.09	-0.31
gs69	-0.24	-0.12
% variation	24.38	21.14

Dry matter content (%DM), net CO_2 assimilation (A), aerial part dry weight (ADW), average tuber weight (ATW), chips color (Chips col), intercellular CO_2 concentration (Ci), ratio between internal and external CO_2 concentration (Ci/Ca), transpiration (E), apparent rate of photosynthetic electron transport (ETR), minimal fluorescence (Fo), maximum photochemical efficiency of PSII (Fv/Fm), non-photochemical quenching (NPQ), flesh tuber color (Pulp col), number of stems (SN), total tuber number (TTN), total tuber weight (TTW), water use efficiency (WUE), effective quantum yield of PSII (Y(II)), quantum yield of nonregulated energy dissipation (Y(NO)), stomatal conductance (gs), and water use efficiency (WUE). Numbers following some variables means the day after planting that was measured.

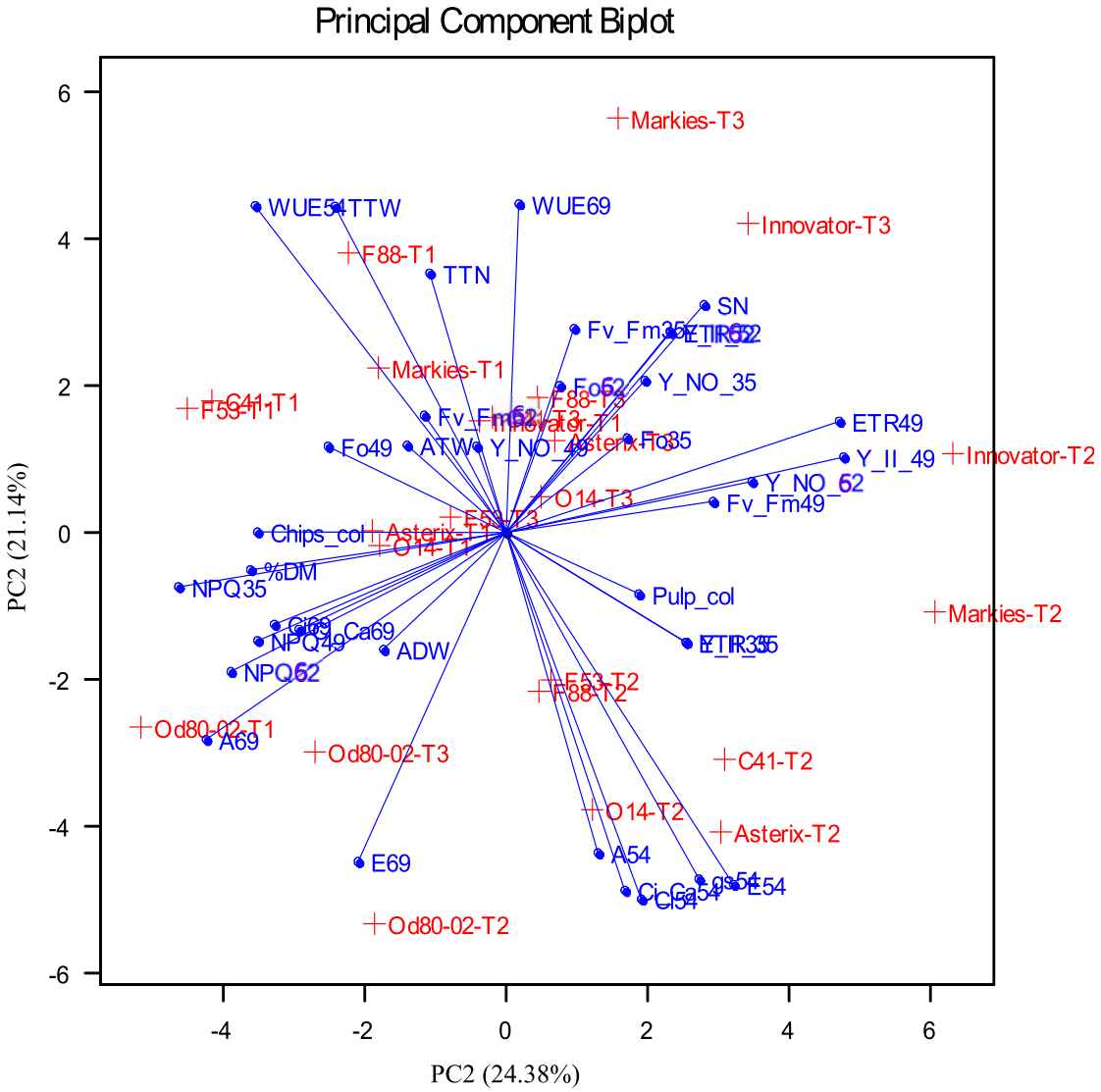

Figure 7. Principal component analysis bi-plot (Component 1 versus Component 2) of eight potato cultivars submitted to three temperature condition treatment (T1: control temp, 14°C-27°C; T2: high temp, 24°C-34°C; T3: mild high temp, 17°C-29°C)

3.4 Dicussion

Fluorescence gives us an idea of the stability and function of the photosynthetic apparatus, during photochemical phase of the photosynthesis, having the control treatment as a normal situation of photosynthetical machinery state and function. On our experimental condition, was observed a low light caption capacity of PSII (Fv/Fm) (PSHIBYTKO; KALITUKHO; KABASHNIKOVA,

2003) before tuber set (35 DAP) (Table 5). Fourteen days later, at the beginning of tuberization, both high temperature and mild high temperature seemed to benefit the efficiency of photons acceptance and energy transference of the PSII, which was even higher than previous evaluation of the same treatment. However, during tuber bulking (62 DAP), the capacity to capture light and transfer energy inside the PSII was diminished (Figure 2).

On this behalf, many authors have suggested the differences on Fo and Fv/Fm are in accordance to the chlorophyll concentration and stability of the thylakoid membrane proteins (Kalaji and Bosa 2011), but Y(NO) values suggest proteins are not damaged. Also was found a connection between the photosynthetic machinery function and tuber initiation (FISCHER et al., 2008; GURURANI et al., 2012), but eventhough evaluations of tuber initiation were not made, previous studies with the same light conditions demonstrated no differences on the time of tuber initiation relative to temperature (KNEIB, 2019). At last, acclimation process to elevated temperature due to long-term exposure was related (OBIERO; MILROY; BELL, 2020), terms that seems to be more acceptable to our results. Because even though, initially, heat limited light caption capacity, also caused an increase of the photosynthetical activity (Y(II) and ETR), which may have promoted later an upgrade of the maximal efficiency of PSII to harvest light and transfer energy. Nevertheless, as adverse condition continued on time, the flow of electrons through the thylakoid membrane proteins was diminished together with work efficiency of PSII, although only Fv/Fm was inferior to the control treatment.

In addition, the chemical phase of photosynthesis, expressed by A, gs, Ci and Ci/Ca, seemed to be advantaged by high temperatures 54 DAP, nevertheless the WUE demonstrated that all the water absorbed was not only used for the production of energy and glucose, but to cool down leaves temperature through E, as well (DEMIREL et al., 2017). This was different under mild-high temperature at this time, where plants demonstrated to behave similar than those grown under control treatment. In accordance to this, previous studies demonstrated that temperatures around 30°C didn´t negatively affect photosynthesis (LAFTA; LORENZEN, 1995). Over time, gas exchange was stable under control temperature, but under high temperature and mild-high temperature condition, there was a significant declination of the process of photosynthesis and an

incapacity of the plant to deal with heat, expressed by an E value similar to the control (Table 6, Figure 3).

In this way, putting together the two phases of photosynthesis can be said that there was an initial partial hinder of light gathering by the antenna complex of PSII (PSHIBYTKO; KALITUKHO; KABASHNIKOVA, 2003) and some time after, the acceleration of the process due to high temperature (WOLF; MARANI; RUDICH, 1990). In a process of acclimation, plants grown under these environments tried to overcome the heat by cooling down with E, but in order to not to waste too much water and energy, closure of the stomata was induced, precluding the gas interchange and so photosynthesis process, as reported by other authors (KAMINSKI et al., 2014; SAGE; KUBIEN, 2007). Potato plant is a C3 plant, and under CO2 deficit in the stroma, Rubisco enzyme is able to capture O2 doing photorespiration (TAIZ et al., 2017). On this state, plants waste too much energy not producing glucose important for tuber bulking (CHEN, Li Qing *et al.*, 2010), at this time (69 DAP) when tubers became the sink organ. For this reason, tuber dry matter (%DM) and tuber yield (Table 7) were lower on plants submitted to intense heat, maybe because of an inefficient tuber bulking due to photorespiration, but as this parameter wasn't measured, can't be assured this is what happened in this case. On the other side, yield of plants grown under mild high temperature was similar to the control treatment, suggesting a better process of adaptation to the environment. In this way, we can confirm that the period that plants are grown under high temperatures besides the intensity of it are determinant factors on the resultant phenotype, this fact was also observed by other authors (HANCOCK et al., 2014; SINGH, Baljeet; KUKREJA; GOUTAM, 2019).

Literature points out a modification of carbohydrate partitioning by heat, proposing that few tubers on plants may be the result of the efficiency of photosynthesis, directing the photosynthates to plant tops (BASU et al., 1999; WOLF et al., 1990). Nevertheless, in our experimental condition, aerial part didn´t have a better progress.

High environmental temperature also affected tuber's quality (Table 7), making them unacceptable for industry, because of the low %DM and darker chips (FERNANDES et al., 2010). However, chips fry color response to heat differed between genotypes and F53, Od80-02, F88, Asterix and Innovator were

unaffected either by high and mild high temperature, while tubers of O14 grown under high environmental temperature produced even lighter color of chips. Asterix, Innovator and Markies are three known dutch cultivars used for French fries industry and, from them, only Markies chips fry color were drastically affected by high temperature, but not by mild high temperature. Opposite to it, Markies flesh color was unnafected by heat, while flesh tuber color of Asterix and Innovator were modified from a light yellow to a mid-yellow, similarly C41 color flesh passed from white to cream.

Color of both fry and fresh tuber respond to their chemical composition, thus many researchers has identified the reducing sugar content as the responsible for potato chip color (DA SILVA PEREIRA; DA SILVA; MARQUES CASTRO, 2016), from which fructose provoked the highest browning followed by glucose (MARQUEZ; AÑON, 1986). However, acid invertase activity (WANG, Yi; BUSSAN; BETHKE, 2012), ascorbic acid, phenolic acids and glutamine content (Rodriguez-Saona and Wrolstad, 1997) also contribute to the final result. Environmental conditions during tuber formation and storage has a direct response over tuber chemical composition (PEREIRA et al., 2007). On this behalf, mild high temperatures promote the conversion of sugars to starch, thus diminishing reducing sugar concentration on tubers (PEREIRA et al., 2007), while too high a temperature inhibit this conversion (KRAUSS; MARSCHNER, 1984), resulting in high reducing sugars. Likewise, our results showed darker chips (Table 7) from tubers grown under heat stress and similar chips color than control from tubers grown under mild high temperature. Differences on this response between genotypes can be attributed to the genetic factor, as revealed by Baroja-Fernández et al. (2009), who found that sucrose synthase activity overexpression favors starch accumulation in tubers.

On the other side, fresh flesh color has been found dependent mainly on sucrose, glucose (PAYYAVULA; SINGH; NAVARRE, 2013), phenolics (NAVARRE et al., 2011) and carotenoids content (BROWN, C.R. et al., 1993), with the highest value for colored genotypes. The profile of these compounds on tubers is a genetic controlled trait, with few or no environmental influence, but the content has in some portion influence of the environment (ANDRÉ et al., 2009; CEBULAK et al., 2023; DE MASI et al., 2020), which could have happened in our experiment. Brown et al., (1993) found that differences between yellow and white

flesh color is due to carotenoid content, which, as the other molecules, have antioxidant properties. It is known that plants produce secondary metabolites as a protection in response to adverse abiotic and abiotic stresses, which in turn gives to the edible organ a valuable phytonutrient for human consumption (PAYYAVULA et al., 2012). However, some studies didn´t find any carotenoid content alteration through different environments (HAYNES et al., 2010), while others did (HAYNES et al., 1996), but in anyway total carotenoid has a very close correlation with yellow-flesh intensity. In this way, we can infer that changes of flesh color in our experiment was due to alteration on carotenoid tuber content, being dependent on the genotype, maybe because of the different zeaxanthin epoxidase transcript levels of each genotype (MORRIS et al., 2004). This flesh color changes, will affect the consumer attraction for the product on the fresh market, which depends on the citizenship, north American and British prefers white-flesh varieties (BROWN, Charles R. et al., 2007; NAVARRE et al., 2011), while Peruvian prefer yellow and colored tubers (DEVAUX, A.; ORDINOLA; HORTON, 2011) and Brazilian, cream (HAYASHI, 2001).

PCA (Figure 7) separated heat treatment (T2) and the other two treatments (T1 and T3) mainly by gas exchange parameters measured at 54 DAP and function of the photochemical phase measured at 35 DAP, opposite to yield parameters and WUE measured at 54 DAP. Suggesting that photosynthesis on initial stages of tuberization (54 DAP) has big influence on final product. In terms of industry quality, PCA also show that tubers grown under high temperatures originated darker potato chips and fewer %DM, being the most affected Innovator and Markies. Instead, potatoes grown under control temperature conditions had the best industry quality, as most of them were located to the left of the graphic. Negative correlation between this characteristics and fluorescence parameters (Fv/Fm, ETR, Y(II)) measured 49 DAP, tell us that at this stage of the plant, photosynthesis has negative influence over tuber quality. Interestingly, ADW was in an opposite direction than SN, which means that stems doesn´t determine the dry weight of the aerial part. Independent on the treatment.

Among genotypes, some called special attention. In the first place, there is Asterix, which yield's was one of the highest among genotypes, fry chips quality didn´t change and flesh color was a little darker under T2. In addition, aerial part of the plant didn´t developed more under high temperature and ADW was low

than the others genotypes. Physiological parameters demonstrate that on tuber set and on the beginning of tuberization, photosynthetic machinery worked better under high temperature, while during tuber bulking stayed as in T1, with a higher performance when compared with the other genotypes. At the same time, this genotype showed a higher and, gs than the rest, at the beginning of tuber bulking (54 DAP).

O14 is also an interesting genotype, as even when the total yield was lower under T2; ATW was higher among genotypes and under T3 kept the same values than under T1. Besides, when grown under high temperatures, Chips col were even lighter, while Pulp col stayed cream and %DM was one of the highest between genotypes. In addition, less SN and ADW under T2, demonstrates carbon partitioning didn´t changed due to high temperature. Fluorescence parameters showed a better biochemical phase photosynthetic performance of this genotype among others. Bigger tubers, light Chips col and high %DM make of this clone suitable for french fries industry.

Different to Asterix and O14, Markies had an stable aerial part development as well as tuber yield and quality in terms of color, however, %DM was one of the lowest. This might be because this cultivar got to an acclimation on high temperature, demonstrated by an initial decrease of Fv/Fm 35, followed by its stabilization.

On the other side, there is Od80-02, which was inferior to the rest when grown under high temperatures, expressed by the 47% less yield when compared to T1, although tuber quality didn´t changed much. It was also observed that aerial part stayed constant. This can be explained by its lowest photosynthetic performance (Fv/Fm, Y(II) and ETR) specially since the beginning of tuberization (49 DAP), besides an elevated water lost, expressed by a high gs, E and WUE. Despite the fact that A was higher over time, there was a problem of carbon partitioning by the preference for aerial part as sink organs.

It´s also interesting to observe that Asterix, O14 as well as Markies lost less water through E on a more advance stage (69 DAP); opposite to Od80-02 whose E was the highest. (Table 5).

For what the average grouping test have shown, gas exchange analysis did not help much to explain morpho-agronomic parameters, maybe of the advanced phenological stage it was measured.

3.5 Conclusion

Photosynthetic parameters of both stages are good indicators of heat tolerance, especially when measured until the beginning of tuber bulking stage.

4 CHAPTER II: Identification of variables and evaluation time for selection of heat tolerant potato genotypes

4.1 Introduction

Potato (*Solanum tuberosum*) is the third most consumed food crop around the world (CIP, 2020), being Brazil between the thirties most important countries that produces it around the world and the second in South America, getting to 3.85 million tons in 116 thousand hectares on 2021 (FAO - Food and Agriculture Organization of the United Nations, 2022). The states that most contribute to this production are Bahia, Goiás, Minas Gerais, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Silveira Wrege et al., 2004) with tropical and subtropical climates. In the tropical regions where potatoes are produced, high temperatures negatively affect the production and quality of tubers (Gandolfi Benites, 2007). At this respect, the potato breeding program in Brazil has as one of its objectives the obtaining of heat tolerant cultivars (Marti Emygdio et al., 2020), without neglecting the requirements of farmers and consumers, either for fresh table-stock or processing.

The creation of a new cultivar is a long breeding process, which includes the selection of hybrid population with desired agronomic and quality traits. After four generations, selected clones are evaluated in controlled environments in order to test their tolerance to different biotic and abiotic stresses, besides the conference of tuber quality. Clones with potential are tested on open fields with different climate characteristics, from where some could be approved as a new cultivar (Pereira et al., 2012).

For many years, potato breeding around the world has aimed the development of all-purpose cultivars. Lately, breeders have focused their efforts on selecting cultivars with more specific applications and production environments (Andrivon, 2017). However, working with potato has some limitations, like the complexity of its physiology, its tetrasomic inheritance, its low multiplication factor and the difficulty in evaluating its phenotype, makes of potato breeding an slow process and, consequently, costly (Bonnel, 2008).

On this behalf, a multidisciplinary scientific knowledge, has made it possible to make far more logical decisions about breeding tactics, breeding objectives, tools, and techniques (Fasoula et al., 2020), and thus reducing time and cost (Slater et al., 2017). Plant physiology is one of this fields that constitute an essential tool for plant breeding, since helps identifying processes that are impacted by the environment and then develop plant mechanisms that adapt to originally adverse conditions.

In this way, the aim of this work was to find characters that can be used on the selection of heat tolerant genotypes and the best phenological stage the evaluation should be done.

4.2 Materials and methods

Plant material

The experiment took place in growth chambers at Embrapa Clima Temperado, Pelotas, Rio Grande do Sul state, Brazil, from September to November 2022. Three cultivars (BRS F63 (“Camila”), Innovator, Markies) and advance clone from Embrapa’s potato breeding program (MB 54-02) were characterized according to their response to different temperature regimes (Table 9).

Table 9. Type, origin vegetative cycle and main characteristic of the genotypes used in the experiment. Pelotas, 2022.

Genotype	Type	Origin	Vegetative cycle	Characteristic
BRS F63	Cultivar	Embrapa - Brazil	Intermediate	Known heat susceptibility. For fresh use.
Innovator	Cultivar	Holland	Intermediate	Firstly used for frozen pre-fried French fries unstable in production with field problems
Markies	Cultivar	Holland	Intermediate	Main cultivar used for frozen pre-fried French fries in Brazil from a quality point of view.
MB 54-02	Advanced clone	Embrapa - Brazil	Late	Resistant to bacterial wilt, developed under tropical Brazilian conditions.

The experimental design was a randomized complete block under factorial arrangement (four genotypes and two temperatures) with four replicates.

Growth conditions

Potato tuber seeds (2.0 to 3.0 cm of length) were planted on September 2nd, 2022 in phenolic foam moistened with nutrient solution. These tubers stayed in the same growth chamber over control temperature treatment for twenty seven days. At that time, uniform tubers (sprouting length of 0.5 to 1.0 cm) were transplanted into 2-liter pots with organo-mineral substrate. The pots were then distributed into two growth chambers calibrated with the same temperature regime for twenty days, when different temperature regimes were programmed for each chamber. T1 was the control, with thermal amplitude from 14 to 24oC and T2 was the heat treatment, with thermal amplitude from 24 to 34oC (Figure 8). Being that control treatment (T1) simulates the ideal temperature for potato growth, while high temperature treatment (T2) refers to a heat stress situation for this crop (TIMLIN et al., 2006; WOLF et al., 1990)

Apart from the temperature, the others environmental parameters were the same in both chambers, photoperiod of 12 hours with 400 µmol m-2 s-1 of luminous intensity. Irrigation during sprouting was twice a day, after planted on pots were drip irrigated and the regime was established differently between treatments and plant phenology.

Plants were maintained in the chambers and evaluations were done three times on four plants/genotype/temperature treatment in a destructive way. For each evaluation date, physiological traits were assessed, leaves samples for biochemical analysis were taken and each plant was destroyed in order to get the morfoagronomic measurements. This procedure was made on the 6th, 13th and 28th day of treatment (DOT), which means 53, 60 and 75 days after planting (DAP) respectively. The rest of the plants were left until senescence, when were harvested.

Treatments started around 45 DAP, because in this moment tuber set starts on precocious genotypes and from there evaluations were done periodically in order to follow the physiological and morpho-agronomical effects of high temperature on potato.

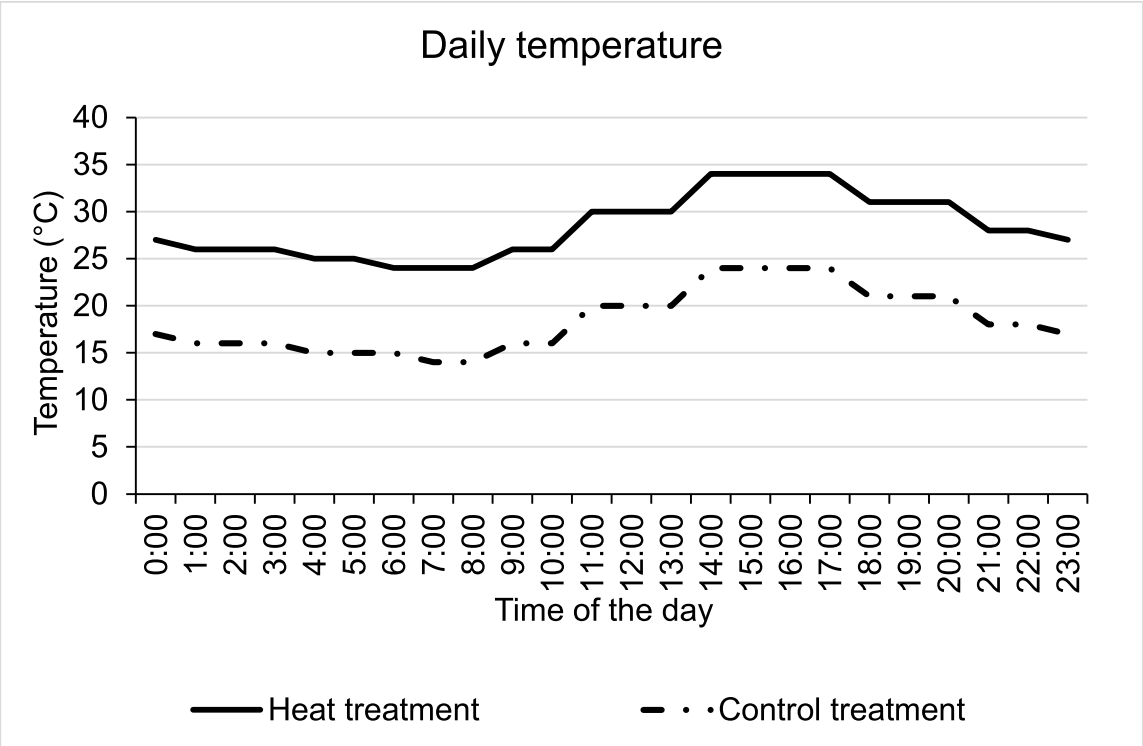

Figure 8. Daily temperatures programmed in growth chambers for two different temperature conditions: control temperature treatment (T1) and high temperature treatment (T2). Pelotas, 2022.

During the period of physiological measurements and leaf collection for biochemical analysis, temperature was established to the highest temperature for each treatment.

Physiological analysis

Physiological traits were assessed on the newest fully expanded leaves (the fourth expanded leaf counting from the top); gas exchange analysis was conducted on the terminal leaflet, while chlorophyll fluorescence measurement was made on the first lateral leaflet.

For gas exchange analysis, values of photosynthetic rate (A), transpiratory rate (E), stomatal conductance (gs), internal CO2 concentration (Ci) and ratio of internal to atmospheric CO2 concentration (Ci/Ca) were determined using infra-red gas analyser IRGA (LI- 6400XT LI-COR, Inc., Lincoln, NE, USA). Before measuring, reference CO2 and flow rate to the sample cell were set at 400 µmol CO2 mol-1 and temperature was set at 24°C (for T1), and 34°C (for T2). Using the lamp annexed to the equipment, the output of quantum sensor was

established at chamber's light intensity. From these results, water use efficiency (WUE) was calculated dividing A by E for each of the measure dates.

For fluorescence measurements, the first leaflet of the fourth expanded leaf of each plant was covered with aluminium foil in chambers where they were grown. Fluorescence was induced by application of saturation pulses of 7000 µmol fótons m-2 s-1 using IMAGING-PAM chlorophyll fluorometer (model PAM-2500 da Walz Heinz GmbH, Effeltrich, Germany). Obtained data was processed in a excel sheet, where maximal PS II quantum yield (Fv/Fm) was calculated according to the equation: Fv/Fm = (Fm - Fo)/Fm, considering the data generated after the first light pulse. Minimal fluorescence (Fo'), effective photosystem II quantum yield (Y(II)), apparent rate of photosynthetic electron transport (ETR) and non-photochemical quenching (NPQ/4) parameters were calculated as the average of the data obtained on light pulse of 280 and 335 PAR.

Morfoagronomic measurements

Using a meter stick each of the sampled plants were height (H) measured in centimeters (cm) from the soil surface to the top of the canopy. Then, the number of stems (SN) and leaves (LN) per plant were counted and leaf area (LA) of each plant was assessed with LI-3100C Area Meter.

Leaves and stems were separated and weighed to obtain leaves and stems fresh weight (LFW and SFW). Afterwards, both of the organs were put in paper bags separately and kept into a forced-air-drying oven for 72 hours at 70° C, after this time dry weight of leaves (LDW) and stems (SDW) were obtained. With LFW, SFW, LDW and SDW, the percentage of dry matter for leaves (%LDM) and stems (%SDM) were calculated. Belowground organs were also measured, thus roots were weighed to obtain their fresh weight (RFW) and, as done with the aerial parts, were put on a paper bag and dried in a forced-air-drying oven for 72 hours at 70°C obtaining roots dry weight (RDW) and the percentage of root dry matter (%RDM) was calculated. On the other side, all the tubers produced per plant were harvested and weighed (TTW) and counted (TTN). From the relation TTW/TTN, was calculated the average tuber weight (ATW). Five commercial tubers without peeling per plant were cut into cubes and a sample of 250 g was weighed (TFW) and put into a forced-air-drying oven for 72 hours at 80° C, after

this time, each sample was weighted (TDW) and the percentage of dry matter (%TDM) was calculated (CIP, 2010).

For the final yield, the rest of the plants were harvested as they reached senescence until completing 109 DAP that all harvesting was completed, even some plants had not entered senescence. From this yield TTW, TTN, ATW, TFW, TDW and %TDM were also obtained.

Biochemical analysis

Leaflets of the fourth leave (counting from the bottom of the plant) and tubers were sampled from each plant that was evaluated at the 53rd, 60th and 75th day after planting, which corresponded to the 6th, 13th and 28th day of treatment.

Biochemical analysis were carried out at the Laboratory of Plant Biochemistry at the Chemical, Pharmaceutical and Food Sciences Center of the Federal University of Pelotas.

a. Proteins

In a microplate, 10 µl of the antioxidant enzymes extract and 250 µl of Bradford were added on each well. After 4 minutes was shaken and absorbance was determined at a 595 nm wavelength. The blank absorbance was obtained with 260 µl of Bradford.

b. Antioxidant enzymes

200 mg of foliar samples were macerated with liquid nitrogen and 50% of PVPP and 1500 µl of and extraction solution were added. The extraction solution was composed by 375 µl of potassium phosphate buffer 400 mM pH 7.8, 15 µl of EDTA 10 mM, 75 µl of ascorbic acid 200 mM and 1035 µl of water. The solution was placed into ependorf tubes and taken to centrifugation of 13000 g for 20 minutes at 4°C, supernatant was collected (extract) and used for the ascorbate peroxidase (APX), catalase (CAT) and superoxide dismutase (SOD) activity analysis. Antioxidant enzymes activity were measure with the SpectraMax M2 spectrophotometer microplate reader.

For APX activity, in each well was put 180 µl of incubation solution (composed by 150 µl of potassium phosphate buffer 50 mM pH 7, 20 µl of

ascorbic acid 2.5 mM and 10 µl of the extract) and incubated for 5 minutes at 25°C in the spectrophotometer. Then, 20 µl of hydrogen peroxide 50 mM was added to the reaction and lecture was made immediately after, in a kinetic mode for 3 minutes with an interval of 10 seconds at wavelength of 290 nm.

For CAT activity, 180 µl of incubation solution (composed by 100 µl of potassium phosphate buffer 200 mM pH 7, 70 µl of distilled water and 10 µl of the extract) was added in each well and incubated for 5 minutes at 28°C. Then, 20 µl of hydrogen peroxide 125 mM was added and the read was immediately made on a kinetic mode for 3 minutes on an interval of 10 seconds at a wavelength of 240 nm.

For SOD, in a dimly lit room, 173 µl of incubation solution (composed by 100 µl of potassium phosphate, 40 µl of methionine 70 mM, 2 µl of EDTA 10 mM and 31 µl of distilled water) was put on each well. Then, 15 µl of NBT 1 mM, 10 µl of the extract and 2 µl of riboflavin 0.2 mM. microplate with the reaction solution was taken on a light box for 10 minutes and when the time was fulfilled, lectures of absorbance at a 560 nm wavelength were done.

On each case, the blank absorbance was obtained by replacing the extract by distilled water or extraction buffer and liquid absorbance was obtained by subtracting the blank absorbance from the sample absorbance.

c. Pigments

Foliar samples of 20mg were put in test tubes with 4 ml of dimethyl sulfoxide (DMSO) with 5% of CaCO3, these were put into a water bath of 65°C for 30 minutes and when took off were kept out of the light until room temperature was reached by the samples.

250 µl of each sample was put into each well of the microplates and absorbance (A) lectures were made with the spectrophotometer on three wavelength (480, 649 and 665 nm), which were then used to calculate pigments content, as follow:

Chlorophyll a (Chl_a) = ((12.19 x A665) – (3.62 x A649))

Chlorophyll b (Chl_a) = ((25.06 x A649) – (6.5 x A665))

Carotenoids (Car) = ((1000 x A480) – (1.29 x Chl a) – (53.78 x Chl b))/220

With these results, total chlorophyll content (T_Chl), the ratio of chlorophyll a to chlorophyll b (Chl_a/Chl_b) and the ratio of total chlorophyll content to carotenoids (T_Chl/Car) were calculated.

d. Lipid peroxidation and Hydrogen peroxide

For extraction, 200 mg samples were macerated with liquid nitrogen and 2 ml of trichloroacetic acid (TCA) 0.1%, the solution was collected into ependorf tubes and taken to centrifugation of 12000 rpm for 20 min at 4°C, finally, the supernatant was collected (extract).

For lipid peroxidation (Perox) test, 850 µl of thiobarbituric acid (TBA) 0.5% and 150 µl of the extract were put together on test tubes (two per sample), which were kept into water bath of 90°C for 20 minutes, then into ice bath for 10 minutes and when taken out, enough time was wait until room temperature was reached. 250 µl of each solution was put into two wells of the microplates and absorbance (A) lectures were made with the spectrophotometer on two wavelength (535 and 600 nm).

For hydrogen peroxide (H2O2), the reaction was made in two wells of the microplate per sample, and was composed by 70 µl of potassium phosphate 10 mM pH 7 buffer, 100 µl of potassium iodate 1M and 30 µl of the extract. The reaction was incubated at 30°C in the spectrophotometer for 10 minutes and the lecture of absorbance was made on a 390 nm wavelength. Absorbance results were used on the equation obtained by reaction of hydrogen peroxide known concentration.

e. Glycolate oxidase

For extraction, 200 mg of foliar samples were ground with liquid nitrogen with 10% polyvinylpolypyrrolidone (PVPV) and then were homogenized with 1.8 mL Tris-HCl buffer, pH 7.8 (composed by Tris-HCl 50 mM, DTT 5mM and Triton X-100 0.1%). This solution was centrifuged at 12,000g for 15 min at 4 °C, after this time, supernatants were collected (extract).

For glycolate oxidase (GO) dose, a mixture of 50 mM Tris-HCl buffer (pH 7.8), 0.009% (v/v) Triton X-100, 3.3 mM phenylhydrazine HCl (pH 6.8 adjusted with KOH) was put in assays tubes and incubated at 25°C. Then, 1.35 mL of plant extract plus distilled water was added and at room temperature, 50 uL of glycolic

acid 300 mM. GO activity was determined by absorvance reads in kinetic mode for 3 minutes on an interval of 10 seconds at a wavelength of 324 nm.

f. Total soluble sugars and aminoacids

For extraction, samples were ground with liquid nitrogen, homogeneized with 8 ml of MCW (methanol: clorofórmio: milli-Q water in the proportion of 12:5:3) and left for 24 hours in the dark. After this period, 2 mL of MCW solution were added and centrifuged at 2500 rpm for 30 minutes. 8 ml of supernatant were collected and 2 ml of chloroform and 3 ml of milli-Q water were added. The new solution was centrifuged for 30 min at 2500 rpm until three phases were formed. The first phase was collected and placed in a 30ºC water bath for 24 hours or until half of the volume was evaporated. From this extract, total soluble sugars, total soluble amino acids and proline were quantified. The levels were calculated by comparing the readings with the standard curve obtained from different known concentrations of each molecule.

Contents of total soluble sugars of leaves and tubers (TSS-L and TSS-T): Quantified from the first extract according to the method described by Graham and Smydzuk (1965). Readings were performed in a spectrophotometer at 620 nm, and the results expressed in mg g-1 FW.

Total soluble amino acid content of leaves and tubers (AA-L and AA-T): Determined according to Yemm et al. (1955) from the first extract. The readings were performed in a spectrophotometer at a wavelength of 750 nm. The values obtained were expressed in µmol g-1 MS.

Proline content of leaves and tubers (Prol-L and Prol-T): The method used for quantification was proposed by Rena and Masciotti (1976), from the first extract obtained. Readings were performed in a spectrophotometer at 515 nm wavelength and compared with the standard curve of known proline concentrations, with the content expressed in µg mg-1 MS.

Statistical analysis

The yield data, in terms of TTW and ATW was analyzed through analysis of variance (ANOVA) and mean values were compared Scott-Knott multiple range test at 5% probability level using Genes statistical program (Cruz, 2001).

All the parameters evaluated were used for the principal component analysis (PCA) and some of them for path analysis (as will be describe later). Both for PCA and path analysis were done using, as well, Genes statistical program (Cruz, 2001).

Principal component analysis (PCA) as well as bi-plot graphical display were performed using the average of four replicates of each genotype and temperature condition treatment per evaluation date.

For path analysis was used the phenotypic correlation data of the three cultivars (BRS F63, Innovator and Markies), as they were grouped together in the PCA. Since the used data presented severe multicollinearity, path analysis under multicollinearity test was done, establishing the lowest K value were variables had the same order in terms of □ value. Two path analysis were done (one for each temperature regime condition), considering the final TTW (TTW) as a dependent variable, and A, Ci/Ca, Y(II) of the first (A-1, Ci/Ca-1, Y(II)-1), second (A-2, Ci/Ca-2, Y(II)-2) and third (A-3, Ci/Ca-3, Y(II)-3) evaluation date, as explanatory variables.

Then, three path analysis per temperature treatment were made, one for each evaluation date, taking TTW as a dependent variable and A, Ci/Ca, Y(II), NPQ/4, Chl_a, Chl_b, Car, T_Chl, GO and TTW of the same and previous evaluation date, as explanatory variables.

4.3 Results

Analysis of variance showed that the genotype x temperature (GxT) interaction was significant for total tuber weight at 60 DAP (TTW-2), average tuber weight (ATW) and total tuber weight (TTW) after senescence. Genotype main effect was significant on the three dates of yield parameters. On the other hand, temperature main effect affected average tuber weight at 75 DAP (ATW-3), total tuber weight at 75 DAP (TTW-3), average tuber weight after senescence (ATW) and total tuber weight after senescence (TTW) (Table 10).

Table 10. Analysis of variance for average tuber weight at 53 DAP (ATW-1), 60 DAP (ATW-2), 75 DAP (ATW-3) and after senescence (ATW), for total tuber weight at 53 DAP (TTW-1), 60 DAP (TTW-2), 75 DAP (TTW-3) and after senescence (TTW), on four potato genotypes grown under two temperature condition treatments (T1: Control temperature, 14°C-24°C; T2: High temperature, 24°C-34°C). Pelotas, 2022.

Source of variance	dF	ATW-1	TTW-1	ATW -2	TTW-2	ATW -3	TTW-3	ATW	TTW
Genotype (G)	3	11.76**	1472.12**	22.72*	5025.94**	31.71*	2631.79**	76.35*	1093.71*
Temperature (T)	1	1.01^{ns}	385.79^{ns}	2.36^{ns}	7.79^{ns}	119.08**	8604.42**	224.11**	12317.44**
GxT	3	1.26^{ns}	109.17^{ns}	4.78^{ns}	1027.53**	12.21^{ns}	112.41^{ns}	82.04*	2731.92**
CV (%)		65.14	62.20	60.43	25.23	38.65	79.53	58.35	17.62

*: significant at 5% probability level, **: significant at 1% probability level, ns: not significant

Scott-Knott mean comparison analysis indicated a lower ATW on MB 54-02 than the rest of the genotypes in all of the evaluated dates. Also was observed that on the last harvest, Innovator had a similar ATW than MB 54-02 (Figure 9-a). On the other side, genotypes showed a different behavior in terms of TTW. At 53 DAP, MB 45-02 produced approximately 97% less weight than the other genotypes. At 60 DAP, MB 54-02 had also less TTW than the rest, with almost the quarter of Innovator´s production, followed by BRS F63, with 60% of Innovator´s TTW. BRS F63 and MB 54-02 had also the lowest production in terms of TTW at 75, being, in average, 67% of the TTW of the other two genotypes. On the last harvest not significant differences were observed between genotypes (Figure 9-b).

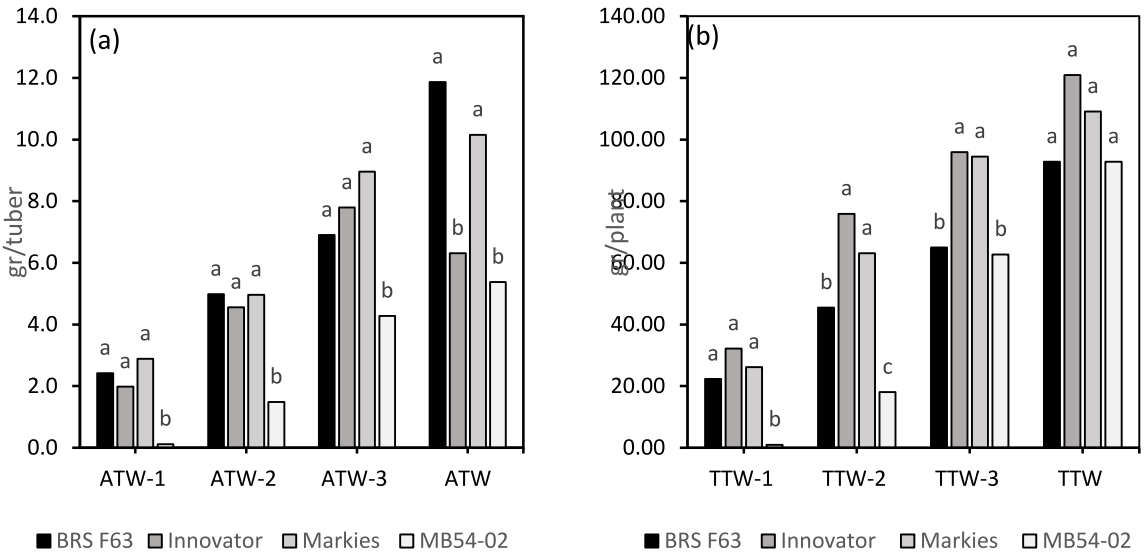

Figure 9. Mean values of yield parameters of four genotypes grown under two temperature treatments: Control temperature (T1: 14°C-24°C) and high temperature treatment (T2: 24°C-34°C). (a) ATW - Average tuber weight at 53 DAP (ATW-1), 60 DAP (ATW-2), 75 DAP (ATW-3) and after senescence (ATW). (b) TTW - Total tuber weight at 53 DAP (TTW-1), 60 DAP (TTW-2), 75 DAP (TTW-3) and after senescence (TTW). Same letters constitute a statistical homogeneous group between genotype at the same evaluation date. $P \leq 0.05$

When temperature treatments were compared by the Scott-Knott mean grouping analysis, significant differences were observed on the last two harvest dates (at 75 DAP and after senescence), with the lowest values for the high temperature treatment, being almost the half of what was obtained under control temperature conditions (Figure 10-a). For TTW occurred the same scenario, since plants grown on the high temperature treatment had less TTW than those grown under control treatment on the last two evaluation dates, with more than 30% less grams per plant (Figure 10-b).

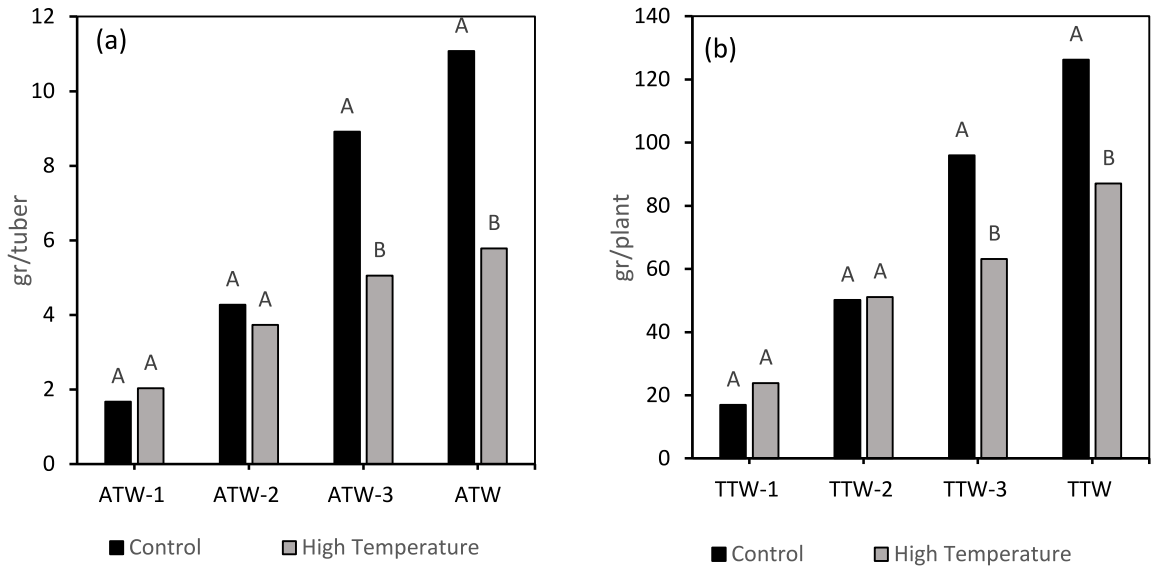

Figure 10. Mean values of yield parameters of four genotypes grown under two temperature treatments: Control temperature (T1: 14°C-24°C) and high temperature treatment (T2: 24°C-34°C). (a) ATW - Average tuber weight at 53 DAP (ATW-1), 60 DAP (ATW-2), 75 DAP (ATW-3) and after senescence (ATW). (b) TTW - Total tuber weight at 53 DAP (TTW-1), 60 DAP (TTW-2), 75 DAP (TTW-3) and after senescence (TTW). Same capital letters constitute a statistical homogeneous group between treatments at the same evaluation date. $P \leq 0.05$

In addition, harvest made after senescence revealed significant differences between genotype´s behavior on each temperature situation. The only cultivar that had less weight per tuber under high temperature situation was BRS F63, with less than the half of what was obtained under control temperature treatment (Figure 11-a). Under high temperature environment, BRS F63 produced almost the quarter of the weight per plant of what was produced under control temperature. Even though there was not significant differences on MB 54-02´s ATW, the TTW was lower when plants were subjected to high temperature condition, approximately 30% less (Figure 11-b).

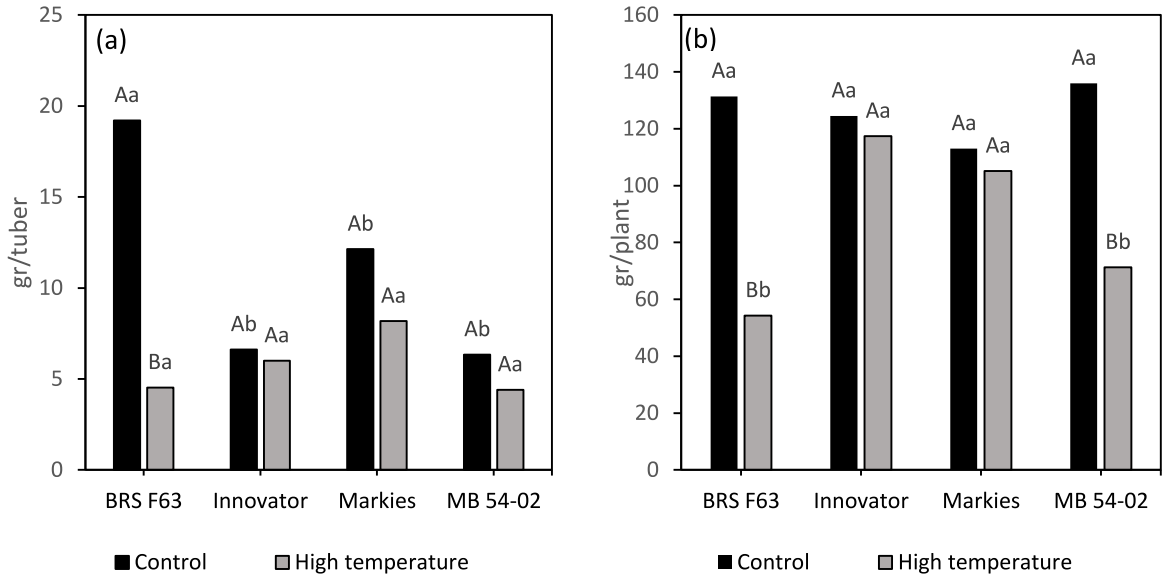

Figure 11. Mean values of yield parameters of four genotypes grown under two temperature treatments: Control temperature (T1: 14°C-24°C) and high temperature treatment (T2: 24°C-34°C). (a) ATW - Average tuber weight evaluated after senescence (ATW). (b) TTW - Total tuber weight evaluated after senescence (TTW). Same capital letters constitute a statistical homogeneous group between treatments of the same genotype. Same lowercase letter constitute a statistical homogenous group between genotypes of the same treatment. $P \leq 0.05$

The principal component analysis of four potato genotypes grown on the two thermal regime based on correlation matrix of 49 traits showed that at 53 DAP, 61.6% of the accumulated variation was explained by the two first components. The maximum variation of 37.4% was explained by first component followed by the second component with 24.2%. The first principal component variables that better contributed to genotypes distribution were mainly related to growth of leaves (LN, LA, LFW, LDW), stems (SFW, SDW) and roots (RFW, RDW). The second principal component has high contribution of tuber growth (TTN, TTW, TFW, TDW) and of aminoacids, in an opposite direction. (Table 11 and Figure 12)

Was also observed that at 60 DAP, the accumulated variation explained by the two first components was 64.3%, from where the first component explained 43.1% of the variation and the second component, the 21.2%. The distribution of the genotypes in the first principal component was strongly associated with tuber matter (TTW, ATW, TFW, TDW) and in an opposite direction with roots, leaves

and stems growth (LN, LFW, SFW, LDW, SDW, RDW), pigments (Chla, Chlb, Car, Chla/Chlb) and secondary metabolism (APX and H2O2). In the second principal component, variables that contributed the most were those related to photosynthesis variables (A, Ci, Ci/Ca, WUE) in opposition to NPQ/4 and H. (Table 11 and Figure 13)

At 75 DAP, principal component analysis indicated the two first components accounted for 69.9% of the total variance. The first principal component accounted for about 39.6% of the total variation and variables that contributed the most to the genotypes dispersion were of photosynthesis and aminoacids component since it included photosynthetic traits (A, Ci, Ci/Ca, Fv/Fm, Y(II), ETR, TChl), leaves matter traits (LA, LFW, LDW) and aminoacids traits (protein, AA-T and prol-T). The second principal component was named biomass accumulation component since it was correlated with WUE, TTW, ATW, TFW, TDW, and with H, SN, SFW, SDW in an opposite direction. This component accounted for 30.3% of the variation (Table 11 and Figure 14).

Table 11. Latent vectors of 49 evaluated variables on four genotypes grown under two different temperature conditions (T1: Control temperature, 14°C-24°C; T2: High temperature, 24°C-34°C). PC1= first principal component, PC2= second principal component. Pelotas, 2022.

Variables*	1st evaluation (53 DAP - 6 DOT)		2nd evaluation (60 DAP - 13 DOT)		3rd evaluation (75 DAP - 28 DOT)	
	PC1	PC2	PC1	PC2	PC1	PC2
	37.4%	24.2%	43.1%	21.2%	39.6%	30.3%
A	0.07	0.03	0.07	0.28	0.19	0.01
E	0.19	0.15	-0.05	0.13	0.10	-0.18
gs	0.16	0.14	-0.07	0.20	0.15	0.11
Ci	0.13	0.05	0.03	0.31	0.20	0.03
Ci/Ca	0.13	0.05	0.02	0.30	0.21	0.04
WUE	-0.18	-0.17	0.00	0.25	0.05	0.22
Fv/Fm	0.05	-0.13	-0.08	0.20	0.18	0.08
Fo'	0.03	0.21	0.09	0.13	-0.13	0.11
Y(II)	0.10	0.06	-0.04	0.15	0.20	0.05
ETR	0.11	0.08	-0.04	0.14	0.18	0.11
NPQ/4	-0.11	-0.22	-0.03	-0.26	-0.14	-0.15
H	0.11	0.21	-0.11	-0.25	-0.08	-0.23
SN	0.06	0.09	-0.13	0.05	0.11	-0.22
LN	0.20	-0.02	-0.20	0.07	0.15	-0.18
LA	0.18	0.12	-0.13	-0.22	0.19	-0.09

LFW	0.20	-0.03	-0.20	-0.02	0.19	-0.10
SFW	0.23	0.01	-0.21	-0.04	0.11	-0.21
LDW	0.21	-0.05	-0.21	0.05	0.19	-0.11
SDW	0.22	-0.07	-0.21	-0.05	0.07	-0.23
%LDM	0.17	-0.07	-0.07	0.12	-0.09	-0.10
%SDM	-0.14	-0.16	-0.15	-0.17	-0.16	-0.14
RFW	0.21	-0.10	-0.18	0.17	0.18	-0.15
RDW	0.20	-0.13	-0.20	0.13	0.16	-0.17
%RDM	-0.11	-0.13	-0.18	-0.09	-0.07	-0.20
TTW	-0.10	0.23	0.19	0.00	0.01	0.24
TTN	-0.10	0.22	0.08	0.00	0.05	-0.15
ATW	-0.11	0.16	0.19	-0.06	-0.01	0.23
TFW	-0.09	0.24	0.19	0.00	0.01	0.25
TDW	-0.12	0.22	0.19	0.06	0.05	0.24
%TDM	-0.20	0.11	-0.11	0.22	0.14	0.10
APX	0.12	0.19	-0.19	-0.02	-0.16	-0.13
CAT	0.17	0.04	-0.17	-0.01	-0.17	-0.09
SOD	0.13	0.12	-0.17	0.04	-0.16	-0.11
Protein	-0.07	-0.22	0.08	0.08	0.21	0.02
Chl_a	0.14	-0.14	-0.19	0.06	0.17	-0.04
Chl_b	0.15	-0.14	-0.21	-0.03	0.11	-0.10
Car	0.20	-0.07	-0.20	-0.06	0.06	-0.17
T_Chl	0.13	-0.08	-0.09	0.19	0.19	0.00
Chl_a/Chl_b	0.15	-0.14	-0.20	0.03	0.16	-0.06
T_Chl/Car	-0.20	-0.04	0.07	0.14	0.17	0.10
Perox	-0.07	-0.13	0.07	0.11	-0.15	-0.04
H_2O_2	0.02	-0.20	-0.20	0.00	-0.03	-0.17
GO	0.10	0.16	-0.12	-0.08	-0.14	-0.03
TSS-L	-0.15	-0.04	0.08	-0.19	-0.12	-0.12
TSS-T	0.20	0.12	0.03	-0.13	0.04	-0.05
AA-L	-0.01	-0.24	-0.17	-0.08	0.10	-0.19
AA-T	0.09	-0.18	0.15	-0.15	-0.20	-0.01
Prol-L	0.01	-0.13	-0.01	-0.01	-0.11	0.16
Prol-T	0.08	-0.20	0.15	0.02	-0.20	-0.04

* **A:** net CO_2 assimilation, **E:** transpiration, **gs:** stomatal conductance, **Ci:** intercellular CO_2 concentration, **Ci/Ca:** ratio between internal and external CO_2 concentration, **WUE:** water use efficiency, **Fv/Fm:** maximum photochemical efficiency of PSII, **Fo':** minimal fluorescence, **Y(II):** effective quantum yield of PSII, **ETR:** apparent rate of photosynthetic electron transport, **NPQ/4:** non-photochemical quenching, **H:** height, **SN:** number of stems, **LN:** number of leaves, **LA:** leaf area, **LFW:** leaf fresh weight, **SFW:** stem fresh weight, **LDW:** leaf dry weight, **SDW:** stem dry weight, **%LDM:** % leaf dry matter, **%SDM:** % stem dry matter, **RFW**: root fresh weight, **RDW:**root dry weight, **%RDM:** %root dry matter, **TTW:** total tuber weight, **TTN:** total tuber number, **ATW:** average

tuber weight, **TFW:** tuber fresh weight, **TDW:** tuber dry weight**, %TDM**: % tuber dry matter, **APX:** ascorbate peroxidase, **CAT:** catalase, **SOD:** superoxide dismutase, **Protein:** proteins, **Chl_a:** Chorophyll a, **Chl_b:** Chorophyll b, **Car:** Carotenoids, **T_Chl:** Total chlorophyll, **Chl_a/Chl_b:** ratio between chlorophyll a and chlorophyll b, **T_Chl/Car:** ratio between chlorophyll and carotenoids, **Perox:** Peroxidase, **H_2O_2:** hydrogen peroxide, **GO:** Glycolate oxydase, **TSS-L:** total soluble sugar of leaves, **TSS-T:** total soluble sugar of tubers, **AA-L:** aminoacids of leaves, **AA-T:** aminoacids of tubers, **Prol-L:** Proline in leaves and **Prol-T:** Proline in tubers.

In the PCA bi-plot, on the 53rd DAP, MB 54-02 independent of the temperature treatment was located on the right inferior quadrant, while the other genotypes grown under control treatment were located on or close to the left inferior quadrant, as well as when grown under high temperature treatment, they were grouped on the right superior quadrant. (Figure 12)

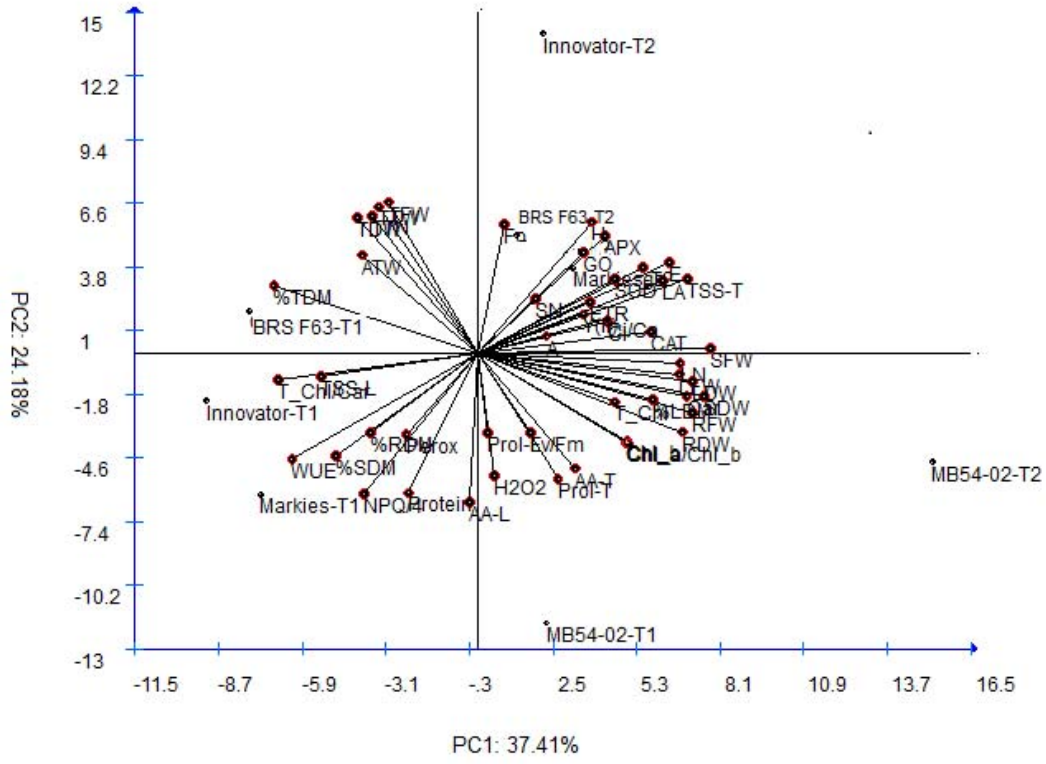

Figure 12. Principal component analysis bi-plot of the first evaluation date (53 DAP, 6 DOT) of four potato genotypes submitted to two temperature condition treatment (T1: Control temperature, 14°C-24°C; T2: High temperature, 24°C-34°C).

Later, on the 60th DAP, MB 54-02 was located on the left side of the bi-plot graphic, while the other genotypes grown under control treatment were located on the right side. Of the latest, those grown under high temperature condition were grouped to the inferior quadrant, while those grown under control temperature were positioned on the superior quadrant (Figure 13).

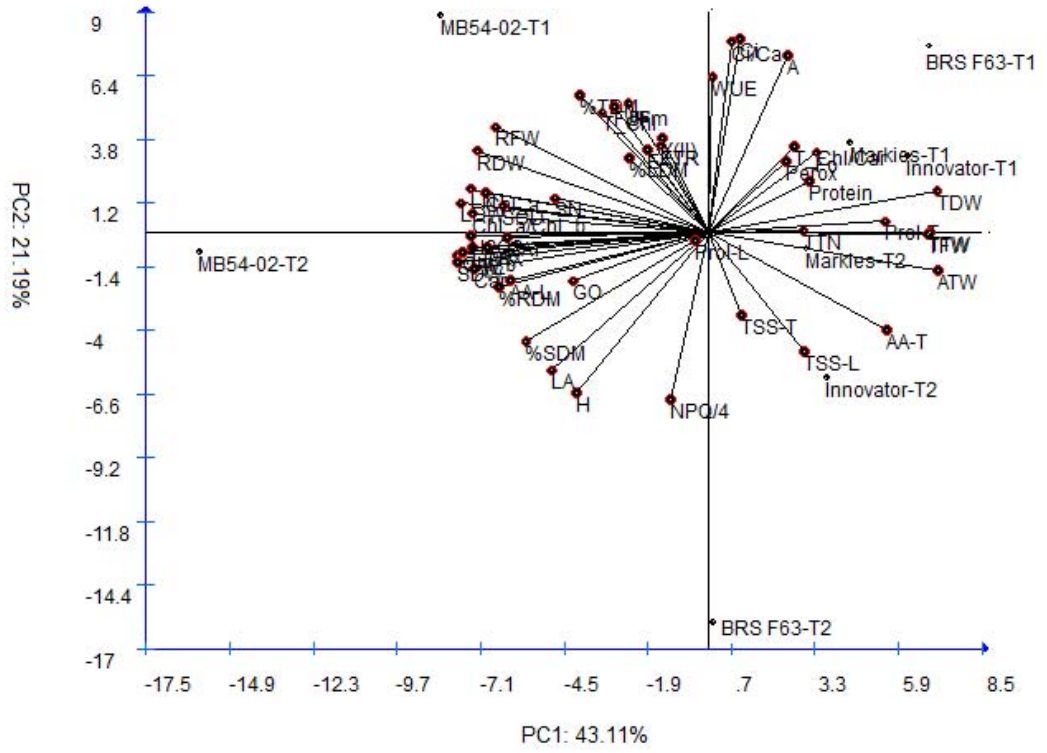

Figure 13. Principal component analysis bi-plot of the second evaluation date (60 DAP, 13 DOT) of four potato genotypes submitted to two temperature condition treatment (T1: Control temperature, 14°C-24°C; T2: High temperature, 24°C-34°C).

At the 75th DAP, the PCA bi-plot was also observed a separation of MB 54-02 from the rest of the genotypes. This time, both treatments of MB 54-02 were localized on the right inferior quadrant, while the rest of the genotypes grown under control temperature environment were set in the center of the upper side and those grown under high temperature environment, on the left inferior quadrant. (Figure 14)

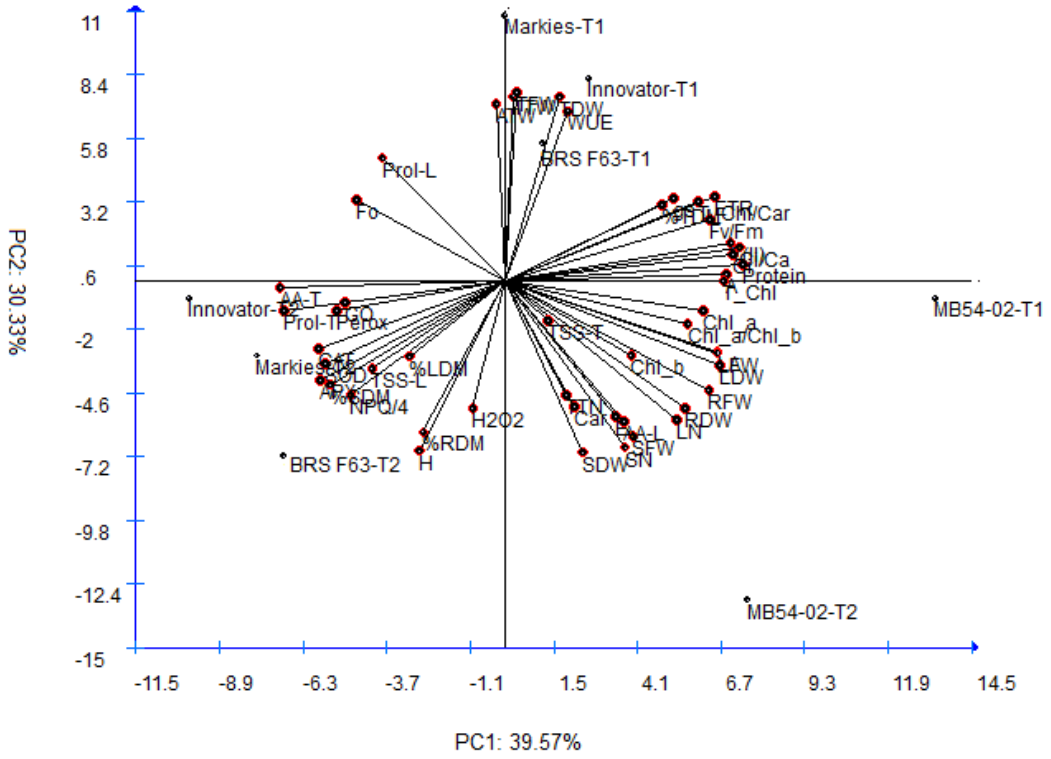

Figure 14. Principal component analysis bi-plot (Component 1 versus Component 2) of the third evaluation date of four potato genotypes submitted to two temperature condition treatment (T1: Control temperature, 14°C-24°C; T2: High temperature, 24°C-34°C).

The path analysis revealed that under control temperature condition, total tuber weight after senescence (TTW) was weakly negative correlated with ratio between internal and external CO2 concentration at 75 DAP (Ci/Ca-3) (-0.199), moderately positive correlated with the effective quantum yield of PSII at 60 DAP (Y(II)-2). Was also observed a strongly positive correlation of TTW with the ratio between internal and external CO2 concentration at 53 DAP (Ci/Ca-1) (0.763) and with the effective quantum yield of PSII at 75 DAP (Y(II)-3) (0.825). In addition, TTW was perfectly correlated to the ratio between internal and net CO2 assimilation at 53 DAP (A-1), 60 dat (A-2) and 75 dat (A-3) (1.000, 0.975 and 0.965 respectively), to the effective quantum yield of PSII at 53 DAP (Y(II-1) (0.913) and to the ratio between internal and external CO2 concentration at 60 DAP (Ci/Ca-2) (0.925). However, the direct effect of all the parameters on the three evaluation dates were low, almost on the same range than their highest

indirect effect values. The highest indirect effect of A-1, A-2 and A-3 on TTW were through Y(II)-1, Ci/Ca-2, Y(II)-3, A-1 (in the case of A-2 and A-3), A-2 (in the case of A-1 and A-3) and A-3 (in the case of A-1 and A-2). While Ci/Ca-1, Ci/Ca-2 and Ci/Ca-3 had their highest indirect effect over TTW through A-1, A-2, Ci/Ca-1 (in the case of Ci/Ca-2 and Ci/Ca-3) and Ci/Ca-2 (in the case of Ci/Ca-1 and Ci/Ca-3). In this case, the determination coefficient was high (0.92) and the residual variable has a weak contribution (0.28) (Table 12).

Table 12. Estimative of direct and indirect phenotypic effects of three explanatory variables evaluated on three dates (53 DAP, 60 DAP and 75 DAP), over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under control temperature treatment (T1: 14°C-24°C). Pelotas, 2022.

Effects	Explanatory variables								
	A-1	Ci/Ca-1	Y(II)-1	A-2	Ci/Ca-2	Y(II)-2	A-3	Ci/Ca-3	Y(II)-3
Direct effect on TTW	0.146	0.120	0.128	0.146	0.141	0.088	0.137	-0.043	0.112
Indirect effect through A-1		0.114	0.132	0.143	0.137	0.096	0.140	-0.032	0.119
Indirect effect through Ci/Ca-1	0.093		0.052	0.107	0.114	0.004	0.068	-0.094	0.032
Indirect effect through Y(II)-1	0.115	0.055		0.102	0.088	0.117	0.126	0.028	0.126
Indirect effect through A-2	0.143	0.129	0.116		0.143	0.072	0.129	-0.060	0.099
Indirect effect through Ci/Ca-2	0.131	0.134	0.097	0.139		0.048	0.112	-0.078	0.077
Indirect effect through Y(II)-2	0.057	0.003	0.080	0.043	0.030		0.074	0.052	0.085
Indirect effect through A-3	0.131	0.078	0.136	0.121	0.109	0.116		0.009	0.129
Indirect effect through Ci/Ca-3	0.010	0.034	-0.009	0.018	0.024	-0.025	-0.003		-0.017
Indirect effect through Y(II)-3	0.091	0.030	0.111	0.076	0.062	0.109	0.106	0.044	
Total correlation (r)	1.000	0.763	0.913	0.975	0.925	0.672	0.965	-0.199	0.825
Determination coefficient	0.92								
K value used on the analysis	0.56								
Effect of the residual variable	0.28								

*__A-1, A-2 and A-3__: net CO_2 assimilation on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively; **Ci/Ca-1, Ci/Ca -2, Ci/Ca -3:** ratio between internal and external CO_2 concentration on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively; **Y(II)-1, Y(II)-2, Y(II)-3:** effective quantum yield of PSII on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively.

When high temperatures were applied, path analysis under multicollinearity (Table 13) showed a strongly negative correlation between TTW and Y(II)-3 (-0.673), yet the direct effect of Y(II)-2 on ATW-4 was very low and negative (-0.013). TTW shown strong positive correlation with Y(II)-1 (0.742) and strong negative correlation with Ci/Ca-3 (-0.748). A-1 (0.962), Ci/Ca-1 (0.976), A-

2, Ci/Ca-2 (0.948) and A-3 (0.902) were perfectly positive correlated to TTW, while the correlation TTW with Y(II)-2 was perfect and negative. Nevertheless, none of this the explanatory variables, has a direct effect on TTW that got to the half value of correlation coefficient. However, those that were perfectly correlated to TTW, had their highest indirect effect through A-1, Ci/Ca-1, Ci/Ca-2 and Y(II)-2 (Table 13).

Table 13. Estimative of direct and indirect phenotypic effects of three explanatory variables evaluated on three dates (53 DAP, 60 DAP and 75 DAP), over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under high temperature treatment (T2: 24°C-34°C). Pelotas, 2022.

Effects		Explanatory variables								
		A-1	Ci/Ca-1	Y(II)-1	A-2	Ci/Ca-2	Y(II)-2	A-3	Ci/Ca-3	Y(II)-3
Direct effect on	TTW	0.131	0.140	0.226	0.097	0.122	-0.200	0.098	-0.038	-0.013
Indirect effect through	A-1		0.131	0.070	0.129	0.131	-0.117	0.129	-0.118	-0.111
Indirect effect through	Ci/Ca-1	0.140		0.081	0.137	0.140	-0.129	0.137	-0.123	-0.115
Indirect effect through	Y(II)-1	0.120	0.130		0.085	0.111	-0.193	0.086	-0.025	-0.001
Indirect effect through	A-2	0.095	0.094	0.036		0.096	-0.077	0.097	-0.093	-0.090
Indirect effect through	Ci/Ca-2	0.121	0.121	0.060	0.121		-0.106	0.121	-0.112	-0.106
Indirect effect through	Y(II)-2	0.179	0.183	0.171	0.160	0.174		0.161	-0.122	-0.104
Indirect effect through	A-3	0.097	0.096	0.037	0.098	0.097	-0.079		-0.094	-0.091
Indirect effect through	Ci/Ca-3	0.034	0.033	0.004	0.037	0.035	-0.023	0.037		-0.038
Indirect effect through	Y(II)-3	0.011	0.011	0.000	0.012	0.012	-0.007	0.012	-0.013	
Total correlation (r)		0.962	0.976	0.742	0.900	0.948	-0.982	0.902	-0.748	-0.673
Determination coefficient		0.96								
K value used on the analysis		0.25								
Effect of the residual variable		0.21								

*__A-1, A-2 and A-3__: net CO_2 assimilation on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively; **Ci/Ca-1, Ci/Ca -2, Ci/Ca -3:** ratio between internal and external CO_2 concentration on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively; **Y(II)-1, Y(II)-2, Y(II)-3:** effective quantum yield of PSII on first (53 DAP), second (60 DAP) and third evaluation (75 DAP), respectively.

At 53 DAP, under normal temperature conditions, path analysis under multicollinearity showed TTW as perfectly correlated to A, Y(II), besides pigments (Chl_a-1, to Chl_b-1, Car-1 and T_Chl) in an opposite direction. There was a high joint contribution of these variables, this is, in each of them what was missing on the direct effect was completed by the other two pigments by an indirect effect. In this conditions, correlation between TTW and GO-1 and NPQ/4 were very

weak (0.017) and weak (-0.376) respectively. Moreover TTW and TTW-1 were strongly negative correlated, but its direct effect was very poor (Table 14).

When high temperature was applied, besides A and Ci/Ca, NPQ/4 was also perfectly correlated to TTW. Additionally, strong positive correlation were observed on TTW with Y(II)) and GO. Of all the mentioned explanatory variables, the their indirect effect it´s of equal importance than the direct effect (Table 15).

Later on, at 60 DAP, TTW appeared to be perfectly correlated to A (0.976), Ci/Ca (0.926), Chl_a (-0.935), Chl_b (-0.983) and T-Chl (-0.952). Besides, NPQ/4 and TTW-1 were strongly negative correlated to TTW, while Y(II) had a moderately positive correlation with the dependent variable. (Table 16). On the other side, under high temperature condition, A (0.900), Ci/Ca (0.948), Y(II) (-0.982), NPQ/4 (-0.984) and TTW-2 (0.970) were perfectly correlated to TTW, from where Y(II) and NPQ/4 are inversely proportional to the TTW (Table 17). In both temperature condition, the direct effect was not enough for them to explain the final TTW, and each parameter acted as an indirect effect for the rest. Although pigments don´t have a direct effect over TTW, Chl_b and T_Chl concentration contributed indirectly through the mentioned variables when heat was applied (Table 17).

At 75 DAP, A, NPQ and Car had the highest contribution to the final TTW, plus Y(II) and Chl_a in a lowest degree under control temperature condition. All of them contributed in a direct and indirect manner, except for pigments that in theory, don´t have a direct effect over tuber yield and different to the earliest evaluation dates, their indirect effect was directly proportional (Table 18). At the same moment, under high temperature condition, the most important variables on the contribution to the final TTW result were A, NPQ, Chl_a, GO, TTW-2 and TTW-3. Differently to what was observed before, their indirect effect of the mentioned explanatory variables, was higher through GO, TTW-2 and TTW-3. Moreover, when compared to earlier situations, in this case the determination coefficient was lower (0.89) and the effect of the residual variable was higher (0.32) (Table 19).

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Table 14. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 53 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under control temperature treatment (T1: 14°C-24°C). Pelotas, 2022

Effects		Explanatory variables									
		A-1	Ci/Ca-1	Y(II)-1	NPQ/4-1	Chl_a-1	Chl_b-1	Car-1	T_Chl-1	GO-1	TTW-1
Direct effect on	TTW	0.144	0.074	0.156	-0.003	-0.150	-0.137	-0.139	-0.149	0.058	-0.079
Indirect effect through	A-1		0.112	0.130	-0.057	-0.144	-0.144	-0.143	-0.144	-0.001	-0.114
Indirect effect through	Ci/Ca-1	0.058		0.032	-0.066	-0.054	-0.061	-0.064	-0.056	-0.047	-0.074
Indirect effect through	Y(II)-1	0.141	0.067		0.006	-0.146	-0.135	-0.130	-0.142	0.066	-0.070
Indirect effect through	NPQ/4-1	0.001	0.003	0.000		-0.001	-0.001	-0.002	-0.001	-0.003	-0.003
Indirect effect through	Chl_a-1	0.149	0.108	0.140	-0.048		-0.147	-0.146	-0.149	0.012	-0.110
Indirect effect through	Chl_b-1	0.137	0.114	0.119	-0.065	-0.135		-0.137	-0.136	-0.012	-0.115
Indirect effect through	Car-1	0.137	0.119	0.115	-0.072	-0.135	-0.138		-0.137	-0.020	-0.120
Indirect effect through	T_Chl-1	0.149	0.113	0.136	-0.055	-0.149	-0.148	-0.147		0.003	-0.115
Indirect effect through	GO-1	0.000	-0.036	0.025	0.053	-0.005	0.005	0.008	-0.001		0.036
Indirect effect through	TTW-1	0.062	0.079	0.035	-0.069	-0.058	-0.066	-0.068	-0.061	-0.049	
Total correlation (r)		1.000	0.764	0.912	-0.376	-0.998	-0.995	-0.987	-1.000	0.017	-0.775
Determination coefficient		0.98									
K value used on the analysis		0.15									
Effect of the residual variable		0.15									

*__A-1__: net CO_2 assimilation, **Ci/Ca-1:** ratio between internal and external CO_2 concentration, **Y(II)-1:** effective quantum yield of PSII, **NPQ/4-1:** non-photochemical quenching, **Chl_a-1:** Chorophyll a, **Chl_b-1:** Chorophyll b, **Car-1:** Carotenoids, **T_Chl-1:** Total chlorophyll, **GO-1:** Glycolate oxidase, **TTW-1:** total tuber weight on first evaluation date (53 DAP, 6 DOT).

Table 15. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 53 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under high temperature treatment (T2: 24°C-34°C). Pelotas, 2022.

Effects		**Explanatory variables**									
		A-1	Ci/Ca-1	Y(II)-1	NPQ/4-1	Chl_a-1	Chl_b-1	Car-1	T_Chl-1	GO-1	TTW-1
Direct effect on	TTW	0.229	0.230	0.141	-0.230	0.081	-0.002	-0.051	0.077	0.126	0.102
Indirect effect through	A-1		0.229	0.122	-0.228	0.099	0.019	-0.026	0.093	0.114	0.090
Indirect effect through	Ci/Ca-1	0.230		0.133	-0.230	0.088	0.007	-0.039	0.082	0.125	0.101
Indirect effect through	Y(II)-1	0.075	0.081		-0.087	-0.075	-0.112	-0.127	-0.078	0.140	0.139
Indirect effect through	NPQ/4-1	0.229	0.230	0.143		0.076	-0.006	-0.052	0.070	0.136	0.113
Indirect effect through	Chl_a-1	0.035	0.031	-0.044	-0.027		0.076	0.069	0.081	-0.046	-0.054
Indirect effect through	Chl_b-1	0.000	0.000	0.002	0.000	-0.002		-0.002	-0.002	0.002	0.002
Indirect effect through	Car-1	0.006	0.009	0.046	-0.012	-0.044	-0.050		-0.044	0.047	0.049
Indirect effect through	T_Chl-1	0.031	0.027	-0.043	-0.023	0.077	0.072	0.066		-0.045	-0.052
Indirect effect through	GO-1	0.063	0.068	0.126	-0.074	-0.072	-0.104	-0.116	-0.074		0.125
Indirect effect through	TTW-1	0.040	0.045	0.101	-0.050	-0.068	-0.090	-0.098	-0.070	0.101	
Total correlation (r)		0.962	0.976	0.742	-0.986	0.169	-0.190	-0.381	0.142	0.715	0.627

Determination coefficient	0.98
K value used on the analysis	0.11
Effect of the residual variable	0.16

*__A-1__: net CO_2 assimilation, **Ci/Ca-1:** ratio between internal and external CO_2 concentration, **Y(II)-1:** effective quantum yield of PSII, **NPQ/4-1:** non-photochemical quenching, **Chl_a-1:** Chorophyll a, **Chl_b-1:** Chorophyll b, **Car-1:** Carotenoids, **T_Chl-1:** Total chlorophyll, **GO-1:** Glycolate oxidase, **TTW-1:** total tuber weight on first evaluation date (53 DAP, 6 DOT).

Table 16. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 60 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under control temperature treatment (T1: 14°C-24°C). Pelotas, 2022.

Effects		**Explanatory variables**										
		TTW-1	A-2	Ci/Ca-2	Y(II)-2	NPQ/4-2	Chl_a-2	Chl_b-2	Car-2	T_Chl-2	GO-2	TTW-2
Direct effect on	TTW	-0.110	0.137	0.130	0.090	-0.124	-0.127	-0.136	-0.078	-0.130	0.028	-0.064
Indirect effect through	TTW-1		0.099	0.106	0.006	-0.108	-0.055	-0.072	0.006	-0.060	-0.048	-0.100
Indirect effect through	A-2	-0.122		0.135	0.067	-0.132	-0.114	-0.126	-0.054	-0.118	0.002	-0.084
Indirect effect through	Ci/Ca-2	-0.124	0.128		0.044	-0.129	-0.095	-0.109	-0.031	-0.100	-0.020	-0.096
Indirect effect through	Y(II)-2	-0.005	0.044	0.030		-0.021	-0.080	-0.071	-0.089	-0.078	0.079	0.035
Indirect effect through	NPQ/4-2	-0.122	0.119	0.123	0.030		-0.081	-0.097	-0.017	-0.086	-0.031	-0.099
Indirect effect through	Chl_a-2	-0.064	0.106	0.093	0.113	-0.083		-0.125	-0.106	-0.127	0.072	-0.010
Indirect effect through	Chl_b-2	-0.088	0.125	0.115	0.108	-0.106	-0.134		-0.099	-0.135	0.056	-0.035
Indirect effect through	Car-2	0.004	0.031	0.019	0.077	-0.011	-0.065	-0.056		-0.063	0.072	0.037
Indirect effect through	T_Chl-2	-0.071	0.112	0.100	0.112	-0.090	-0.130	-0.129	-0.105		0.068	-0.017
Indirect effect through	GO-2	0.012	0.000	-0.004	0.025	0.007	-0.016	-0.012	-0.026	-0.015		0.022
Indirect effect through	TTW-2	-0.058	0.039	0.047	-0.025	-0.051	-0.005	-0.016	0.031	-0.008	-0.050	
Total correlation (r)		-0.775	0.976	0.926	0.671	-0.881	-0.935	-0.983	-0.588	-0.952	0.235	-0.425
Determination coefficient		0.97										
K value used on the analysis		0.25										
Effect of the residual variable		0.19										

*__A-2__: net CO_2 assimilation, **Ci/Ca-2:** ratio between internal and external CO_2 concentration, **Y(II)- 2:** effective quantum yield of PSII, **NPQ/4-2:** non-photochemical quenching, **Chl_a-2:** Chorophyll a, **Chl_b-2:** Chorophyll b, **Car-2:** Carotenoids, **T_Chl-2:** Total chlorophyll, **GO-2:** Glycolate oxidase, **TTW-2:** total tuber weight on first evaluation date (60 DAP, 13 DOT), **TTW-1:** total tuber weight on first evaluation date (53 DAP, 6 DOT).

Table 17. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 60 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under high temperature treatment (T2: 24°C-34°C). Pelotas, 2022.

Effects		**Explanatory variables**										
		TTW-1	A-2	Ci/Ca-2	Y(II)-2	**NPQ/4-2**	Chl_a-2	Chl_b-2	Car-2	T_Chl-2	GO-2	TTW-2
Direct effect on	TTW	0.046	0.132	0.133	-0.115	-0.131	-0.089	-0.132	-0.054	-0.109	-0.030	0.113
Indirect effect through	TTW-1		0.010	0.016	-0.035	-0.022	-0.042	-0.018	-0.046	-0.037	0.038	0.036
Indirect effect through	A-2	0.029		0.131	-0.105	-0.127	-0.075	-0.129	-0.038	-0.098	-0.046	0.101
Indirect effect through	Ci/Ca-2	0.046	0.132		-0.116	-0.132	-0.089	-0.133	-0.054	-0.109	-0.030	0.112
Indirect effect through	Y(II)-2	0.088	0.092	0.100		-0.107	-0.109	-0.103	-0.093	-0.114	0.033	0.115
Indirect effect through	NPQ-2	0.063	0.126	0.130	-0.122		-0.101	-0.130	-0.070	-0.117	-0.011	0.119
Indirect effect through	Chl_a-2	0.082	0.051	0.059	-0.084	-0.068		-0.063	-0.084	-0.086	0.051	0.086
Indirect effect through	Chl_b-2	0.053	0.130	0.132	-0.119	-0.132	-0.094		-0.061	-0.113	-0.022	0.115
Indirect effect through	Car-2	0.053	0.016	0.022	-0.043	-0.029	-0.051	-0.025		-0.046	0.043	0.045
Indirect effect through	T_Chl-2	0.090	0.081	0.090	-0.109	-0.098	-0.107	-0.094	-0.094		0.041	0.109
Indirect effect through	GO-2	-0.025	0.010	0.007	0.008	-0.002	0.017	-0.005	0.024	0.011		-0.010
Indirect effect through	TTW-2	0.090	0.087	0.095	-0.113	-0.103	-0.109	-0.099	-0.095	-0.113	0.038	
Total correlation (r)		0.627	0.900	0.948	-0.982	-0.984	-0.872	-0.965	-0.679	-0.961	0.098	0.970
Determination coefficient		0.97										
K value used on the analysis		0.26										
Effect of the residual variable		0.18										

*__A-2__: net CO_2 assimilation, **Ci/Ca-2:** ratio between internal and external CO_2 concentration, **Y(II)- 2:** effective quantum yield of PSII, **NPQ/4-2:** non-photochemical quenching, **Chl_a-2:** Chorophyll a, **Chl_b-2:** Chorophyll b, **Car-2:** Carotenoids, **T_Chl-2:** Total chlorophyll, **GO-2:** Glycolate oxidase, **TTW-2:** total tuber weight on first evaluation date (60 DAP, 13 DOT), **TTW-1:** total tuber weight on first evaluation date (53 DAP, 6 DOT).

Table 18. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 75 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under control temperature treatment (T1: 14°C-24°C). Pelotas, 2022.

Effects		**Explanatory variables**										
		TTW-2	A-3	Ci/Ca-3	Y(II)-3	NPQ/4-3	Chl_a-3	Chl_b-3	Car-3	T_Chl-3	GO-3	TTW-3
Direct effect on	TTW	-0.090	0.159	-0.054	0.130	0.159	0.126	0.031	0.167	0.099	0.112	-0.145
Indirect effect through	TTW-2		0.015	-0.088	-0.015	0.016	-0.016	-0.067	0.042	-0.033	0.089	-0.082
Indirect effect through	A-3	-0.027		0.010	0.150	0.159	0.150	0.085	0.151	0.136	0.049	-0.090
Indirect effect through	Ci/Ca-3	-0.052	-0.003		-0.021	-0.003	-0.022	-0.047	0.013	-0.031	0.050	-0.042
Indirect effect through	Y(II)-3	0.021	0.123	0.051		0.123	0.130	0.102	0.104	0.127	-0.003	-0.034
Indirect effect through	NPQ-3	-0.028	0.159	0.010	0.150		0.149	0.084	0.151	0.135	0.050	-0.091
Indirect effect through	Chl_a-3	0.022	0.118	0.051	0.126	0.118		0.100	0.099	0.124	-0.004	-0.032
Indirect effect through	Chl_b-3	0.023	0.017	0.028	0.025	0.017	0.025		0.008	0.028	-0.020	0.012
Indirect effect through	Car-3	-0.078	0.159	-0.041	0.133	0.159	0.131	0.041		0.109	0.098	-0.132
Indirect effect through	T_Chl-3	0.036	0.084	0.057	0.096	0.084	0.097	0.088	0.064		-0.023	-0.006
Indirect effect through	GO-3	-0.111	0.035	-0.104	-0.002	0.035	-0.004	-0.072	0.066	-0.026		-0.108
Indirect effect through	TTW-3	-0.132	0.082	-0.114	0.038	0.083	0.036	-0.057	0.115	0.008	0.139	
Total correlation (r)		-0.425	0.965	-0.201	0.824	0.966	0.816	0.291	0.999	0.688	0.550	-0.764
Determination coefficient		0.98										
K value used on the analysis		0.10										
Effect of the residual variable		0.13										

*__A-3__: net CO_2 assimilation, **Ci/Ca-3:** ratio between internal and external CO_2 concentration, **Y(II)- 3:** effective quantum yield of PSII, **NPQ/4-3:** non-photochemical quenching, **Chl_a-3:** Chorophyll a, **Chl_b-3:** Chorophyll b, **Car-3:** Carotenoids, **T_Chl-3:** Total chlorophyll, **GO-3:** Glycolate oxidase, **TTW-3:** total tuber weight on first evaluation date (75 DAP, 28 DOT), **TTW-2:** total tuber weight on first evaluation date (60 DAP, 13 DOT).

Table 19. Estimative of direct and indirect phenotypic effects of ten explanatory variables evaluated at 75 DAP, over total tuber weight per plant after senescence (TTW) from three different potato genotypes, grown under high temperature treatment (T2: 24°C-34°C). Pelotas, 2022.

Effects		**Explanatory variables**										
		TTW-2	A-3	Ci/Ca-3	Y(II)-3	NPQ/4-3	Chl_a-3	Chl_b-3	Car-3	T_Chl-3	GO-3	TTW-3
Direct effect on	TTW	0.123	0.123	-0.106	-0.097	-0.099	-0.103	0.016	-0.085	-0.056	0.131	0.131
Indirect effect through	TTW-2		0.095	-0.070	-0.058	-0.115	-0.117	-0.028	-0.108	-0.088	0.117	0.114
Indirect effect through	A-3	0.095		-0.119	-0.114	-0.060	-0.065	0.056	-0.044	-0.012	0.115	0.118
Indirect effect through	Ci/Ca-3	0.060	0.102		-0.106	-0.024	-0.029	0.072	-0.009	0.019	0.084	0.089
Indirect effect through	Y(II)-3	0.046	0.090	-0.097		-0.012	-0.016	0.073	0.002	0.028	0.070	0.075
Indirect effect through	NPQ/4-3	0.092	0.048	-0.023	-0.012		-0.099	-0.055	-0.098	-0.091	0.076	0.072
Indirect effect through	Chl_a-3	0.097	0.054	-0.028	-0.017	-0.103		-0.054	-0.101	-0.092	0.082	0.078
Indirect effect through	Chl_b-3	-0.004	0.007	-0.011	-0.012	0.009	0.008		0.011	0.013	0.001	0.003
Indirect effect through	Car-3	0.074	0.030	-0.007	0.002	-0.084	-0.084	-0.057		-0.082	0.057	0.053
Indirect effect through	T_Chl-3	0.040	0.005	0.010	0.016	-0.052	-0.051	-0.048	-0.054		0.026	0.022
Indirect effect through	GO-3	0.124	0.122	-0.104	-0.095	-0.101	-0.105	0.012	-0.088	-0.060		0.131
Indirect effect through	TTW-3	0.121	0.125	-0.109	-0.101	-0.095	-0.099	0.021	-0.082	-0.052	0.131	
Total correlation (r)		0.970	0.902	-0.748	-0.673	-0.817	-0.841	0.021	-0.725	-0.518	0.998	0.990
Determination coefficient		0.89										
K value used on the analysis		0.81										
Effect of the residual variable		0.32										

*__A-3__: net CO_2 assimilation, **Ci/Ca-3:** ratio between internal and external CO_2 concentration, **Y(II)- 3:** effective quantum yield of PSII, **NPQ/4-3:** non-photochemical quenching, **Chl_a-3:** Chorophyll a, **Chl_b-3:** Chorophyll b, **Car-3:** Carotenoids, **T_Chl-3:** Total chlorophyll, **GO-3:** Glycolate oxidase, **TTW-3:** total tuber weight on first evaluation date (75 DAP, 28 DOT), **TTW-2:** total tuber weight on first evaluation date (60 DAP, 13 DOT)

4.4 Discussion

Average tuber weight (ATW), considered as one of the most important yield component of the total tuber yield (DE LA MORENA; GUILLÉN; DEL MORAL, 1994), gives us also an idea of size of tuber (Lung'aho cited by ASNAKE; ALEMAYEHU; ASREDIE, 2023). For his reason, can be also an indicator of the vegetative cycle of the plant, when all different genotypes are harvest at the same time. In this way could be seen that MB 54-02 started the tuberization stage later than the other genotypes, as it has showed significantly less ATW-1 during the whole crop life cycle.

It can be seen that plants grown under high temperature conditions differed of the ones grown under control conditions in physiological terms and that the variables that contributed to the separation of treatments changed over time.

At 53 DAP, variables that contributed to the separation of MB 54-02 to the other genotypes were those related to pigments (Chl_a, Chl_b, Car, T_Chl, Chl_a/Chl_b), aerial (LN, LFW, LDW, SFW, SDW) and root growth (RFW and RDW). In the case of the three cultivars, the separation between treatments were mostly induced by, Fo, H, APX and GO, in opposition to WUE, %SDM, %RDM, %TDM, T_Chl/Car and TSS-L (Figure 12).

At 60 DAP, the PCA bi-plot shows a separation between temperature treatments of all of the genotypes in terms of the second principal component, which is constituted by photosynthetic parameters, being located on the upper side of the graphic, those grown under control temperature and, on the lower side, those grown under high temperature treatment. The separation between MB 54-02 and the rest of the genotypes was oriented by the first component, where negative values favored MB 54-02 to be apart from the others. The variables that contributed to the separation of BRS F63, Innovator and Markies, grown under control and high temperature condition, were related to tuber growth and TSS on both, leaves and tubers, in opposition to A, T_Chl/Car, Perox, Protein and TDW (Figure 13).

On the PCA bi-plot based on data from the 75th DAP, the control treatment was completely influenced by the second principal component, thus the variables that most explained this treatment were related to tuber growth (ATW, TTW, TFW) as well as by WUE (Figure 14).

Being photosynthesis the most vulnerable physiological process to stresses, any changes on it, in order to maintain leaf gas exchange, when subjected to stress, are reliable markers of the plant's stress tolerance (WAHID et al., 2007).

In this way, at 53 DAP, on the sixth day of treatment, plants grown under high temperature condition showed a low T_Chl/Car suggesting a higher Car concentration in relation to T_Chl. Pigments are important for photosynthesis, because they capture light, transforming sunlight into electronic excitation (SCHEER, 2006). However, Car also preserve PSII by releasing excess energy created by either light or heat stress (RATH et al., 2022). At this respect, Havaux and Tardy (1996) observed a short-term adaptive response to high temperatures through the availability of violaxanthin for de-epoxidation (pathway of xanthophyll) in the lipid phase of thylakoid membrane, making it more fluid and increasing the stability of PSII to heat stress (KOTAKIS et al., 2018), which could explain the initial elevated Fv/Fm observed in our study. However, availability of Car to the deepoxidase system means the detachment from peripheral light-harvesting pigments (LHCII), resulting in a lower efficiency transferring excitation energy from accessory carotenoid pigments to antenna chlorophylls (Fo) (HAVAUX et al., 1991).

Under high temperature conditions, pigments has been related not only to mobilize for the photosynthetic apparatus protection. Chlorophyll content diminution could be also a consequence of the damage of thylakoid membranes (RISTIC; BUKOVNIK; PRASAD, 2007) or, to the degradation of protein due to the activity of proteolytic enzymes (HARDING; GUIKEMA; PAULSEN, 1990) caused by oxidative stress. In any case, many authors have suggested that the pigments loss is one of the reasons for the decline of photosynthesis (HALDIMANN; FELLER, 2004; MOUSTAKAS; CALATAYUD; GUIDI, 2021), because it´s not possible for them to perform their function in the photosynthetic system (HAVAUX, 1993; SATTAR et al., 2020). In this way, over time (Figure 9), the exposure of plants to high temperature environment resulted on chlorophyll content reduction and, consequently, on a limited electron transport function (Y(II) and ETR). Besides, NPQ/4 appeared to be increased at 13 DOT, mainly for BRS F63, which might emphasize on the oxidative damage of the photosynthetic apparatus.

On the other side, initial high gs and E suggest another protection mechanism of plants grown under high temperature, which consists on evaporative cooling (TAIZ et al., 2017). Over time, high temperature caused stomata closure, denoted by low gs and E, and a consecutive reduction of biochemical phase of the photosynthesis (A, Ci/Ca) (ZHANG et al., 2005). As a result, WUE was always low on plants grown under high temperature condition. First, at six DOT, constant heat exposure produced continuous water loss trying to cool down leaves (TAIZ et al., 2017). Seven days later, at 13 DOT, high photorespiration and low photosynthesis rate, led to low biomass production and consequently low WUE (MARTINEZ et al., 2015; PARRY et al., 2013), which persisted on the last evaluation date.

Aside carotenoids, APX and SOD also contribute to the protection of the photosynthetical apparatus against oxidative stresses, being considered as the key enzymes for reactive oxygen species (ROS) detoxification in the chloroplast (TANG et al., 2006). As the concentration increases with oxidative stress (PETRIK et al., 2023), it is also taken as stress indicators. In this way, on the sixth DOT, the high APX and SOD activity on plants grown under high temperature conditions tell us about the stress situation caused by heat and the capacity of these plants to overcome it.

In addition, it is known that under high temperature condition, photorespiration is enhanced due to the higher availability of O2 in relation to CO2 for Rubisco, besides RuBP oxygenation is stimulated under high temperatures more than RuBP carboxylation is (FOYER et al., 2009). In this circumstance, peroxisomal GO activity on levels that helps to avoid glycolate, and thus glyoxylate, accumulation in chloroplast is of high importance (CUI et al., 2016), otherwise excess of the latest could impede photosynthesis (LU et al., 2014). On this way, higher GO activity at six DOT, might be an indicator of self-protection against oxidative stress. However, on the persistence of high temperature and declination of photosynthesis process (as seen on upper lines), GO activity alone shows an undesirable scenario, where poor carbohydrate quantity is produced.

Total soluble sugars are the first products of photosynthetic carbon absorption (CHEN, Li-Qing, 2014), which are then distributed to the growing organs, however this partition is environmental dependent (ROBREDO et al.,

2011). Temperature is one of these factors and, the synthesis rate response, will depend on the tolerance level and phenological stage of the plant (BASU et al., 1999). In this way, on the sixth DOT, even though no differences were observed on the three cultivar´s (BRS F63, Markies and Innovator) for TAW between treatments, there was higher TSS on tubers and less TSS on leaves under high temperature environment. This may respond to the fact that heat first positively contributed to the photosynthates production, transporting them to tubers, as they were on bulking stage.

Nevertheless, over time, as high temperature conditions persisted, plants showed an increase of TSS on leaves. At this respect, many authors have related the stress buffering role of sugars in leaves, maintaining osmotic homeostasis, buffering cellular redox potential, keeping good membrane stability, or maintaining cell water potential in plant tissues under high temperature (FAROOQ et al., 2008; IBA, 2002; WAHID et al., 2007). The increased amount of sucrose generated in the leaves aided, in some degree, in the diminished of photosynthesis (KAMINSKI et al., 2014) as well as, in the faster transfer of photosynthates (BASU; MINHAS, 1991), being favored to the aerial parts of the plant by heat (TIMLIN et al., 2006). On tubers, at 28 DOT, elevated temperature caused a higher TSS, due to the inhibition of the conversion into starch (KRAUSS; MARSCHNER, 1984). Sugar accumulation on tubers is not favorable, once it make tubers inappropriate for industry (BUSSE; WIBERLEY-BRADFORD; BETHKE, 2019), however, on the biplot of PCA, this character had low influence on the separation of treatments.

Even though, at the beginning of the stress (6 DOT), heat caused higher plants, with more leaf area, stems had poorer dry matter composition, evidencing thicker stems, as related by other authors (DEMIREL *et al.*, 2017; SINGH, Baljeet; KUKREJA; GOUTAM, 2020). Later on, at 13 DOT, elevated temperature caused lower dry matter accumulation on both aerial and underground organs, though with less weight per tuber. Finally, at 28 DOT, control temperature condition favored yield variables on the three cultivars, while heat favored leaves and root dry matter. Chen and Setter (2021) suggested that the inhibitory response in tubers was triggered by photosynthate status.

In summary, at 53 DAP, when the three cultivars, BRS F63, Innovator and Markies, were six days exposed to the heat treatment, physiological and

biochemical, specifically geared toward photosynthetic protection against high temperature impacts, were the most important characters that differenced temperature treatments. Seven days later (13 DOT) those were the photosynthetical variables and, at 28 DOT, the antioxidant molecules and tuber production.

It´s important to highlight that even though these three cultivars were always grouped on the same bi-plot quadrant, there seemed to be a little difference in terms of heat tolerance between them. On the second evaluation date (13 DOT) BRS F63 showed the lowest WUE, and a pronounced NPQ/4 accompanied by the lowest Fv/Fm, suggesting a stronger oxidative damage on this cultivar (Figure 13). Moreover, it´s the only cultivar that showed significant differences between treatments on ATW and had the same TTW than MB 54-02, which started tuberization later (Figure 11).

Path analysis, considering photosynthetic parameters for tuber yield, was done on both temperature treatments, in order to analyze the influence temperature has on this respect. On both temperature condition, the perfect correlation between A and TTW confirms the importance of photosynthesis in plant metabolism, as it is the starting point for most processes that lead to mass production (MURCHIE; PINTO; HORTON, 2009). However, the low direct effect has over TTW suggests the importance of other parameters, which in turn, is not in the same level during the whole life cycle of the plant and it´s temperature dependent (CHEN, Chien Teh; SETTER, 2021).

In this way, was seen that on both temperature condition at 53 DAP, when plants were 6 DOT, the effect of A over TTW depended also of Ci/Ca and Y(II). Besides, A-1 and Y(II)-1 were essential for the influence of A on TTW on all evaluated dates. Suggesting that the assimilation of carbon and production of energy at the beginning of tuberization is determinant for the final yield result. Under high temperature condition was different, because the relationship of A and TTW during tuber growth was mostly influenced by A-1, Ci/Ca-1, A-2, Ci/Ca-2 and Y(II)-2. At this respect, it is important to consider that under high temperature condition, photosynthesis process occurs faster.

The interaction photosynthetic parameters between evaluation dates, lead to the decision to make path analysis for some biochemical compounds, in order to deepen the knowledge about the effect of high temperature over potato plants.

To do so, one path analysis for each evaluation date and temperature condition was performed, having considered as a normal situation the observation under control temperature condition.

At 53 DAP, plants were at the stage of tuber initiation, this is, underground pith cells were in process of enlargement followed by cell division (MELIS; VAN STADEN, 1984), so, new organs are new requires for photosynthesis products. Thus, a joint effect of photochemical and biochemical phase of photosynthesis (A, Y(II) and pigments) on final TTW was observed. About this, it´s important to consider that pigments don´t have a direct effect over tuber production thus, only the indirect effects are considered for this study, which are inversely proportional to TTW. This might be because at this phenological stage, photosynthates were used to maintain above ground organs as tuber requirement was low (BEHERA et al., 2009). When high temperature was applied, because the plants were on the same phenological stage, photosynthetic parameters (A, Ci/Ca, Y(II)) had a good contribution to final TTW. Although NPQ/4 appeared to be perfectly correlated to TTW, in reality it doesn´t have a direct effect and its indirect effect would be only possible through Y(II) which is negligible, for this reason won´t be taken into account. In addition, GO showed a strong correlation with TTW, and its indirect effect through photosynthetical parameters strengthen the protective role of this enzyme under high temperature condition (CUI et al., 2016). Interestingly, the amount of tuber obtained at this time is not determinant for the final tuber yield, as the total correlation is not strong and the direct effect is low in both temperature condition.

Seven days later, plants appear to be in the tuber bulking stage. According to Egúsquiza (2000), at this stage, photosynthesis might be stronger than respiration, preventing the products of photosynthesis from having another draining organ than tubers. It brings that, among evaluated variables, CO2 capture (A, Ci/Ca) have the highest effect on TTW. Again, although path analysis shows NPQ/4 as an equal contributor, will not be taken in consideration for the reasons already described. On the other side, elevated temperatures added an inversely proportional effect of Y(II), Chl_b, T_Chl and NPQ/4 to the variables that contributed the most to TTW. Although pigments don´t have a direct effect over TTW, Chl_b and T_Chl concentration contributed indirectly through the mentioned variables when heat was applied. At this respect, many authors have

related the increment of Chl b concentration due to high temperature environmental condition, which in turn brings to an inefficient energy transfer (RATH et al., 2022). This is consistent with the reduction of Y(II) at this stage, observed previously in PCA (Figure 13), which might be the reason of the negative direct and indirect effect of this variable and the negative indirect effect of NPQ/4 through Y(II). However, a joint effect of these variables with other photosynthetic characters strengthens the importance of photosynthesis to overcome heat stress during tuber bulking. In addition, the direct and indirect effect on the final yield (TTW) of this stage's TTW (TTW-2) appeared to be positive and higher than on previous situation, suggesting it would be a good moment to infer whether the final production would be high or not. However, it might be accompanied by physiological evaluations.

Finally, at 75 DAP, photosynthesis continue being important for tuber bulking, then A and Y(II), together with Chl_a, Car and NPQ/4 had a joint effect on TTW. While Car works on quantum harvest, Chl_a is responsible for energy transfer, being more efficient than Chl_b (KALAJI et al., 2016). On the other side, Car is both the main acceptor of photons for photosynthesis and photoprotector pigment on the non-photochemical quenching process. Thus, under normal temperature condition, at this stage of the plant, photosynthesis is occurring normally, while there is a need of other energy dissipation through NPQ/4. At this respect, Ierna (2007) observed a decrease of chlorophyll content with the age of the plant, decreasing the activity of PSII (HARDING; GUIKEMA; PAULSEN, 1990), besides the increase of tilakoid membrane permeability, leading to the enhancement of mechanisms of photosynthetic apparatus protection (HONG et al., 2000). Similarly, on plants grown under high temperature condition, the most important contributors to TTW were A, Chl_a and NPQ/4, besides GO, TTW-2 and TTW-3. Nevertheless, this was not a joint effect, since the only indirect effect that contributed to their direct effect were through GO and TTW-3, resulting in a highest effect of the residual variable, which means there are other characters that are influencing on the final TTW on this experimental condition. The high importance of GO over final TTW suggest that the long-term elevated temperature and natural process of senescence led to photorespiration process, with which the increment of dry matter was not possible. This may also explain

the directly proportional direct effect of TTW-2 and TTW-3 on TTW, because there was not a significant increment on tuber yield.

4.5 Conclusion

The greatest differences between potato genotypes in terms of heat tolerance were detected when the heat stress is applied in the beginning of tuber initiation stage for two weeks, through the measurement of photosynthetic traits.

5 FINAL CONSIDERATIONS

As a whole, both studies demonstrated that high temperatures negatively affect tuber production and alter aerial part growth of the plant on all tested genotypes.

Through photosynthetic measurements was possible to visualize an acclimation process once the temperature is elevated, at the beginning of the application of the stress, but longer periods of heat reduced the activity of photosynthesis and gas exchange.

In both studies could be seen that the level of damage caused is genotype dependent.

On the first study was concluded that physiological measures help to identify less stressed genotypes under high temperature conditions.

On the second study was added biochemical analysis in order to have a better understand of potato response to heat and was confirmed that photochemical variables are helpful for heat tolerance.

For better discriminations of genotypes the stress should be applied in the beginning of tuber initiation stage, for two weeks.

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