FACULTY OF AGRICULTURAL SCIENCES

Institute of Agricultural Sciences in the Tropics
(Hans-Ruthenberg-Institute)

Department of Management of Crop Water Stress in the Tropics and Subtropics (490g)

Prof. Dr. Folkard Asch

UNIVERSITY OF HOHENHEIM

Screening tools for late drought resistance in tropical potato

Dissertation

submitted in fulfillment of the requirements for the degree
"Doktor der Agrarwissenschaften"
(Dr. sc. agr. / Ph.D. in Agricultural Sciences)
to the
Faculty of Agricultural Sciences

presented by

Julia Hölle
Born in Hechingen, Germany
Stuttgart, April 2023

This thesis was accepted as a doctoral thesis (Dissertation) in fulfillment of the regulations to acquire the doctoral degree "Doktor der Agrarwissenschaften" (Dr.sc.agr. / Ph.D. in Agricultural Sciences) by the Faculty of Agricultural Sciences at University of Hohenheim on April 26th, 2023.

Date of the oral examination: 29.09.2023

Examination Committee

Supervisor and Reviewer: Prof. Dr. Folkard Asch

Co-Reviewer: Dr. Awais Khan

Additional examiner: Prof. Dr. Georg Cadisch

Chairperson of the oral examination: Prof. Dr. Stefan Böttinger

Affidavit

pursuant to Sec. 8(2) of the University of Hohenheim's doctoral degree regulations for Dr.sc.agr.

1. I hereby declare that I independently completed the doctoral thesis submitted on the topic „Screening tools for late drought resistance in tropical potato"

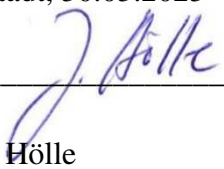
2. I only used the sources and aids documented and only made use of permissible assistance by third parties. In particular, I properly documented any contents which I used - either by directly quoting or paraphrasing - from other works.

3. I did not accept any assistance from a commercial doctoral agency or consulting firm.

4. I am aware of the meaning of this affidavit and the criminal penalties of an incorrect or incomplete affidavit. I hereby confirm the correctness of the above declaration.

I hereby affirm in lieu of oath that I have, to the best of my knowledge, declared nothing but the truth and have not omitted any information.

Albstadt, 30.03.2023



Julia Hölle

To all the people, who always believed in me

To the most understanding person I know

To my family

Space to think

Space to develop

Space to be

Acknowledgments

Long journey to the end or is it a new beginning? I don't know yet, but I am happy this chapter is over now. So many feelings and even more people involved in this wonderful project. First of all, I would like to thank to Folkard. He always believed in me, never gave up, even after long, and apparently terminal drought spells in my brain. After "re-watering" I learned to think out of the box and around it. Your favorite question always was: What would you do, if you are a plant? Thank you for your guidance, ideas, advices and hours and hours of talking and reviewing my texts. Thank you for your visits in Peru, nice learning lessons for all of us.

Muchas gracias a todo la gente de CIP me han acogido muy bien y me han ayudado a orientarme en el nuevo país. David, Wendy y claro que si, Jorge, que estuvo a mi lado con palabras y hayuda cuando no sabía cómo funciona un dispositivo o generalmente las cosas en el campo. Hubert, siempre auxiliar en el campo y taxi diario. Gracias por todo a mis amigos, con quiees sigo en contacto: Emily, Trini, Anthony. Saludos a mis primeros estudieantes Mayron y Jesus en mi perimer año en St. Rita. A todos estudiantes diligentes, ayudando en el campo 10 y mas horas por dia. Gracias por pasar su tiempo libre conmigo, en el ovalo en St. Rita, Navidad, Nochevieja. Gracias a toda la gente de St. Rita, Jorge del hostal, a mi segunda familia en Perú. Juanita, Rosa, con su ayuda incansable en el campo, la Migda, que aseguró mi almuerzo. Todos que ustedes han hecho de mi intenso y largo tiempo en Perú algo hermoso que siempre me gusta recordar. Gracias por su constancia y paciencia con la que me hasn enseñado todo el español.

Staying in Germany I was pleased to had all the nice colleagues around me. Thanks to my office, lunch and "mental hygiene" colleagues: Sarah Glaetzle, Nadja Reinhardt, Marc Schmierer, Sabine Stürz, Julia Asch, Gabriele Schmid and Gabriele Kircher. Thank you Sabine for being there, when I needed urgent help, to meet any deadline by yesterday as well as motivating words and support.

And of course thank you to all my family. Dear Mum, dad, you always believed in me and let me choose my way. Whatever idea I had and still have, you are supporting me. I never heard words like: Oh don't do that, or what a bad idea. Thank you Mum for your great support, caring for the children while I was working. For that I am very grateful. Andy, to be with me, now about double time, like my dissertation lasted, is really incredible. We went through so many steps together in our lives, amazing. You supported me in this journey and gave me power if I needed, even online or in real! Thank you. A grateful thank goes to my parents in law. Always,

when I needed time to work you took care of Jonna and Amida and filled this time with nice experience and adventure for them. Also thanks to all other child sitter in our life: Louisa, Julia and many more. Finally, thanks to my friends Linda and Ina which help me whenever I need them. My new team from the “FREIE SCHULE Zollernalb” which gave the freedom I need to finish my thesis and a place to be and work.

Table of Content

List of Abbreviations

BBCH	Biologische Bundesanstalt für Land- und Forstwirtschaft, Bundessortenamt und chemische Industrie
BD	Bulk density
CIP	International Potato Center
DAP	Days after planting
DAPM	Days after the stage of physiological maturity
DAWW	Days after withholding water
FC	Field capacity
FDR	Frequency domain reflectometry
FI	Full irrigation
G	Genotype
LAI	Leaf area index
Loam	Loamy sand
NDVI	Normalized difference vegetation index
NIR	Near infrared (900 nm)
PASM	plant available soil moisture
PAR	Photosynthetically active radiation
PCA	Principal component analyze
PPFD	Photosynthetic photon flux density
PRI	Photochemical reflectance index
PSII	Photosystem II
PW	Permanent wilting point
Red	Red-waveband (680 nm)
R_{531}	Radiation at waveband 531 nm
R_{570}	Radiation at waveband 570 nm

RH	Relative air humidity
Sand	Sandy soil
SD	Standard deviation
SSI	Stress severity index
T	Treatment
T1	Treatment 1, fully irrigated control
T2	Treatment 2, early drought, initiated at 50 days after planting
T3	Treatment 3. Intermediate drought, initiated at 75 days after planting
T4	Treatment 4, late drought initiated at 90 days after planting
ΔT	DeltaT is the difference of the air temperature - leaf temperature
T_{air}	Temperature of the air
Temp.	Temperature of the air
T_{leaf}	Temperature of the leaf
TD	Drought treatment
TFW	Tuber fresh weight
TubRed	Tuber yield reduction
TYTD	Tuber yield under terminal drought
TYFI	Tuber yield under full irrigation
VPD	Vapor pressure deficit
WUE	Water use efficiency

List of Figures

List of Tables

Zusammenfassung

Die Kartoffel (*Solanum tuberosum* L.) ist eine empfindliche Kulturpflanze gegenüber Trockenheit. Meist reicht nur eine kurze Trockenperiode oder unregelmäßige Bewässerung während der Stolonentwicklung, der Knollenbildung oder des Knollenwachstums, um die Erträge stark zu verringern.

Um die Kartoffelgenotypen zu identifizieren, welche mit weniger Wasser gleichbleibende oder nur gering reduzierte Knollenerträge hervorbringen, führt die Wissenschaft der Selektionsforschung seit Jahren Studien durch. Oft wird eine große Anzahl an verschiedenen Kartoffelgenotypen auf Trockentoleranz getestet und eine schnellere Vorgehensweise würde Zeit und Geld sparen. Da in die Eigenschaft der Trockenstresstoleranz eine Vielzahl von Genen involviert ist, wäre ein entsprechendes Screening Tool, welches eine Reihe an physiologischen Reaktionen auf Trockenstress evaluiert, hilfreich um den Selektionsprozess zu beschleunigen.

Eine ganze Reihe von morphologischen und physiologischen Merkmalen und Anpassungsstrategien können die Erträge der Kartoffel unter Trockenheit verbessern. Dazu zählt die Anpassung der Phänologie an Trockenstress. Weitere wichtige physiologische, Parameter sind die Reflektion der Pflanzen, wie zum Beispiel der Normalisierte Vegetations Index (NDVI) und der photochemische Reflektions Index (PRI). Ein weiterer wichtiger Parameter ist die Blattflächentemperatur, welche hilft die Transpirationskühlung zu beschreiben. Alle Parameter mit ihrer entsprechenden Anpassung helfen den Pflanzen Trockenstressperioden zu überstehen. Diese Merkmale entwickeln sich jedoch in Abhängigkeit zur phänologischen Phase bei Beginn des Trockenstresses, der Dauer des Trockenstresses und natürlich der Stressintensität, welche wiederrum vom Bodentyp abhängig ist. Dies führt dazu, dass verschiedene Kartoffelgenotypen dasselbe Feuchtigkeitsdefizit im Boden unterschiedlich intensiv wahrnehmen und dementsprechend differenziert darauf antworten.

In zahlreichen Studien wird die zentrale Rolle der oberirdischen Biomasse für die Ertragsbildung beschrieben. In der Züchtung ist eine visuelle Evaluation der oberirdischen Biomasse eine wichtige Methode. Die unterirdische und die oberirdische Entwicklung der Kartoffel ist in der Literatur als eng und linear zusammenhängend beschrieben. Diese Synchronie führt dazu, dass viele Studien den Zustand oder das phänologische Stadium der oberirdischen Biomasse dazu nehmen um auf die unterirdische Entwicklung zu schließen, ohne die Pflanzen zu ernten. Bis heute liegt keine Studie vor, die die Auswirkung von Trockenstress

auf die Synchronie der ober- und unterirdischen Entwicklung untersucht hat. Neben dem phänologischen Stadium zu Beginn der Trockenheit, sind die Dauer und die Intensität des Wasserdefizits zwei weitere wichtige Aspekte in der Toleranzforschung. Um die Reaktionen von Genotypen auf verschiedenen Längen von Trockenheit in verschiedenen Umgebungen, Jahren und Bodentypen vergleichen zu können, benötigt man einen Index, der die Phänologie, Trockenstressintensität und Dauer widerspiegelt. Bei der Trockenstressintensität spielt der Bodentyp eine zentrale Rolle. Während das Wasser bei einem spezifischen Wassergehalt in einem Lehmboden pflanzenverfügbar ist, besteht in einem Sandboden schon ein Wasserdefizit. Der erforderliche Index sollte also auf Informationen der Bodenwasserspannung und einer Gewichtung der Phänologie nach Sensibilität beinhalten. Durch die Akkumulation der einzelne Werte kann so ein Stressintensitätsindex (SSI; Stress Severity Index) ermittelt und verglichen werden. Der nächste und letzte Schritt war es, den neu entwickelten SSI mit physiologischen Messungen zu verbinden, um mit Hilfe von Fernerkundung schnell und einfach eine große Vielzahl von Genotypen auf Trockentoleranz zu Testen. Zu den schnellen Methoden der Fernerkundung zählt die Messung der Pflanzenreflektion und die Messung der Blattflächentemperatur. Mit Hilfe der Reflektionsdaten kann der normalisierte differenzierte Vegetationsindex (NDVI) und der photochemische Reflektionsindex (PRI) berechnet werden. De NDVI gibt Auskunft über die Grüne der Pflanze und der PRI über den Status des Xythophylls. In Kombination mit der Blattflächentemperatur entsteht ein Bild über den aktuellen Status der Pflanze.

In einem Feldversuch haben wir auf zwei verschiedenen Böden dreizehn unterschiedliche Kartoffelgenotypen drei verschiedenen Trockenszenarios ausgesetzt. Die Ernte, sowie die oberirdische und zeitglich die unterirdische phänologische Entwicklung und die physiologischen Parameter wurden in fünf bis zehn Tagesintervallen gemessen und dokumentiert. Die Bewässerung wurde an 50, 65 und 80 Tagen nach der Pflanzung bis zur finalen Ernte nach 120 Tagen eingestellt. Die Synchronie zwischen der oberirdischen und der unterirdischen Entwicklung ist vom Wasserdefizit als auch vom Entwicklungsstadium zu Beginn der Trockenheit anhängig. Bei früh induzierter Trockenheit, während der Stolonbildung zum Beispiel, wurde die oberirdische Entwicklung beschleunigt und unterirdische Entwicklung verzögert. In späteren Entwicklungsstadien, während der Knollenfüllung war diese Verhältnis genau umgekehrt. Die phänologische Entwicklung der oberirdischen Biomasse war verzögert,

während die Knollenbildung und Knollenfüllung beschleunigt wurde. In weiteren Experimenten ist es also wichtig, die Pflanzen komplett zu ernten und nicht von der oberirdischen Biomasse auf die unterirdische zu schließen. Der SSI ermöglicht den Vergleich der Ergebnisse von verschiedenen Dürrebehandlungen unabhängig von Standort, Jahr, Jahreszeit und Bodentypen. Der SSI ist ein unabhängiger Indikator für den Stress, was eine Bewertung der Reaktionen einer Pflanze auf einer standortunabhängigen Basis ermöglicht. Mit Hilfe des SSI bis 1000 sind wir in der Lage zwischen sensitiven und toleranten Genotypen zu differenzieren. Bei SSI Werten über 1000 gingen die Erträge um mehr als 60 % zurück, und eine Differenzierung zwischen den Genotypen war nicht mehr möglich. Der SSI ermöglicht eine Aufsummierung der Stressschwere, und je höher der Ertrag bei einem hohen SSI ist, desto stärker sind die Abwehr- und Anpassungsmechanismen der Pflanzen. Die Cluster-Analyse des SSI mit Ertragsverlusten, NDVI, PRI und Thermografie, identifizierte drei Gruppen mit den entsprechenden physiologischen Reaktionen bei Trockenheit. Die erste Gruppe umfasste Genotypen mit einem SSI von <1000, welche durch einen schnell abnehmendem NDVI, PRI und Temperaturdefizit charakterisiert war. In der zweiten Gruppe waren die Genotypen mit einem SSI-Wert von 1000 bis 2000. Diese wiesen konstante NDVI und Temperaturdefizite auf. In der dritten Gruppe mit SSI>2000 fanden wir nur kleinen Veränderungen von NDVI, PRI und Blattflächentemperatur. Die Kombination dieser vier Parameter (Ertragsminderung, NDVI, PRI, Thermografie) erklärte 76 % der Varianz, was darauf hindeutet, dass diese Kombination einen wertvollen Datensatz zur Analyse der Trockentoleranz bei Kartoffeln liefert. In Kombination mit dem SSI können wir die Pflanzenreflexionsmessungen als geeignetes Screening Tool für Trockentoleranz bei Kartoffeln identifizieren.

Summary

Potato (*Solanum tuberosum* L.) is a drought sensitive crop, and even short drought spells or infrequent irrigation during stolon formation, tuber initiation, or tuber bulking reduces tuber yields. A number of morphological traits have been described that potentially improve genotypic performance of potato under moisture deficit conditions. In breeding processes, a large set of genotypes are tested at the same time and because the genotypes differ in their phenology, various phenological stages occur simultaneously in the field. Consequently, during a drought spell different varieties will be subjected to soil moisture deficit at different phenological stages.

We tested thirteen contrasting genotypes under field conditions in a desert in South Peru in four different irrigation treatments at two different soil types. The irrigation was withheld after 50, 65 and 80 days after planting until final harvest after 120 days. Sequential harvests, remote sensing and phenological evaluation was conducted in five to ten-days intervals.

In literature, the belowground and aboveground development of potato has been described as closely and linearly related, meaning that in many studies belowground development is estimated according to aboveground development. The synchrony of the aboveground and belowground development is strongly influenced by both, water deficit and development stage at drought initiation. Under early drought, the aboveground development was accelerated and belowground development slowed. The opposite was found at later development stages. The earlier drought was initiated, the longer the tuber-filling phase, while the bulking phase was shortened. Water deficit also slowed down the aboveground development of flowering by a couple of days. In further drought experiments it is important to evaluated the belowground development separately, as we cannot conclude from the above to the belowground development stage. In conventional breeding experiments often only one final harvest is used to analyze the final tuber yield. This proceeding do not describe under which circumstances like stress intensity the tuber yield was achieved. Genotype evaluation in breeding experiments often relies only on visual evaluation of the aboveground biomass with no harvest of the plant. Besides the phenological stage at drought initiation the stress severity is another important aspect to determinate the drought stress response of potato genotypes. The stress severity depends on the water availability in term of soil water tension and the drought duration. In this study we developed a stress severity index (SSI) which combines all three important parameters, phenology, soil water tension and drought duration.

With this SSI the selection processes should be improved and genotypes can be compared independently from environment, seasons and years. The SSI combines the yield response of potato to water deficit based on the soil tension the genotype was subjected to for the duration of the stress modified by the development stage of the genotype and drought duration. SSI allows for comparison of genotypic performance independent of year, location, season, soil type effects, and drought scenario. An SSI value of up to 1000 is able to differentiate between sensitive genotypes from more resistant genotypes. Beyond 1000, yields were generally reduced by more than 60% and a differentiation between genotypes was not possible anymore. SSI allows accumulating stress severity and thus, the higher the yield at a high SSI the stronger are the plants defense and adaptation mechanisms. Therefore, other indices that have looked into stay-green syndrome, rooting depth adaptations, leaf surface temperature, or canopy reflectance indices with only medium success, may benefit from including SSI in their indices to identify the underlying mechanisms of drought tolerance in potato. Remote sensing allows to evaluated many genotype simultaneously at field level. Proven indicators in drought tolerance screening are the normalized vegetation index (NDVI), the photochemical reflectance index (PRI) and thermography which describes the transpirational cooling of the leaves. Therefore, the last objective of this study was to validate the suitability of the SSI in remote-sensing stress diagnosis.

The cluster analysis, including SSI, tuber yield reduction, NDVI, PRI and thermography identified three SSI groups with their corresponding physiological reactions under drought. The first group include SSI<1000 with fast decreasing NDVI, PRI and temperature deficit, in the second group matched SSI values from 1000 to 2000 with almost constant NDVI and temperature deficit and in the third group we found SSI beyond 2000 with corresponding small changes of NDVI, PRI and temperature deficit. The combination of these four parameters (tuber yield reduction, NDVI, PRI, thermography) explained 76 % of the variance which indicates this combination as valuable dataset analyzing drought tolerance in potato. Thus, combining these indicators with SSI and tuber yield reduction proved to be a first promising step for a new screening method for drought tolerance in a wider genotypic range. Whereas reflectance data can be recommended for assessing responses under mild to moderate stress severity, thermal imaging should rather be used to screen under mild or early drought stress.

1 General Introduction

1.1 *Solanum tuberosum* L. and yield constraints

The name potato refers to the belowground starchy tubers as well as the parts aboveground. The cultivation of potato (*Solanum tuberosum* L.) goes back 10.000 years (Harris & Hillmann, 2014). About 8,000 years ago, the first potatoes were cultivated in Peru and Bolivia (Lutaladio & Castaldi, 2009). The potato was introduced to Europe from South America by the Spanish in the second half of the 16th century (Salaman, 1985) and the potato slowly spread from Spain to whole of Europe.

Since the 16th century, potato consumption as well as production has been constantly increasing all over the world. In 2020, the global potato yield reached 359 million tons (FAO 2020). Potato is known for its productive water use and nutritional value. Per applied unit of water the potato produces double to three times more dietary energy than other crops (FAO, 2008). Nevertheless, the potato is considered a drought-sensitive crop. Short drought spells can lead to significant reductions in tuber yield (Obidiegwu, 2015; Onder et al., 2005). Since 1980, breeders at the International Potato Center (CIP, Lima, Peru) generated and selected new potato clones out of wild clones and landraces as well as improved germplasm. However, due to sexual incompatibility, the introduction of traits can take 15-20 years (Halterman et al., 2015). Climate change will reduce the worldwide water availability. Irrigated as well as rain-fed potato production will be affected by shifting rainfall patterns and reduced water availability and therefore, rising irrigation costs.

Another difficulty is that drought tolerance depends on multiple traits, meaning long-lasting experiments in which many parameters would need to be measured. Extensive screening experiments are expensive and require significant resources. Therefore, fast, and effective screening tools are needed to speed up the breeding process and reduce associated costs.

1.2 Drought, drought stress and tolerance

Before outlining tools to identify drought tolerant potato genotypes, we will first take a glance at some definitions:

1. How is drought defined?
2. How does drought affect potato growth?
3. What is meant by drought tolerance in potato?

In general, drought from a biological perspective, describes dry soil because of absence of water or low rainfall or due to long periods without any water supply, neither via rain or artificial irrigation. Even if the definition of drought is clear, different drought scenarios are developed, as there is no universal definition of drought intensity. Droughts are described with field capacity, soil or leafe water potential, water amounts in Milliliter or just by X days without water.

Drought affects potato above and belowground growth in various ways. Belowground development like root traits, including root length, root dry mass, and stolon number change depending on the stress intensity, duration, and phenological stage at onset of drought (Albiski et al., 2012; Tourneux et al., 2003a). Additionally, tuber yield traits such as, tuber number, yield, misshapes, tuber dry matter, tuber water content were affected by drought (Lefèvre et al., 2012; Luitel et al., 2015). The canopy traits like canopy growth, stem length, leaf number, stem eight, leaf area, were changed in potato plants in different drought scenarios under field conditions (Aliche et al. 2018; Deblonde and Ledent 2001; Lahlou et al., 2003). The lack of water reduces $C0_2$ uptake as the stomata close. The whole photosynthesis process is lowered or stopped (Muthoni & Shimelis, 2020). The first visible changes are the reduction in above and belowground growth. Early senescence and resorption of tubers might be other effects of drought.

It is known, that a soil water tension of -70 kPa is a critical point for potato growth (Mould & Rutherfoord, 1980). Satisfactory yields were measured at a soil moisture tension of -50 kPa throughout the whole growing season. However, measurements of soil water and a definition of soil water tension under drought treatment is rarely found in the literature. In one of the studies where information about soil water is available, the soil water potential was -185 kPa for deficit irrigation in tomato (Jensen et al. 2010). Moderate drought conditions were described with -1500 kPa in Deblonde et al., (1999) and in Schittenhelm et al., (2006) with 30 % of plant available water. Each study defines a different stress severity and uses different treatment protocols. In general, drought is a lack of water but how severe or intense a moderate or low drought stress is, is not yet clearly defined in potato research. This applies also to other crops, like maize, rice and soybean (Santini et al., 2022). The multivariable attributes of drought depend on magnitude, frequency, duration and timing, makes generalization and definition of drought intensity so difficult.

With different drought scenarios and different protocols in literature – how can drought tolerance be defined? The terms drought resistance, water-use-efficiency and yield potential

are often misunderstood (Blum, 2005). However, with crops grown under drought, the efficiency to use the available soil moisture is the key mechanism, which then is expressed in lower water-use-efficiency (WUE). However, selecting only for high WUE may discriminate plants which are able to increase the net plant production or change their biochemistry to enhance assimilation (Blum, 2005). However, how drought indices are calculated, and which selection criteria are used to define tolerant genotypes is variable. The available harvest indices (relative drought index, tolerance, stress tolerance index, drought intensity index, mean productivity etc.) could help to identify drought-tolerant genotypes. However, which yield level (200 g plant^{-1} or 1000 g plant^{-1}) is used as the standard depends on the genotypes as well as the research focus. Other measured parameters (water content, biomass, root length etc.) should also be considered and related to tuber yield performance.

1.3 Potato research in drought screening

Screening for drought tolerance can include destructive and non-destructive parameters. The general idea of a screening tool is to detect a defined condition. With the help of thresholds and genotypic responses, drought tolerant or/and sensitive genotypes can be distinguished from each other.

Investigation of the morphology, physiology, and phenotyping of potato are classical methods to screen and identify drought tolerant potato genotypes (Figure 1.1). The latest biotechnological approaches such as high-throughput phenotyping, functional phenomics, remote sensing technology, and molecular and genetic component analysis complete the knowledge and extend the scientific expertise. However, it seems that there is little research interest in drought-related phenotypic response in potato (Hill et al., 2021). The majority of investigation into the drought response of potato are at least 10-years-old. Hill et al. (2021) assume the disinterest in morphophysiological research may result from the new research focus on genetic and biotechnological methodologies, paired with the belief that morphophysiological traits have already been thoroughly explored. However, many important studies that establish general effects of drought on potato, need to be implemented in combination with current available technology.

Figure 1.1: Field Design in Santa Rita de Siguas, Arequipa, in the desert in South Peru.

A broad range of morphophysiological parameters have been used to measure drought-stress responses of potato in greenhouse, laboratory, or fields. The studies between the late 1980's and early 2000's explained the effect of drought on yield (Jefferies & Mackerron, 1989; Levy, 1986), canopy development (Deblonde and Ledent 2001; Lahlou et al., 2003) and root growth (Tourneux et al., 2003b). A number of physiological and morphological adaptive traits already have been identified and evaluated; however, no single trait has been shown to be highly correlated with yield performance (Schafleitner et al., 2006). Several morphophysiological traits were associated with water-use-efficiency; like transpirational cooling; paired with stomata behavior, biomass accumulation and canopy architecture.

The greenness of leaves is linked with canopy reflection, carbon storage, and allocation. The existing gap between yield potential based on adaptive traits and final tuber yield performance must be considered in a breeding strategy for drought tolerance. To understand the various mechanisms of drought tolerance research should use different tools to consider plant mechanisms:

- Screening based on the potato tuber yield
- Screening based on the plant's phenology and morphology
- Screening based on the plant's physiology

In breeding, studies focusing on tuber yield parameters such as tuber yield, tuber yield reduction, and various statistical drought resistance indices based on tuber yield are well-established. Experiments with tuber yield and drought resistance indices are documented in various studies (Beyene et al. 2019; Muthoni & Kabira 2016). The selection of genotypes is

often based on tuber yield information reached under drought and well-watered conditions. However, the 17 developed drought resistance indices based on tuber yield, have difficulties in describing drought-stress intensity (Hill et al., 2021). These indices have been developed to identify potato genotypes with high yields and/or high yield potentials under drought. Under which stress intensity and magnitude these yields have been reached is not considered, as the stress intensity depends on the phenological stage and drought duration. These factors should be included in further reasearch.

All development stages of potato are considered sensitive to drought (Spitters & Schapendonk, 1990). Depending on the phenological stage, drought-stress intensity and duration affects emergence, stolon initiation, flowering, tuber initiation, or the bulking phase. The emergence, stolon and tuber initiation as well as tuber filling stage, are very sensitive to drought which lead to significant reduction in tuber yield under field conditions under short- and long-term drought conditions (Carli et al., 2014; Obidiegwu et al., 2015; Saravia et al., 2016). Mapping genotype-phenotype relationships is currently ongoing, but has yet to have a large impact on global crop breeding efforts (Rahaman, et al., 2015). Several studies have emphasized that phenotypic plasticity might be even more important in the face of climate change than genetics, as plasticity is particularly large under extreme conditions, like drought (Gratani, 2014; Vitasse, et al., 2010). Protocols for screening germplasm, mapping populations or mutants, transgenic lines and other breeding material are well-established in the scientific community. However, the protocols for field experiments are diverse, with little interoperability.

Potato has been classified as sensitive to even minor drought spells partly due to its shallow root system, as the potato plant appears to be an ineffective soil water extractor (Weisz et al., 1994). To ensure water and nutrient uptake, root architecture is determining access to soil water. The main root system in potato is 30 cm depth (Iwama, 2008) and drought severely affects potato genotypes with small root systems (Wishart et al., 2014). In the study from Wishart et al. (2014), root mass including root length and stolon number is positively correlated with shoot mass and final tuber yield. Not many studies are available about root studies under field conditions in potato because it is time-consuming, laborious, expensive, and imprecise. Hill et al., (2021) concluded, that due to the unpredictable effect of factors on root growth during drought, and challenges in quantifying root growth accurately, it may be more productive to focus on aboveground growth.

The amount of water for transpiration depends on plant height and leaf area. Above-ground biomass, shoot dry weight, and plant height are important morphological parameters determining photosynthetic capacity and transpiration (Fig. 1.2). In a greenhouse pot experiment, shoot dry weight and plant height were not affected by drought treatment, regardless if the plants were drought-acclimated or not (Banika et al., 2016). Under terminal drought, total biomass and the sum of leaf, stem and root weight were significantly reduced in field studies (Saravia et al., 2016, Auber et al., 2013). As a dynamic and adaptive parameter, leaf area in potato is decreased due to natural senescence processes as well as drought. Jefferies and Mackerron (1993) concluded that the sustainability of leaf development under drought conditions with increasing soil water deficit would improve productivity of potato genotypes.

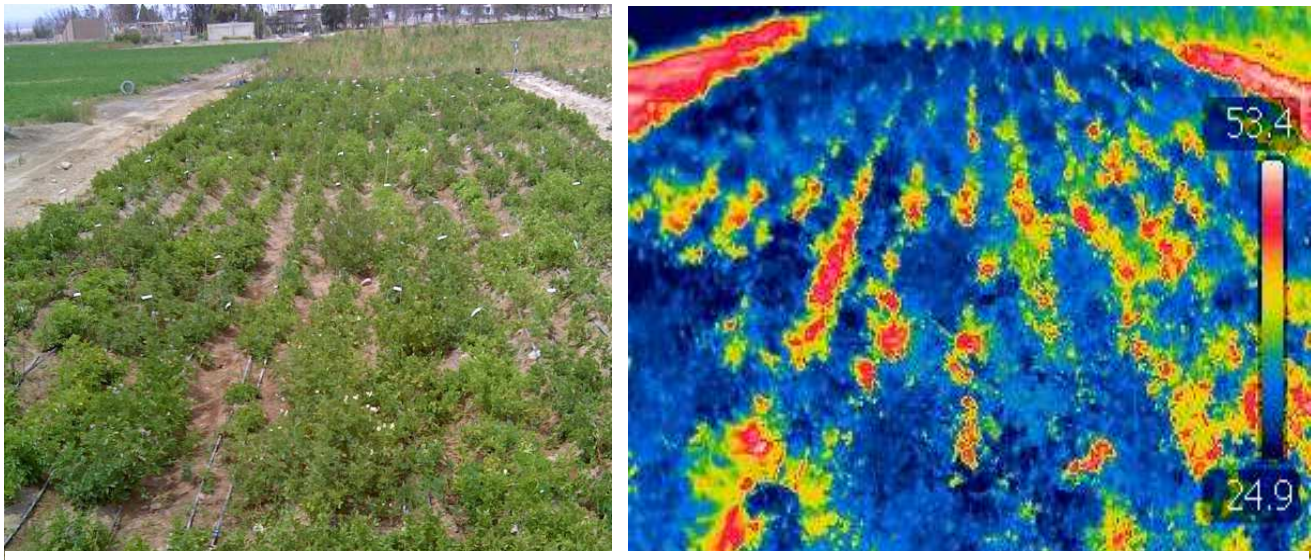


Figure 1.2: Screening of aboveground biomas via visual evaluation and thermal imaging. Colours representing temperature in °C.

Agronomic and morphological traits and various physiological parameters are tested to identify drought tolerant potato genotypes. The two physiological measurements covering a broad range of physiological mechanisms are thermography and reflectance measurements.

Thermography of canopy temperature allows to estimate stomatal control over transpirational water losses (Grant et al. 2012; Jones et al. 2009; Merlot et al., 2002). Due to a rise in air temperature by 1.2 to 1.8 °C by 2039 and up to 3.2 °C by 2050, Hijmans (2003) modelled that the yield of non-adapted potato genotypes will decrease by 10 to 19 % in the years 2010-2039, and 18 to 32% in 2050. Thermography is used to study plant-water kinetics, with a

focus on stomatal conductance. The driving force determining leafs temperature is the rate of evaporation from the leafs surface. The conversion of each mole of water into water vapor, needs energy which is taken from the leaf, resulting in cooling (Jones et al., 2009). Consequently, potato plants under drought close their stomata, reduce transpiration, and thereby increase leaf temperature, which can be measured by thermography (Idso, 1982; Idso et al., 1981; Jones, 1999). Heat generation due to respiration can be neglected, as it has no detectable effect at the leaf level (Breidenbach et al., 1997; Jones, 2002). In tropical climates, maize genotypes with better adaptation to drought, exhibit lower canopy temperatures under drought conditions (Romano et al., 2011). With thermography, many genotypes in a largescale field trial can be measured at the same time using drones or trucks with integrated ladders. Therefore, this technique can be used as a remote sensing tool for diagnosing drought stress at plant level (Auber, et al., 2014; Jones et al., 2009).

In addition to thermography, reflectance which estimates photosynthesis and stay-green mechanisms, can actually be used for yield estimations (Ferrio et al., 2005). Including remotely sensed indices like the normalized difference vegetation index (NDVI) and photochemical reflectance index (PRI), based on the visible and near-infrared spectral regions, it can be used to study canopy photosynthesis and even net primary production (Peñuelas & Filella, 1998; Sellers, 1985, 1987). Additionally, these techniques provide information about the spatial and temporal variability of soil and crops. Remote indices can be calculated from the reflectance, which is measured from the waveband 325 up to 1075 nm. Flexible sampling and individual selection of specific wavebands make this evaluation feasible. There are only a few publications on hyperspectral imaging under field conditions as a screening tool (Broge & Mortensen, 2002; Romero et al., 2017). Reflectance indices mostly have been used to determine biomass growth and/or changes in leaf water content due to drought. The NDVI is a proxy for canopy density or total aboveground biomass (Verhulst & Govaerts, 2010). Reflection of green and healthy vegetation is low in the red visible spectral range (600-700 nm) and high in near infrared (700 – 1300 nm). The more green and vigorous a plant is the greater the reflection in near infrared, which means there is a high amount of chlorophyll in the leaves. NDVI varies between -1.0 and +1.0, where negative values indicating water and values from 0 to 0.2 senescence vegetation or vegetation free area. Values around +1 indicating the presence of green vegetation. In general, higher reflections in the near infrared waveband indicate longer photosynthetic activity and therefore may lead to higher yields under drought. Using NDVI to select for drought tolerant

genotypes has been validated with various crops like maize (Araus & Cairns, 2014), potato (Tuberosa, 2012), scrubs, annuals and trees (Sims & Gamon, 2003).

The PRI is used to investigate the photosynthetic activity of potato under drought stress conditions (Gerhards, et al., 2016; Romero et al., 2017) and tomato (Ihuoma & Madramootoo, 2019). It measures the xanthophyll cycle activity, which is related to photosynthetic light-use efficiency in plants (Coops et al. 2010) and serves as an indicator of different water stress levels (Ihuoma & Madramootoo, 2019). The PRI is sensitive to diurnal changes in canopy temperature, stem water potential and stomatal conductance (Suárez et al., 2008). Additionally, the PRI can be used to estimate the carbon assimilation at canopy level.

Among others, cloudiness, soil background, and canopy geometry are just a few factors that can complicate the measurement of canopy reflectance under changing weather conditions. Another constraint is measuring wilted plant material and partly senescent plants.

1.4 Objectives

Screening tools considering multiple traits that contribute to drought tolerance in potato are needed to identify genotypes suitable for production under water-limited conditions, thereby accelerating breeding efforts. As drought tolerance is comprised of several traits representing different strategies, various parameters should be measured to identify drought-tolerant potato genotypes. Even if phenological, morphological and agronomic parameters are collected, datasets may remain incomparable, as the stress intensity to which plants have been subjected, often remains unknown or inconsistent. In literature, the duration of the droughts is described in days and the intensity in terms of water potentials or just water volume. The comparability and transferability of data for different experimental settings, stress levels and severities as well as genotypes is difficult. This study investigates the relationship between drought and phenology and the corresponding physiological effects. Furthermore, this study proposes a stress severity index which makes different genotypes, physiological reactions, and environments comparable with each other.

The main objective of this study was to screen potato genotypes for drought tolerance and investigate underlying mechanisms and strategies with the specific objectives:

- to investigate the influence of drought on the synchrony of the above- and belowground phenology of potato.

- to develop and define a stress severity index under consideration of the phenological stage of potato, soil water tension and drought duration.
- to investigate the suitability of the drought Stress Severity Index in remote-sensing stress diagnosis in potato.

2 Drought affects the synchrony of above and belowground phenology in tropical potato

This chapter is submitted as:

Hoelle, J., Asch, F., Khan, A., 2023. Drought affects the synchrony of above and belowground phenology in tropical potato. Journal of Agronomy and Crop Science.

Keywords: abiotic stress, water deficit, phenological development, *Solanum tuberosum*

Abstract: Literature describes the belowground and aboveground phenology of potato to be linearly related. Bud formation is synchronous with tuber initiation and flowering with tuber filling. Many agronomic and breeding studies in potato use non-destructive aboveground phenology to assess belowground development. No information is currently available on the influence of water deficit on the synchrony of above- and belowground development in potato. Five contrasting potato genotypes were subjected to four irrigation treatments on two different soil types. The irrigation treatments were: fully watered, early, intermediate, and late drought. In 5-day intervals after withholding water detailed belowground and aboveground development was recorded. Results showed that the synchrony between aboveground and belowground development is strongly influenced by both, water deficit and development stage at drought initiation. Under early drought, the aboveground development was hastened and belowground development delayed. The opposite was found in later development stages. The earlier the drought was initiated, the longer was the tuber filling phase, while the bulking phase was shortened. We concluded that under terminal drought conditions above and belowground development need to be evaluated separately and cannot follow the standard evaluation system that uses aboveground phenology as a proxy for tuber formation belowground development rates.

2.1 Introduction

The belowground and aboveground development of potato (*Solanum tuberosum* L.) has been described as closely and linearly related (Meier, 2001; Obidiegwu et al. 2015). The first principal growth stage, the formation of sprouts and roots from the tuber, ends with emergence, when the sprouts become visible above the soil surface. Above-ground increasing leaf area and shoot branching coincides with belowground root growth, the formation of basal side shoots,

and stolon initiation. Main stem elongation and further leaf area increase occurs in parallel with tuber initiation. At flowering, in varieties that flower, and at maximum aboveground biomass, tuber formation and tuber filling take place. Finally, during the aboveground senescence process, development and ripening of the fruits, the skin of the tubers sets (=bulking phase). Tubers are physiological mature and tuber dry matter at its maximum when the skin at the apical end of the tuber cannot be removed by thumb. When combining the above and below ground development stages, the potato cycle can be described in a linearly way (Figure 2.1): 1. Growth initiation (sprouting, root formation, emergence), 2. Vegetative stage (leaf development with flowering paired with stolon and tuber initiation), 3. Reproductive stage with tuber filling and fruit development and 4. Tuber bulking process with aboveground senescence.

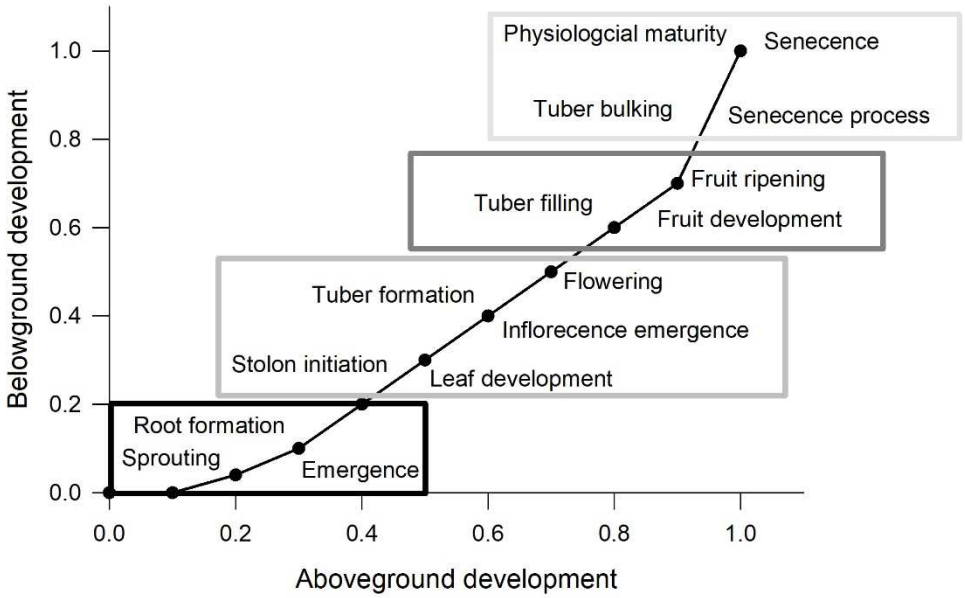


Figure 2.1: Makro-BBCH scale of the aboveground and belowground phenological development according to Meier (2001).

The main limiting factor of potato production under rainfed conditions is drought stress due to inadequate irrigation or erratic rainfall. Drought shortens growth duration (Minhas & Bansal, 1991) and reduces tuber number and size (Hughes, 1974), leaf area (Jefferies, 1993), harvest index (Auber et al., 2013) and final tuber yield (Deblonde et al., 1999). The effect of water deficit on yield depends strongly on the combination of stress severity and phenological stage. E.g., severe water deficit during tuber filling hastened aboveground senescence which resulted

in severe yield reductions (Kuppinger et al., 2014). On the other hand, drought during tuber bulking resulted in longer bulking periods under drought and increased yields (Hoelle et al., 2020).

Many agronomic and breeding studies on drought effects in potato use aboveground phenological observations to conclude on belowground development. Yields are often evaluated with a single harvest at the end of the growing cycle (e.g. Deblonde & Ledent, 2001; Lahlou & Ledent, 2005) even when plants were subjected to water deficits during specific phenological stages, such as stolon initiation (Minhas & Bansal, 1991), tuberization (Rodríguez et al., 2016), or bud formation (Li et al., 2019).

Studies on long-term effects of drought on above and below ground phenological development are not available and no information is currently available if water deficit affects the synchrony of aboveground and belowground development in potato. In addition to continuous observations of the below and above ground phenology, water deficits initiated at and thus affecting different phenological stages are lacking. In this study, we investigated the synchrony of above- and below ground phenological development of 5 potato genotypes subjected to different levels of drought stress at different phenological stages. Additionally, we investigated the genotype specific phenological responses to drought and to identified corresponding adaptation and/or escape strategies.

2.2 Materials and Methods

2.2.1 Site description

Field trials were conducted over two seasons at an experimental station of the “Instituto Nacional de Innovacion Agraria“ in St. Rita de Siguas (16°28'35"S; 72°6'18"W), Peru. The photoperiod in Majes is 13 hours in December and 11 hours in July.

Meteorological date was recorded with a HOBO® Weather station close to the experimental plots. Air temperature, air humidity, wind and gust speed, and photosynthetically active radiation at 2 m height were recorded in 15 min intervals. No rainfall occurred during the field trials. Climate data for the two experimental periods are shown in Figure 2.2. Fields chosen for the field experiments, although classified as arenosol according to IUSS Working Group (WRB 2006), contrasted in soil type. In the first season the soil consisted of a loamy sand, whereas in the second season a neighboring field consisting of sand was selected (Tab. 2.1). For each field, 5 soil samples were taken in a diagonal transect for two depths (0 to 15 and 15 to 30 cm) before

planting. Soil pH, texture, bulk density, field capacity, and permanent wilting point were determined at the soil testing laboratory at the Universidad Agraria La Molina, Lima, Peru.

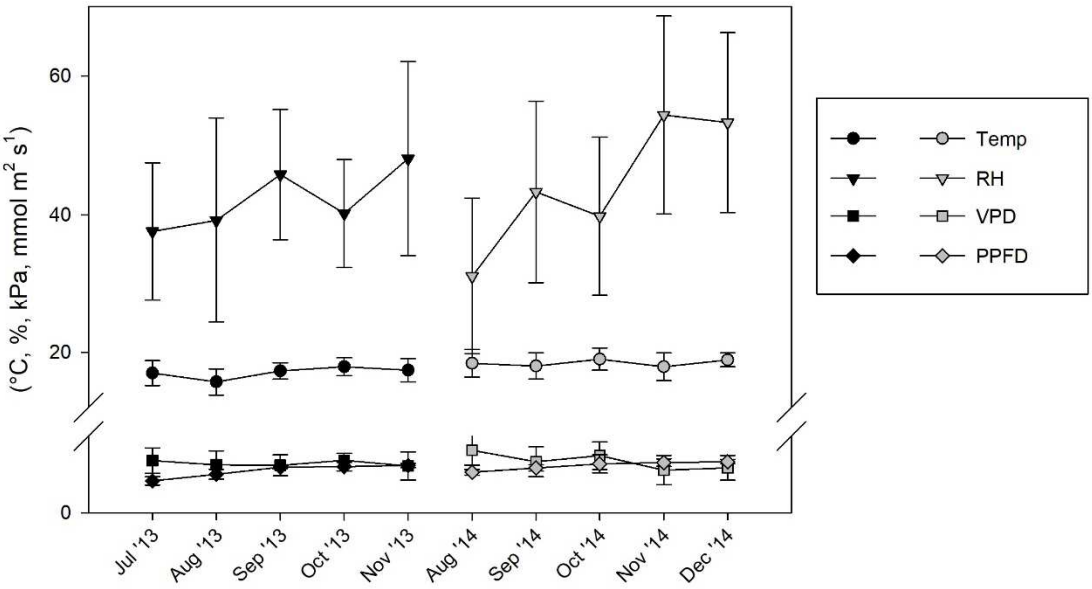


Figure 2.2: Weather conditions during the experimental periods in 2013 and 2014 in St. Rita de Siguas, Arequipa, Peru. Data are shown as monthly averages of daily mean values. Temp=Temperature (°C), RH = relative air humidity (%), VPD = vapor pressure deficit (kPa) and PPFD = photosynthetic photon flux density (mmol m^2 s^1). The error bars representing the standard deviation.

Table 2.1: Soil analyses and water relations for the two experimental fields. Sand = sandy soil; Loam = loamy sand; OM = organic matter; BD = bulk density; FC = field capacity (pF 1.8); PW = permanent wilting point (pF 4.2); PASW = plant available soil water.

			Soil texture				**BD**	**Soil water**		
Soil type	Depth (cm)	pH	Sand (%)	Clay (%)	Silt (%)	OM (%)	g cm^{-3}	FC (vol %)	PW (vol %)	PASW (mm)
Loam	0-15	8.1 ± 0.18	80.8 ± 1.79	11.2 ± 1.79	8.0 ± 1.41	1.5 ± 0.49	1.18	23.2	8.5	58.8
	15-30	7.9 ± 0.19	81.6 ± 1.67	10.0 ± 1.41	8.4 ± 1.67	1.0 ± 0.25				
Sand	0-15	7.4 ± 0.24	94.0 ± 3.46	4.4 ± 0.89	0.4 ± 0.89	0.9 ± 0.18	1.15	20.8	5.0	63.2
	15-30	7.5 ± 0.41	96.0 ± 1.41	4.0 ± 1.41	0.0 ± 0.00	0.7 ± 0.13				

2.2.2 Genotypes, experimental design, and crop management

In both years, the same drought tolerant and susceptible genotypes were used. The five potato genotypes (G1-G5; *Solanum tuberosum)* were obtained from the International Potato Center (CIP). CIP's codes, maturity group, heat tolerance level, and virus resistance level are presented in the Appendix. The five genotypes were planted in a randomized split-plot design with three replications.

Each experimental plot was 3 m long and 2.7 m wide (8 m^2) per genotype and replication. Each plot consisted of 3 rows with row distance of 0.9 m and 0.3 m space within the row. Each row contained 11 plants of the same genotype and 9 plants of the middle row were used for sampling whereas the outer rows were treated as border rows. Before planting, 1000 kg ha^{-1} Guano was applied into the furrows and pre-sprouted seed tubers were placed by hand with the sprouts upside. Mineral fertilizer was applied manually as 162 kg ha^{-1} potassium sulfate (50 % K_2O, 18 % S, INTI), 81 kg ha^{-1} ammonium nitrate (33% N – 3% P_2O_5 – 0% K_2O, MISTI S.A.), and 244 kg ha^{-1} Fertiphos®-Plus (20 % P_2O_5; 36 % CaO; 6 % S, 17 % SiO_2; 1.08 % Fe_2O^3; 0.9 % MgO; Micronutrients Zn, Mn, Cu, B). An additional top-dressing of 120 kg ha^{-1} ammonium nitrate followed during hilling. Seed tubers were disinfected with Homai (BASF) and afterwards with Decis (Bayer) against potato beetle (*Leptinotarsa decemlineata*). Fungicides and insecticides were applied in approximately 20 day intervals according to the instructions of the suppliers. Following products were used: Sorba 50 EC (Syngenta), Ultra Pegasol (Farmagro S.A), Rover (Sipcam Pacific), Pentacloro Farmex, Cipermex (Farmex), Confidor 350 SC Fitoraz (Bayer), Evisect 50 SP (Arysta). Insecticides with changing functional groups were applied to avoid build-up of resistances in the field. Manual weeding was done in 14 day intervals.

2.2.3 Assessment of phenology and soil moisture

Detailed observations of plant growth, and growth responses to environmental changes, as well as timing of fertilizer application or plant protection measures, are commonly related to specific development stages of the plants. The BBCH scale has been developed to describe the phenology of various mono- and dicotyle crops (Meier, 2001). In this scale, the penology of potato is divided into 10 macro stages and within each stage 10 related micro stages. For each aboveground development step a corresponding belowground process has been defined which

are linearly related (Figure 2.1). The macro stages of the BBCH scale are defined as 0-0.9- sprouting/germination, 1.0-1.9 - leaf development, 2.0-2.9 - formation of basal side shoots below and above soil surface, 3.0-3.9 - main stem elongation, 4.0-4.9 - tuber formation, 5.0-5.9 - inflorescence emergence, 6.0-6.9 - flowering, 7.0-7.9 - development of fruit, 8.0-8.9 - ripening of fruit and seed, 9.0-9.9 - senescence. For the purpose of this study we adapted the stages to a linearly incrementing above ground macro development: 50 % of the plants germinated (=0.1), 50 % with flowers (=0.5), 50 % of the plants with wilting symptoms (=0.75) and 50 % of the plants senescence (=1). The aboveground development was evaluated in 7 day intervals.

The belowground phenology was evaluated in 10 day intervals at one plant per genotype and replication (n=33). For each development stage, following codes were used: 50 % of the plants germinated (=0.1), 50 % of the plants at stolon initiation (=0.25), 50 % of the plants at tuber initiation (=0.5), 50 % of the plants at the tuber filling stage (=0.75) and, 50 % of the tubers were physiologically mature (=1). Physiological maturity/end of tuber bulking was defined as tuber skin is connected to tuber flesh and the skin cannot be easily removed by peeling.

The daily above and belowground development was calculated as follows:

$$\text{Daily development} = \frac{\text{difference between developement code}}{\text{days to next development stage}}$$

For example, for genotype X needed 15 days between stolon initiation (= 0.25) to tuber initiation (= 0.5). Therefore, daily development rate was calculated:

$$\frac{0.5 - 0.25}{15} = 0.016 \text{ daily development rate}$$

In both years, four irrigation treatments were implemented: fully irrigated plants (T1), early drought (T2) with withholding irrigation at 50 days after planting (DAP), intermediate drought (T3) with irrigation withheld after 75 DAP and at 80 DAP named late drought.

Table 2.2: Water supply in liter per plant (L plant^{-1}) for the fully irrigated control (T1) to individual plants. Respectively for the drought treatments T2 and T3 in % water supply per plant of fully irrigated control. Water was withheld after 50 days after planting (DAP) in the early drought (T1), at 75 DAP in the intermediate drought (T3) and at 80 DAP in the late drought treatment (T4).

	Loamy sand	**Sand**
	(L plant^{-1})	
T1	152	83
	% of control	
T2	32	45
T3	47	51
T4	59	57

In 3 to 5 day intervals, depending on irrigation schedule, soil moisture was assessed via frequency domain reflectometry (FDR, PR2 Soil Moisture Profile Probe, Delta T-Device). The profile probe measures soil moisture from 0-40 cm depth, in 10 cm increments, through glass fiber access tubes that were installed for each genotype and replication. Soil moisture was measured 3-4 hours after irrigation. The water loss in comparison to the irrigated control ranged in the early drought from 10 % after 10 days without water up to 33 % in the first season in loamy sand and 55 % in the second season on sand after 30 days without water (Figure 2.3). In the intermediate and late drought water loss was up to 20-30 % of the full irrigated control.

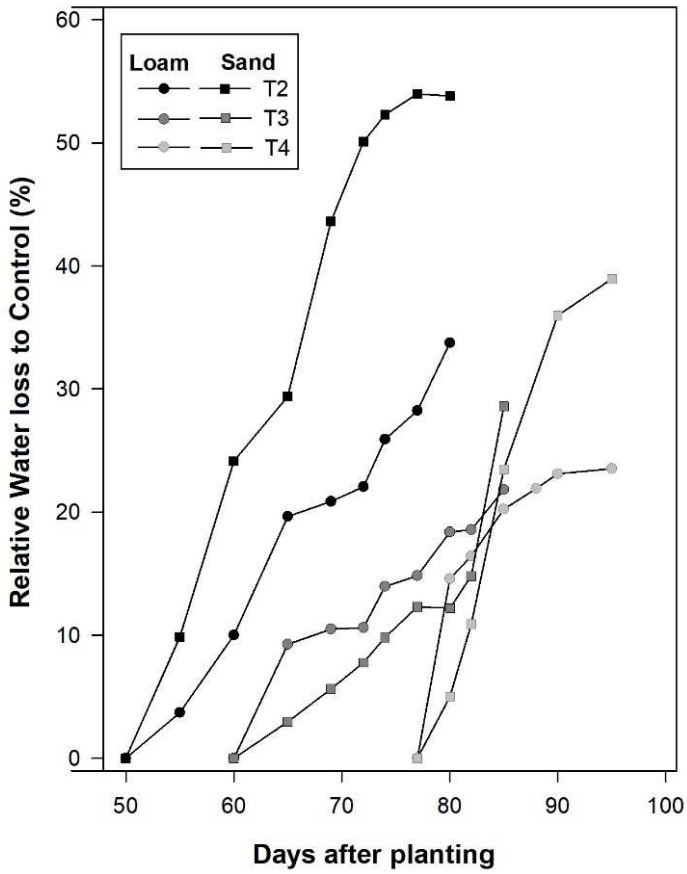


Figure 2.3: Development of soil moisture in vol. % at days after planting for the four irrigation treatments (T1-T4) in loam sand (Loam) and sandy soil (Sand). Measurements were taken in 5-day intervals per genotype, treatment, and replication. Each data point represents a mean of 15 measurements of the average soil moisture from 10-40 cm depth. Error bars have been omitted for readability.

2.2.4 Calculation of percentage of development cycle

For each genotype and replication, above and belowground were evaluated separately The total number of days to maturity was set as 100 and percentage share of each development stage was calculated relative to the total duration. The time to emergence was taken out of the total duration as it was the same for all genotypes and treatments. All graphs were created with SigmaPlot 12.5, Systat Software, Inc., Erkrath, Germany.

2.3 Results

2.3.1 Genotypic phenological responses to drought

Soil type and irrigation treatment affected the above ground and below ground phenology of the five potato genotypes included in this study, except for emergence which was affected by neither soil type nor irrigation treatment, with G5 being the slowest to emerge (19 days after planting (DAP) on average across treatments) and G4 the fastest (12 DAP on average across treatments) and stolon initiation which was equally affected by neither with G5 showing the earliest stolon initiation (5 DAP on average across treatments) and G4 being the latest (on average 12 DAP across treatments, Table 2.3, Table 2.4) Soil type strongly affected time to flowering and tuber filling, however, only in plants grown on sand significant effects of the drought treatments on the duration of tuber filling were found. Grown on sand, flowering was observed about 14 days earlier on average across genotypes and drought treatments, whereas tuber filling was delayed by 12 days on average across genotypes and drought treatments with the exception of G5 where tuber filling occurred about 4 days earlier on sand than on loamy sand. Since irrigation treatments were initiated as a function of DAP and not executed by phenological stages of the individual varieties, water deficit was introduced during earlier development stages on sand (flowering observed between 40 and 46 DAP on average across treatments) than on loamy sand (flowering between 56 and 59 DAP across treatments). Late drought treatments significantly increased the period of tuber filling in plants grown on sand but had no effect on plants grown on loamy sand.

Table 2.3: Aboveground development in potato in days after planting (DAP) in the for irrigation treatments T1–T4 and for the 5 genotypes (1-5). The first treatment (T1) represents the fully irrigated control. Water was withheld after 50 DAP in the early drought (T2), at 75 DAP in the intermediate drought (T3) and at 80 DAP in the late drought treatment (T4). L.Sand= loamy Sand, Sand = sandy soil. Model used: Phenological stage=G+T+Replication+G*T, LSD=least significant difference. Genotypes (G) 1–5, see Appendix A.1.

			Emergence (DAP)		Flowering (DAP)		Senescence (DAP)	
	T	G	L.Sand	Sand	L.Sand	Sand	L.Sand	Sand
	1	1	14 ± 1 *ab*	14 ± 1 *ab*	55 ± 3 *a*	47 ± 3 *ab*	100 ± 1 *a*	85 ± 3 *b*
	1	2	14 ± 0 *ab*	14 ± 1 *ab*	55 ± 2 *a*	58 ± 3 *a*	115 ± 4 *a*	104 ± 4 *a*
	1	3	14 ± 1 *ab*	14 ± 1 *ab*	65 ± 2 *a*	44 ± 3 *ab*	101 ± 1 *a*	87 ± 4 *a*
	1	4	13 ± 1 *b*	13 ± 1 *b*	56 ± 2 *a*	42 ± 4 *ab*	88 ± 2 *a*	108 ± 2 *a*
	1	5	19 ± 2 *a*	19 ± 1 *ab*	51 ± 2 *a*	37 ± 6 *b*	116 ± 3 *a*	109 ± 3 *a*
LSD			*5.3*	*5.8*	*14.8*	*16.9*	*33.1*	*23.4*
	2	1	16 ± 1 *ab*	16 ± 1 *ab*	64 ± 2 *a*	48 ± 1 *a*	88 ± 4 *a*	90 ± 3 *a*
	2	2	20 ± 1 *a*	20 ± 1 *a*	50 ± 2 *a*	44 ± 1 *a*	92 ± 3 *a*	86 ± 3 *a*
	2	3	15 ± 1 *ab*	15 ± 2 *ab*	54 ± 1 *a*	40 ± 1 *a*	82 ± 4 *a*	85 ± 3 *a*
	2	4	11 ± 1 *b*	11 ± 1 *b*	57 ± 2 *a*	49 ± 4 *a*	85 ± 3 *a*	78 ± 3 *b*
	2	5	15 ± 1 *ab*	15 ± 2 *ab*	54 ± 1 *a*	44 ± 2 *a*	97 ± 7 *a*	77 ± 3 *c*
LSD			*7.6*	*8.5*	*13.5*	*11.5*	*19.5*	*7.0*
	3	1	13 ± 2 *a*	14 ± 1 *ab*	53 ± 2 *a*	41 ± 1 *a*	87 ± 5 *a*	86 ± 5 *a*
	3	2	12 ± 9 *a*	19 ± 1 *a*	63 ± 1 *a*	42 ± 3 *a*	95 ± 5 *a*	86 ± 4 *a*
	3	3	16 ± 2 *a*	14 ± 1 *ab*	55 ± 2 *a*	40 ± 1 *a*	78 ± 8 *a*	79 ± 5 *a*
	3	4	12 ± 1 *a*	11 ± 1 *b*	54 ± 8 *a*	48 ± 9 *a*	86 ± 8 *a*	86 ± 4 *a*
	3	5	12 ± 2 *a*	11 ± 1 *b*	57 ± 2 *a*	43 ± 2 *a*	99 ± 6 *a*	86 ± 5 *a*
LSD			*12.0*	*6.7*	*14.8*	*13.0*	*26.9*	*12.0*
	4	1	16 ± 2 *a*	16 ± 1 *a*	53 ± 2 *b*	38 ± 2 *a*	86 ± 2 *b*	85 ± 3 *a*
	4	2	12 ± 1 *a*	12 ± 1 *a*	60 ± 3 *ab*	43 ± 3 *a*	92 ± 4 *ab*	102 ± 4 *a*
	4	3	15 ± 1 *a*	17 ± 2 *a*	59 ± 4 *ab*	43 ± 5 *a*	85 ± 2 *b*	86 ± 1 *a*
	4	4	12 ± 1 *a*	12 ± 1 *a*	60 ± 2 *ab*	47 ± 2 *a*	86 ± 3 *b*	94 ± 3 *a*
	4	5	18 ± 1 *a*	16 ± 5 *a*	61 ± 2 *a*	37 ± 2 *a*	112 ± 4 *a*	96 ± 4 *a*
LSD			*8.0*	*9.0*	*7.9*	*13.3*	*24.5*	*19.9*
Means								
	1		15 ± 2 *a*	15 ± 2 *a*	57 ± 5 *ab*	45 ± 8 *a*	104 ± # *a*	98 ± # *a*
	2		15 ± 3 *a*	15 ± 3 *a*	56 ± 5 *ab*	45 ± 4 *a*	89 ± 6 *b*	83 ± 5 *c*
	3		15 ± 2 *a*	15 ± 3 *a*	56 ± 4 *b*	42 ± 3 *a*	88 ± 8 *b*	85 ± 3 *b*
	4		113 ± 3 *a*	14 ± 2 *a*	59 ± 3 *a*	42 ± 4 *a*	92 ± # *b*	92 ± 7 *a*
LSD			*3.1*	*2.8*	*4.7*	*5.3*	*10.3*	*9.5*

In general, drought treatments did neither affect the period of tuber bulking nor the onset of senescence significantly, however, in plants grown on sand, onset of above ground senescence was hastened as compared to plants grown on loamy sand and occurred on average about 5 days earlier across treatments and genotypes with the strongest effect in G5 with an average of 18 days earlier. A similar effect was observed for the tuber bulking period for plants grown on sand, however genotypic differences in the below ground development were less pronounced.

Late drought (T4) in plants grown on sand significantly delayed physiological maturity on average by 18 days when compared to plants subjected to late drought on loamy sand and 15 days when compared to fully watered plants grown on sand, respectively. Strongest effects in this regard were observed in G1 and G4 with a delay of about 30 days each (Table 2.3, Table 2.4).

Table 2.4: Belowground development of potato in days after planting (DAP) in the for irrigation treatments T1–T4 and for the 5 genotypes (1-5). The first treatment (T1) represents the fully irrigated control. Water was withheld after 50 DAP in the early drought (T2), at 75 DAP in the intermediate drought (T3) and at 80 DAP in the late drought treatment (T4). Model used: Phenological stage=G+T+Replication+G*T, Genotypes (G) 1–5, see Appendix A1.

			Stolon initiation (DAP)				Tuber filling duration (Days)				Tuber bulking duration (Days)				Physiological maturity (DAP)			
	T	G	L.Sand		Sand		L.Sand		Sand		L.Sand		Sand		L.Sand		Sand	
	1	1	28 ± 4 *a*		26 ± 2 *a*		37 ± 2 *a*		47 ± 2 *a*		23 ± 1 *ab*		13 ± 2 *ab*		87 ± 7 *a*		85 ± 6 *b*	
	1	2	27 ± 3 *a*		26 ± 3 *a*		48 ± 3 *a*		56 ± 2 *a*		23 ± 4 *ab*		11 ± 1 *ab*		98 ± 10 *a*		94 ± 6 *ab*	
	1	3	26 ± 2 *a*		26 ± 3 *a*		36 ± 2 *a*		56 ± 1 *a*		24 ± 2 *ab*		3 ± 3 *b*		86 ± 5 *a*		85 ± 6 *b*	
	1	4	26 ± 3 *a*		25 ± 3 *a*		37 ± 3 *a*		47 ± 3 *a*		13 ± 3 *b*		13 ± 3 *ab*		76 ± 7 *a*		85 ± 6 *b*	
	1	5	27 ± 3 *a*		28 ± 3 *a*		37 ± 2 *a*		49 ± 3 *a*		40 ± 1 *a*		47 ± 3 *a*		105 ± 5 *a*		124 ± 9 *a*	
LSD			*5*		*5*		*14*		*14*		*26*		*36*		*33*		*37*	
	2	1	25 ± 1 *a*		28 ± 3 *a*		36 ± 1 *a*		47 ± 3 *a*		15 ± 4 *ab*		11 ± 1 *ab*		76 ± 5 *a*		85 ± 6 *b*	
	2	2	28 ± 3 *a*		25 ± 1 *a*		56 ± 2 *a*		47 ± 2 *a*		42 ± 3 *a*		10 ± 0 *ab*		126 ± 7 *a*		82 ± 3 *b*	
	2	3	25 ± 1 *a*		27 ± 3 *a*		57 ± 3 *a*		58 ± 3 *a*		21 ± 1 *ab*		1 ± 1 *b*		103 ± 3 *a*		87 ± 7 *b*	
	2	4	25 ± 1 *a*		28 ± 3 *a*		41 ± 2 *a*		47 ± 3 *a*		7 ± 2 *b*		12 ± 2 *ab*		73 ± 3 *a*		87 ± 8 *b*	
	2	5	27 ± 3 *a*		26 ± 2 *a*		47 ± 3 *a*		59 ± 3 *a*		12 ± 4 *ab*		43 ± 2 *a*		87 ± 8 *a*		129 ± 8 *a*	
LSD			*6*		*5*		*27*		*15*		*34*		*34*		*61*		*38*	
	3	1	23 ± 1 *a*		24 ± 1 *a*		46 ± 1 *a*		40 ± 0 *a*		14 ± 2 *ab*		10 ± 2 *a*		83 ± 2 *a*		74 ± 2 *a*	
	3	2	17 ± 9 *a*		25 ± 1 *a*		63 ± 2 *a*		40 ± 1 *a*		15 ± 1 *a*		8 ± 2 *a*		95 ± 10 *a*		74 ± 2 *a*	
	3	3	27 ± 4 *a*		24 ± 1 *a*		42 ± 3 *a*		61 ± 1 *a*		5 ± 2 *b*		10 ± 2 *a*		75 ± 6 *a*		95 ± 2 *a*	
	3	4	24 ± 1 *a*		23 ± 1 *a*		41 ± 1 *a*		42 ± 3 *a*		8 ± 4 *ab*		9 ± 4 *a*		73 ± 5 *a*		74 ± 7 *a*	
	3	5	23 ± 2 *a*		22 ± 2 *a*		44 ± 1 *a*		50 ± 0 *a*		7 ± 1 *ab*		10 ± 0 *a*		74 ± 2 *a*		82 ± 2 *a*	
LSD			*15*		*4*		*23*		*23*		*9*		*6*		*24*		*26*	
	4	1	27 ± 3 *a*		26 ± 3 *a*		46 ± 2 *b*		77 ± 2 *a*		16 ± 2 *ab*		14 ± 4 *a*		89 ± 5 *ab*		117 ± 8 *a*	
	4	2	25 ± 2 *a*		27 ± 2 *a*		38 ± 3 *b*		56 ± 1 *a*		21 ± 1 *a*		12 ± 4 *a*		85 ± 5 *b*		107 ± 16 *a*	
	4	3	28 ± 4 *a*		29 ± 4 *a*		46 ± 1 *b*		57 ± 3 *a*		12 ± 2 *ab*		14 ± 4 *a*		86 ± 6 *ab*		100 ± 8 *a*	
	4	4	25 ± 2 *a*		24 ± 1 *a*		48 ± 3 *b*		77 ± 3 *a*		13 ± 3 *ab*		12 ± 2 *a*		86 ± 7 *ab*		113 ± 5 *a*	
	4	5	25 ± 3 *a*		25 ± 5 *a*		78 ± 3 *a*		88 ± 4 *a*		7 ± 3 *b*		11 ± 1 *a*		111 ± 6 *a*		125 ± 9 *a*	
LSD			*6*		*9*		*29*		*35*		*10*		*5*		*25*		*31*	
Means	1		27 ± 1 *a*		26 ± 1 *ab*		39 ± 5 *b*		51 ± 5 *b*		25 ± 10 *a*		17 ± 17 *a*		90 ± 11 *a*		95 ± 2 *b*	
	2		26 ± 1 *ab*		27 ± 1 *ab*		47 ± 10 *ab*		51 ± 6 *b*		20 ± 14 *ab*		15 ± 16 *a*		93 ± 22 *a*		94 ± 20 *b*	
	3		23 ± 3 *b*		24 ± 1 *b*		47 ± 9 *ab*		47 ± 9 *b*		10 ± 4 *c*		9 ± 1 *a*		80 ± 9 *a*		80 ± 9 *b*	
	4		26 ± 1 *ab*		26 ± 2 *ab*		51 ± 16 *a*		71 ± # *a*		14 ± 5 *bc*		13 ± 1 *a*		91 ± 11 *a*		113 ± 9 *a*	
LSD			*3*		*3*		*10*		*11*		*9*		*10*		*15*		*16*	

2.3.2 Environmental factors shift the synchrony between below and above ground development

Due to large genotypic differences in the overall duration from planting to physiological maturity, which in turn is affected by genotype x environment interactions, comparing phenological responses based on absolute numbers of days does not allow analyzing the environmental effect on the genotypic phenology. Genotypes varying in duration can be compared regarding the effects of environmental factors on critical phenological stages across using values representing the share of the individual phenological stage in the overall duration. Figure 2.4 compares the relative shares of above and below ground development stages with in the overall duration for genotypic responses to soil type and drought. On both soils, the relative share of all above- and belowground phenological stages after withholding irrigation was influenced by drought. In general, drought increased the relative tuber filling phase and senescence while the relative time to flowering was shortened. It can be expected from the data presented in Figure 2.1 that 50% of the below ground development constitute the sink filling phase (tuber filling, bulking, maturity) which happens after sink dimensioning (tuber formation) and after full source development (flowering) which concludes 70% of the above ground development. In the current study, under full irrigation, the sink filling phase constituted 70% of belowground development which occurred after at flowering 70% of above ground development was concluded on loamy sand whereas on sand the sink filling phase accounted for 75% of belowground development and the time to flowering accounted for 65% of the above ground development. Early drought treatments shifted this relationship by reducing the remaining aboveground development after flowering to 18% and 25% of the total cycle on loamy sand and sand, respectively during which 70 % and 75% of the sink filling occurred on loamy sand and sand, respectively. The largest share of the later tuber development was attributed to tuber filling whereas the share of tuber bulking was strongly shortened under drought. The earlier irrigation was withheld, the larger was the deviation between above- and belowground phenology. Accelerated above ground development combined with slower below ground development led to a large disparity between below ground and above ground development. As a result, above ground development is no longer indicative for below ground development.

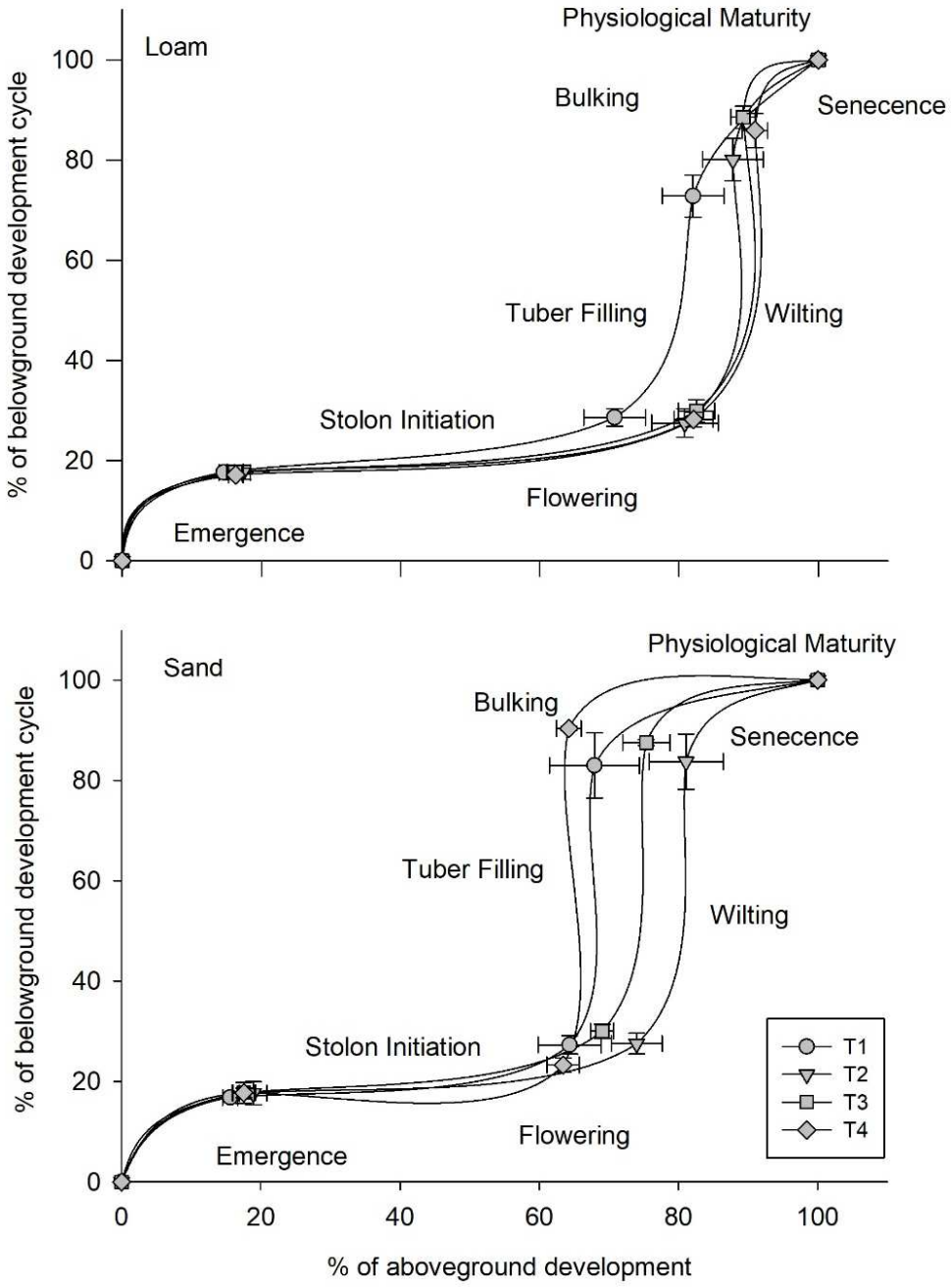


Figure 2.4: The synchrony of above- and belowground phenology in potato averaged over all 5 potato genotypes grown in loamy sand (Loam) and sandy soil (Sand). The first treatment (T1) represents the fully irrigated control. Water was withheld after 50 days after planting (DAP) in the early drought (T2), at 75 DAP in the intermediate drought (T3) and at 80 DAP in the late drought treatment (T4).

2.4 Discussion

Above and below ground phenology were adversely affected by soil type and stress intensity. In general, above ground phenology was hastened whereas below ground phenology was delayed. The earlier the drought was initiated, the longer was the tuber filling phase, while the bulking phase was shortened, leading to significant differences in stress intensity during specific growth stages for the various drought treatments on the two soil types. In addition, these effects were strongly modified by genotypic responses to these factors, increasing the disparity of treatment effects created by the different soil types on a genotypic level.

2.4.1 Phenology and environmental factors

In order to exclude confounding effects of water availability, soil type by genotype interactions are best studied under full irrigation. Genotypes varied significantly in the length of their respective phenological cycles due to late (Genotype 5) or early maturity (Genotype 1, Ranjbar, et al., 2012) and genotypes with delayed germination showed early tuberization and flowering (Wurr, Fellows, & Allen, 1992). Since in potato the desired product is not a seed but a storage organ, the relative time the plant invests in building up the storage (sink) and filling it (source) makes the differences in genotypic yields and not flowering time. To evaluate treatments effects on phenology in genotypes differing in overall duration, the duration of individual phenological stages needs to be standardized as the share in the respective overall duration, making it possible to compare soil type effects on duration among different genotypes. Both soil types, sandy loam and sand, had optimal physical growing conditions for potato. Aboveground, the date of flowering differed significantly between the two soil types in the fully irrigated control. On average in plants grown on sandy soil, genotypes flowered 10 days earlier than in plants grown on loamy sand. Belowground under full irrigation, stolon initiation, bulking duration, senescence, and day of maturity were not affected by soil type. But differences in soil type resulted in differences in the duration of tuber filling. In plants grown on sand, tuber filling duration was 12 days longer than in plants grown on sandy loam. Most studies evaluate tuber development by tuber yield, size, dry matter partitioning and starch content (Geremew et al., 2007; Khan et al., 2015; Viola, 2000) since repeated measurements of stolon and tuber development to evaluate tuber filling period are difficult to perform, as digging up and measuring the same plant several times during the growing period may negatively influence stolon and mini tubers development. In addition, several phenological stages are present simultaneously in the same plant as new tubers

develop while others approach physiological maturity (Ewing & Struik, 1992), all of which renders the exact determination of a belowground phenological stage, and thus the period of tuber filling, difficult. Since tuber initiation is independent from stolon initiation, flowering, and the duration of the whole cycle (Celis-Gamboa et al., 2003), we evaluated genotypic stolon initiation and tuber filling over the entire vegetation period.

2.4.2 Phenology and drought stress

Withholding irrigation in staggered intervals resulted in different drought severities which in turn affected genotypic phenology differently which may have partly been caused by competition for assimilates between foliage and tubers (Ivins & Bremner, 1965). In general, drought hastened above ground phenology and delayed below ground phenology, which resulted in significant genotypic differences in stress intensity during specific growth stages (Hoelle et al., 2020).

Drought shortened the duration of tuber bulking, reduced canopy growth, and induced early foliage senescence, which is in line with earlier observations by Spitters & Schapendonk (1990) who reported strongest effects on tuber yields for early drought which induced early tuber bulking while leaf area was still small. In the present study, drought advanced foliage senescence by up to 15 days, with genotypic differences most pronounced in early drought in plants grown on loamy sand and late drought in plants grown on sand.

Drought significantly affected belowground development, particularly late drought prolonged the duration of tuber filling. Earlier studies related canopy size at tuber initiation with tuber growth and foliage senescence (Ivins & Bremner, 1965; Slater, 1963), however, in the experiment reported here irrigation was withheld when the canopy was already fully developed and potential tubers already initiated. The extended duration of tuber filling effectively decoupled belowground development rates from aboveground development rates. Thus, drought broke the synchrony between above and belowground phenology by prolonging the duration of tuber filling while shortening the time to flowering and senescence. Smaller amounts of plant available water and thus a faster drying of the soil for plants grown on sand, shifted the severeness of the drought into earlier phenological stages with an even stronger effect on the synchrony. This way, the tubers developed into a more severe water deficit than the aboveground biomass, indicating a shift in source – sink relationship in favor of storage organ formation. In contrast, under fully irrigated conditions,

development rates of above and belowground biomass showed no shift in partitioning preferences.

Many agronomic studies use the aboveground phenology as a proxy for the belowground development, although, even under optimal growing conditions, there is no physiological link between flowering and tuber development, as some genotypes do not flower per se or abort buds (Jefferies & Lawson, 1991). The observed, drought-induced shift in phenological synchrony in favor of faster aboveground development clearly supports the findings of Celis-Gamboa et al. (2003) and indicates that the system of linear development from Meier (2001) cannot be applied to potato grown under water deficit conditions. However, the interaction between drought, phenological stages and tuber yield still need more systematic research as we could not confirm the findings of van Loon (1981) that the tuber bulking period is the most drought sensitive stage with regard to final tuber yield.

2.5 Conclusion

Above and below ground phenology were adversely affected by environmental factors, such soil type and water deficit. In general, above ground phenology was hastened whereas below ground phenology was delayed, leading to significant differences in stress intensity during specific growth stages for the various drought treatments on the two soil types. In addition, these effects were strongly modified by genotypic responses to these factors, increasing the disparity of treatment effects created by the different soil types on a genotypic level. We concluded that under terminal drought conditions above and belowground development need to be evaluated separately and cannot follow the standard evaluation system that uses aboveground phenology as a proxy for tuber formation belowground development rates.

Author Contributions: Conceptualization, J. H. and F. A.; methodology, J. H. and F.A.; formal analysis, J. H.; investigation, J. H., L. K. and J. Z.; resources, CIP, D; data curation, J. H.; writing—original draft preparation, J. H and F.A..; writing— review and editing, J. H. and F.A.; visualization, J. H. and F. A.; supervision, F. A.; project administration, J. H.; funding acquisition, M. B. and Team.

All authors have read and agreed to the published version of the manuscript.

Funding: Financial support by the German Ministry for Collaboration and Development (GIZ No. 11.7860.9-001.00)

Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: The authors thanks INIA-Arequipa for providing facilities. We are grateful to Jesus Zumaran and Leah Kuppinger for their support during the field trials. Competent technical assistance by Jorge Vega, Anthony Quello, Elisabeth Torreblanca and Trinidad Unda is gratefully acknowledged.

3 Phenology-adjusted stress severity index to assess genotypic responses to terminal drought in field grown potato

This chapter is published as:

Hoelle, J., Asch, F., Khan, A., Bonierbale, M. 2020. Phenology-Adjusted Stress Severity Index to Assess Genotypic Responses to Terminal Drought in Field Grown Potato. *Agronomy* 10(9):1-17. https://doi.org/10.3390/agronomy10091298.

Keywords: development stage, drought index, *Solanum tuberosum* L., water deficit, Van Genuchten

Abstract: Potato is a drought susceptible, often rain-fed crop suffering strongly from even short periods of soil water deficit. With global environmental conditions changing, potato clones resistant to variable water supply are needed and identifying them a major task. Many indices assessing potato tolerance to water deficit have been proposed, albeit none of them takes into account the severity of the stress or the sensitivity of the developmental stage during which the stress occurs. As a result, data obtained on genotypes in one location or season are normally not useful in another location or in a different season. We have developed an index evaluating yield responses of potato to water deficit based on the soil tension the genotype was subjected to for the duration of the stress modified by the development stage of the genotype. The sum of the daily values was combined in a stress severity index (SSI). In total thirteen genotypes differing in duration and sensitivity to drought were subjected to four levels of deficit irrigation on two soil types at different development stages over two years. Early drought (early tuber filling) reduced yields up to 95% whereas late drought (late tuber bulking) reduced yields significantly less. SSI depended on the genotypic phenological development and on the soil tension values and ranges between 25 and 3500. The index differentiated genotypic responses well across treatments and soil types, even with these relatively advanced development stages, up to a value of 1000. Beyond 1000, yields were generally reduced by more than 60% and a differentiation between genotypes was not possible anymore. SSI constitutes a method that renders site, location, year, season, and soil

type effects comparable for responses of potato clones to soil water deficit. Combining this measure of stress severity with other proposed indices may improve upon their current weaknesses in finding or identifying the underlying traits drought tolerance in potato.

3.1 Introduction

Potato (*Solanum tuberosum* L.) is the most important vegetable staple crop worldwide and is grown in more than 100 countries (Levy & Veilleux, 2007). Potato varieties maturing between 120 and 150 days require between 500 – 700 mm water on average (FAO, 2015). Potato is a drought sensitive crop, commonly grown on light sandy soils, with 65-80% of its root mass concentrated in the upper 0.4 m of the soil (Stalham & Allen, 2001). Even short drought spells or infrequent irrigation during stolon formation, tuber initiation, or tuber bulking can reduce tuber yields significantly (Dalla et al., 1997; Obidiegwu et al., 2015; Onder et al., 2005; Ramírez et al., 2016; Saravia et al., 2016; Schafleitner et al., 2007). Efforts are being made to (1) decrease potatoes water requirements to reduce irrigation water requirements in systems with seasonal water shortages (Carli et al., 2014; Reddy et al., 2016), and (2) to increase genotypic resistance to soil moisture deficit in predominantly rainfed systems with little or no irrigation facilities (Rauf et al., 2016). A number of morphological traits have been described that potentially improve genotypic performance of potato under moisture deficit conditions. Genotypes with deeper and larger roots systems maintain better access to soil stored moisture (Lahlou & Ledent, 2005; Puértolas et al., 2014). Varieties forming a smaller number of tubers perform better than those forming many (MacKerron & Jefferies, 1986). Reduction of leaf growth and area reduces transpirational water loss (Tourneux et al., 2003; Vos & Haverkort, 2007), changes in canopy architecture influence the canopy microclimate (Schittenhelm et al., 2006), or stay green traits improve the water use efficiency (Cabello et al., 2013). These morphological traits develop during different phenological stages and whereas some are generally phenotypically expressed, others are triggered only under water deficit conditions, which may not concur with the appropriate phenological stages of the genotype. In addition, genotypes may perceive the same level of soil moisture deficit differently, depending on their level of resistance to soil moisture deficit and on the phenological stage they are in when the water deficit occurs. The phenological

cycles vary from 80 to 150 days for early, intermediate, and late maturing potato genotypes (Rodríguez et al., 2016; Wang et al., 2011). In a large set of genotypes sown at the same date, various phenological stages occur simultaneously. During a drought spell, therefore, different varieties will be subjected to soil moisture deficit in different phenological stages, resulting in genotypic responses that depend on the sensitivity of the respective phenological stage and the overall resistance strategy expressed in the respective genotype. Thus, in order to evaluate the performance of individual genotypes the severity of the stress needs to be expressed as a function of plant available soil moisture and the sensitivity of the respective phenological stage.

The irrigation amount or soil moisture measurements alone are not sufficient to describe the severity of the stress at plant level, as plant available water content varies among soil types. Several authors have shown that soil matrix potential rather than soil moisture content affects plant physiological responses to soil moisture deficit, for example in oil seed rape (Jensen et al., 1996), wheat (Ali et al., 1999), maize (Rivera-Hernández et al., 2009) and potato (Lahlou & Ledent, 2005; MacKerron & Jefferies, 1986). Mould and Rutherfoord (1980)) observed negative effects on potato quality and yield beyond a threshold in soil matrix potential of 700 hPa. Since roots take up water and the aboveground biomass loses water through transpiration, evolution of soil matrix potential during a drought spell is not only determined by the soil type but also by the water use of the crop, which in turn depends on the prevailing climatic conditions and on the adaptation mechanisms of the genotype (Asch et al., 2009). Adaptation mechanisms, such as leaf area reduction or increased rooting depth are triggered by the stress itself, thus, the potential of maintaining a marketable yield under suboptimal conditions depends on the effectiveness of resistance mechanisms of a genotype in a specific stress situation during specific development stage. Therefore, the comparative evaluation of genotypic performance needs to be based on a comparable stress severity indicator considering not only the abiotic stressor but also the biotic response to it.

Many studies on drought tolerance of potato report on performance of individual cultivars under a given set of environmental parameters (e.g. Haverkort et al., 1990; Saravia et al., 2016; Stark et al., 2013) without quantifying soil borne stress severity or the phenological

stage during which the stress occurs. This renders comparisons of genotypic responses to water deficit across sites or years almost impossible. We propose a stress severity index (SSI) that takes into account the changes in the soil matrix potential during water deficit, the sensitivity of the respective phenological stage, and the duration of the stress, allowing assessing genotypic performance over a range of climatic conditions, soil types, and water deficit intensities.

3.2 Materials and Methods

3.2.1 Site description

Field trials were conducted over two years at an experimental station of the "Instituto Nacional de Innovacion Agraria" in St. Rita de Siguas (16°28'35"S; 72°6'18"W), Peru, from July to November 2013 and from August to December 2014.

The environmental conditions at the experimental site are characterized as arid climate with little inter-annual variation. Air temperature, air humidity, wind speed, and photosynthetically active radiation at 2 m height were recorded in 15 min intervals with a HOBO® Weather station close to the experimental plots (Table 1). No rainfall occurred during the field trials. Two neighboring fields differing in soil texture were selected. Soil samples were taken with a cylindrical auger (Delta T-Device) as bulk samples from 0-15 cm and 15-30 cm along a diagonal transect with five replications for each field and depth before planting. Soil samples were analyzed at the soil laboratory at the Universidad Agraria La Molina, Lima, Peru. Soil texture, pH, and organic matter content are given in Table 2. For the full soil analyses, including electrical conductivity, nutrients and exchangeable cations, refer to appendix A.1. The soil type was defined according to IUSS Working Group (WRB 2006) as Arenosol.

Table 3.1: Weather conditions during the experimental periods in 2013 and 2014 in St. Rita de Siguas, Arequipa, Peru. Data are shown as monthly averages of daily mean values. VPD = vapor pressure deficit, PPFD = photosynthetic photon flux density, SD = standard deviation.

Month/Year	Mean air temperatur	Mean relative air	Mean VPD	Mean daily PPFD	Mean wind speed
	(°C) ± SD	(%)± SD	(kPa) ± SD	(mol m^{-2} s^{-1}) ± SD	(m s^{-1}) ± SD
Jul '13	17 ± 2	38 ± 9.9	1.4 ± 0.3	833 ± 109	0.88 ± 0.3
Aug '13	15.7 ± 2	39 ± 15	1.3 ± 0.4	1005 ± 128	0.75 ± 0.1
Sep '13	17.3 ± 1	46 ± 9.4	1.2 ± 0.3	1189 ± 40	0.81 ± 0.2
Oct '13	17.9 ± 1	40 ± 7.8	1.4 ± 0.2	1203 ± 115	0.74 ± 0.1
Nov '13	17.4 ± 2	48 ± 14	1.2 ± 0.4	1233 ± 59	1.03 ± 0.3
Aug '14	18.4 ± 2	31 ± 11	1.6 ± 0.4	1058 ± 73	1.17 ± 0.2
Sep '14	18 ± 2	43 ± 13	1.3 ± 0.4	1168 ± 83	1.23 ± 0.2
Oct '14	19 ± 2	40 ± 11	1.5 ± 0.4	1275 ± 237	1.55 ± 0.3
Nov '14	17.9 ± 2	54 ± 14	1.1 ± 0.4	1309 ± 96	1.34 ± 0.3
Dec '14	18.9 ± 1	53 ± 13	1.2 ± 0.3	1333 ± 60	1.23 ± 0.1

Table 3.2: Soil analyses and water relations for the two experimental fields. Sand = sandy soil; Loam = loamy sand; OM = organic matter; BD = bulk density; FC = field capacity (pF 1.8); PW = permanent wilting point (pF 4.2); PASM = plant available soil moisture.

			Soil texture				BD	Soil water		
Soil type	Depth (cm)	pH	Sand (%)	Clay (%)	Silt (%)	OM (%)	g cm^{-3}	FC (Vol%	PW (Vol%	PASW (mm)
Loam	0-15	8.1 ± 0.18	80.8 ± 1.79	11.2 ± 1.79	8.0 ± 1.41	1.5 ± 0.49	1.18	23.2	8.5	58.8
	15-30	7.9 ± 0.19	81.6 ± 1.67	10.0 ± 1.41	8.4 ± 1.67	1.0 ± 0.25				
Sand	0-15	7.4 ± 0.24	94.0 ± 3.46	4.4 ± 0.89	0.4 ± 0.89	0.9 ± 0.18	1.15	20.8	5.0	63.2
	15-30	7.5 ± 0.41	96.0 ± 1.41	4.0 ± 1.41	0.0 ± 0.00	0.7 ± 0.13				

3.2.2 Genotypes, experimental setup, and crop management

Thirteen genotypes from the International Potato Center (CIP) breeding program were planted on 17.07.2013 and 13.08.2014 for the first and second year, respectively. For reasons of simplicity, genotypes are named G1-G13 in the text. A list of all genotypes and CIP identification codes is given in appendix A.2. Before planting, seed tubers were disinfected with Homai (BASF) and afterwards with Decis (Bayer) against potato beetle (*Leptinotarsa decemlineata*).

The experiments were laid out in a strip plot design with three replications. The size of the experimental subplots was 8.1 m^2 (3 m x 2.7 m). Plants were arranged in three rows of 11 plants each with 0.9 m between and 0.3 m within the rows for all genotypes. Observations, measurements, and samplings were conducted in the middle row and the neighboring rows served as border plants. Before planting, 1000 $kgha^{-1}$ Guano was applied into the furrows and pre-sprouted seed tubers were placed by hand with the spouts upside. Mineral fertilizer mixture of 160 $kgha^{-1}$ potassium sulfate (50 % K_2O, 18 % S, INTI), 80 $kgha^{-1}$ stabilized ammonium nitrate (33% N – 3% P_2O_5 – 0% K_2O, MISTI S.A.) and 250 $kgha^{-1}$ Fertiphos®-Plus (20 % P_2O_5; 36 % CaO; 6 % S, 17 % SiO_2; 1.08 % Fe_2O_3; 0.9 % MgO; Micronutrients Zn, Mn, Cu, B) was placed manually between the seed tubers. A second nitrogen dose was top-dressed manually as ammonium nitrate (120 $kgha^{-1}$) during hilling. Fungicides and insecticides were applied in approximately 20-day intervals according to the instructions of the suppliers. Following products were used: Sorba 50 EC (Syngenta), Ultra Pegasol (Farmagro S.A), Rover (Sipcam Pacific), Pentacloro Farmex, Cipermex (Farmex), Confidor 350 SC Fitoraz (Bayer), Evisect 50 SP (Arysta). Insecticides with changing functional groups were applied to avoid build-up of resistances in the field. Manual weeding was done in 14-day intervals.

3.2.3 Irrigation treatments and soil moisture measurements

Irrigation of the experimental plots was established via drip irrigation with 0.3 m distance between individual drips and one dripline per row until hilling and two driplines per row thereafter. The full irrigation treatments were targeted to 85 % field capacity of the respective fields (T1). Irrigation was withheld at 50 days after planting (DAP) for T2, at 65 DAP for T3, and at 80 DAP for T4. The total amount of irrigation for each treatment is given in Table 3.3.

Table 3.3: Water supply for irrigation treatments 1-4 (T1-T4) to individual plants during the experimental period in liter per plant (L plant^{-1}).

	Loam	Sand
	(L plant^{-1})	
T1	152	83
T2	48	37
T3	71	42
T4	89	47

Soil moisture was measured in the plots planted with G1-G5 for each treatment and replication in 3 to 5 day intervals via frequency domain reflectometry (FDR, PR2 Soil Moisture Profile Probe, Delta T-Device). The four sensors of the profile probe measure in 10 cm increments in 0-40 cm depth via access tubes made of fiberglass. For each value, three measurements were taken with the probe rotated by approximately 120 degrees for each measurement to account for suboptimal soil contact of the access tube and the gap in the sensor ring. The upper 10 cm were excluded in further presentation, as the soil dried down very fast in this horizon and the FDR probe did not measure adequately at soil moisture content under 5 vol. %. Soil moisture dynamics under the different irrigation treatments and soil types are shown for the experimental period in Figure 3.1.

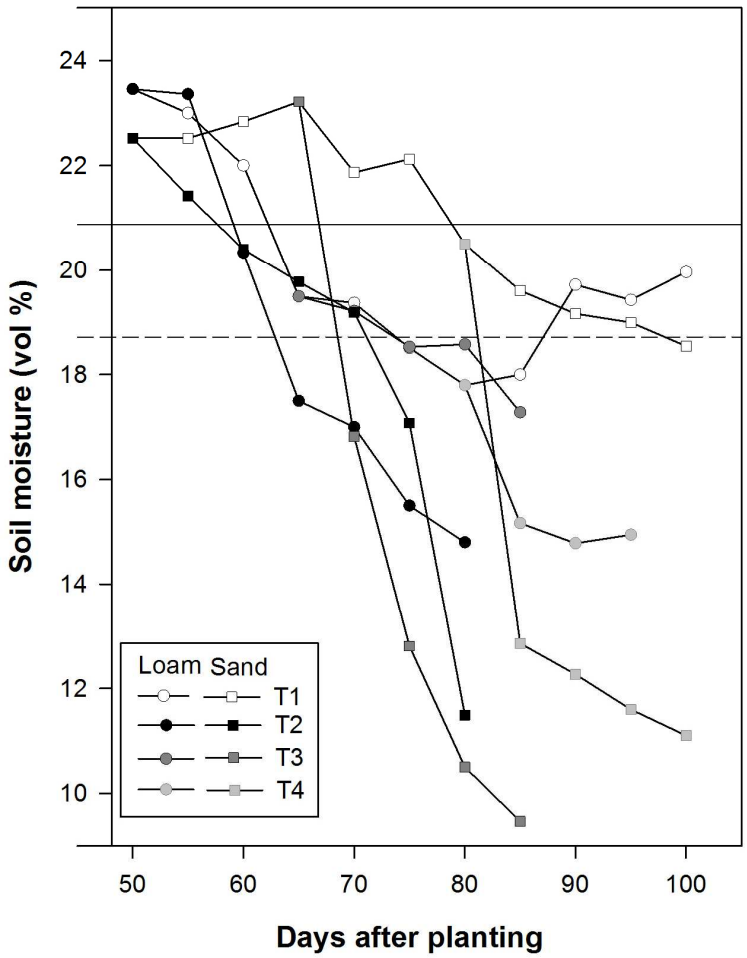


Figure 3.1: Evolution of mean soil moisture by treatment in volume percentage for the four irrigation treatments (T1-T4) in loamy sand (Loam) and sandy soil (Sand). Measurements were taken in 5-day intervals per genotype (G1-G5, appendix A.2), treatment, and replication. Each data point represents a mean of 15 measurements of the average soil moisture from 10-40cm depth. Error bars have been omitted for readability. Solid horizontal line = irrigation target loam, broken horizontal line = irrigation target sand.

3.2.4 Samplings, yield and yield components

One randomly selected plant per genotype, replication, and treatment was sampled destructively at 10, 20, and 30 days after withholding water. Care was taken that each sampled plant was in the center of eight neighboring plants to avoid border effects. Roots and tubers were carefully excavated, adhering soil removed, average root length was measured, and tubers were counted. Leaves, stems, and roots were separated and dried in paper bags for 3 days at 80 °C until constant weight. Dry matter and fresh tuber weight

were determined with a fine balance (KERN und Sohn, Type 440). Differences in tuber yield relative to the fully watered treatment (ΔTY; %) were calculated as:

$$\Delta TY\ (\%)\ = 100 - \left(\frac{TY_{TD} * 100}{TY_{FI}}\right) \qquad (1)$$

with TYTD and TYFI, for fresh tuber yield in grams per plant under water deficit and fully irrigated control.

Leaf area index (LAI, $m^2\ m^{-2}$) was measured non-destructively before each destructive sampling with AccuPAR LP-80 (Decagon Device, Inc.). The external PAR sensor to measure incoming radiation was installed at 2 m height on a portable rack.

3.2.5 Phenology and development stage specific sensitivity to moisture deficit stress

Belowground phenology was evaluated non-destructively in 10-day intervals from planting to physiological maturity from one plant per genotype and replication (n=3) in five genotypes (G1-G5, appendix A.2).

In order to be able to compare genotypic responses across development stages, genotypic development was standardized to range between 0 (planting) and 1 (physiological maturity). Based on the scales for development proposed by Doorenbos & Kassam (1979) and Obidiegwu et al. (2015), cardinal points in genotypic development were set as: 50 % of the plants germinated = 0.1, 50 % of the plants at stolon initiation = 0.2, 50 % of the plants at tuber initiation = 0.4, 50 % of the plants at the tuber filling stage = 0.65, and 50 % of the tubers were physiologically mature = 1. Physiological maturity/end of tuber bulking was defined as tuber skin connected to tuber flesh and not removable by peeling. The below ground development rate was calculated as the difference between two standardized development stages divided by the number of days required to reach from one stage to the next.

A sensitivity score for the different development stages was developed based on results on yield and growth responses in potato under drought published earlier by Doorenbos & Kassam (1979), van Loon (1981) and other (MacKerron & Jefferies, 1986; Muthoni & Kabira, 2016; Obidiegwu et al., 2015; Spitters & Schapendonk, 1990). The sensitivity score ranges from 1 (not sensitive) to 9 (highly sensitive), reciprocally corresponding to the drought

response score developed by Boguszewska-Mańkowska et al. (2020), with tuber initiation and tuber filling being the most sensitive development stages (Figure 3.2).

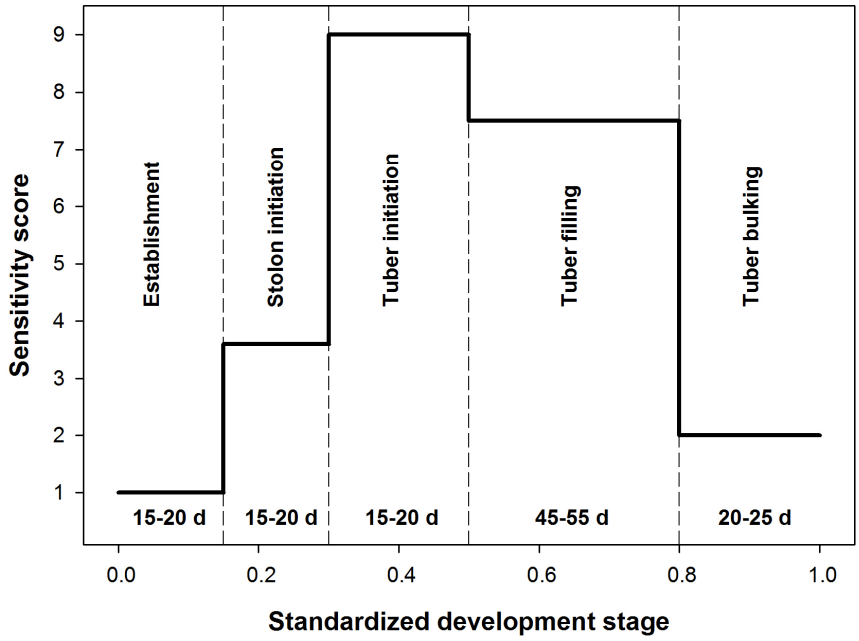


Figure 3.2: Literature based sensitivity score for standardized development stages (0 = planting; 1 = physiological maturity) of potato. Development stages and durations adapted from Doorenbos and Kassam (1979) and Obidiegwu et al. (2015).

3.2.6 Soil water and Stress Severity Index

Soil water retention curves with corresponding field capacity and plant available water were modelled with the van-Genuchten-Mualem function. The parameters for the van-Genuchten-Mualem function were estimated with "RosettaLite" in HYDRUS-1D (Simunek et al., 2008). The soil texture and soil density used in "RosettaLite" is given in appendix A.1. With the van-Genuchten-Mualem function, field capacity and permanent wilting point were calculated at 23.2 % and 8.5 % for the loamy sand and 20.8 and 5 % for the sandy soil, respectively (Table 3.2).

Irrigation was targeted to 0.85 * field capacity, however, since irrigation was based on time and not volume, variability in the drip points resulted in a varying moisture level for irrigated plots for both soils (Figure 3.1). Withholding irrigation resulted in all treatments in rapid soil drying and, depending on the treatment and the soil type, resulted in a loss of plant available water of 30 to 80 %, thus, creating relatively severe stress levels for the plants. Taking into

account the varying sensitivity to water deficit of the different development stages (Figure 3.2) a stress severity index was calculated.

The stress severity index (SSI) comprises of the soil water tension experienced by the plant weighted by the relative genotypic sensitivity of the respective phenological stage (Figure 3.2), cumulated for the duration of the water deficit treatment.

3.2.7 Data analysis

Statistical analysis was performed with R Statistical Program (R Foundation for Statistical Computing, Vienna, Austria, 2008). All data were tested for normal distribution and homogeneity of variances using the Bartlett's test and outliers were removed. We used an ANOVA-pairwise comparison with Bonferroni adjustment for completely randomized block design. All statistical analyses used a nominal alpha of $p < 0.05$. Graphs and regressions were generated with SigmaPlot 12.5, Systat Software, Inc., Erkrath, Germany.

3.3 Results

3.3.1 Genotypic performance under water deficit

Table 3.4 shows the agronomic and morphological results exemplary for five potato clones subjected to four irrigation treatments on two contrasting soil types. Under fully irrigated conditions tuber yields ranged on loam and sand between 1080 g pl^{-1} and 622 g pl^{-1} and 1282 g pl^{-1} and 472 g pl^{-1}, respectively. Withholding irrigation significantly reduced tuber yields across genotypes by 77 %, 50 %, and 22 % for early, medium, and late drought treatments, respectively, on loam and 86 %, 85 %, and 62 %, respectively, for the same treatments on sand. Aboveground biomass, mean root length and leaf area index (LAI) were strongly negatively affected by withholding irrigation and in all instances the effects were most severe under early drought and more pronounced in sand than in loam. Whereas tuber number was also reduced by about 50 % under early drought on both soil types the stronger

yield losses on sand were mainly due to a reduced tuber size, whereas, on average under drought, tuber number was less affected. Mean tuber size in sand under the drought treatments was only about 50 % of that in loam. Genotypes responded differently to both soil type and drought treatments. Whereas genotype 1 and 2 yielded above average in in loam, genotype 3 and 4 out yielded the others in sand under full irrigation. Early drought reduced yields in loam by about 72 % - 78 % except for genotype 5 with 92 % and in sand by 79 % -

85 % except for genotype 5 and 4 with 91 % and 94 %, respectively. Withholding irrigation later resulted in better genotypic performance, however, genotype 5 always performed worse than the other four, particularly in sand (Table 3.4).

Table 3.4: Tuber yield, number of tubers per plant, above ground biomass, mean rooting depth, and maximum leaf area index for five genotypes subjected to four irrigation treatments on two contrasting soil types. Treatment 1 (T1) to Treatment 4 (T4) see Table 3, Genotype 1-5.

		Max. tuber yield				Tuber number				Above ground biomass				Mean root length				Max. leaf area index			
G	T	L.Sand		Sand		L.Sand		Sand		L.Sand		Sand		L.Sand		Sand		L.Sand		Sand	
		g pl^{-1}	SE	g pl^{-1}	SE		SE		SE	g pl^{-1}	SE	g pl^{-1}	SE	cm	SE	cm	SE	m^2 m^{-2}	SE	m^2 m^{-2}	SE
1	1	1080 ±	62	736 ±	56	14 ±	0.5	15 ±	1.9	35 ±	0.7	29 ±	0.8	20 ±	2.0	13 ±	1.4	3.0 ±	0.1	2.1 ±	0.2
2	1	1024 ±	75	689 ±	31	27 ±	0.7	22 ±	2.1	77 ±	1.0	64 ±	2.0	19 ±	0.6	16 ±	0.2	4.0 ±	0.2	3.3 ±	0.2
3	1	901 ±	40	683 ±	33	13 ±	1.1	18 ±	1.5	74 ±	5.0	25 ±	0.0	21 ±	0.2	11 ±	0.2	3.5 ±	0.1	2.2 ±	0.0
4	1	876 ±	29	1124 ±	51	23 ±	0.5	20 ±	0.7	47 ±	2.0	53 ±	2.0	17 ±	0.5	14 ±	0.9	3.7 ±	0.3	2.5 ±	0.2
5	1	622 ±	79	472 ±	28	23 ±	0.5	22 ±	1.4	83 ±	4.0	101 ±	4.0	21 ±	0.2	22 ±	3.0	3.5 ±	0.3	3.0 ±	0.2
1	2	287 ±	20	192 ±	36	15 ±	1.4	10 ±	2.3	10 ±	0.3	24 ±	1.8	10 ±	0.7	6 ±	0.0	2.3 ±	0.1	2.1 ±	0.1
2	2	216 ±	23	150 ±	21	8 ±	0.9	21 ±	2.6	19 ±	3.0	19 ±	1.0	11 ±	0.7	15 ±	0.7	2.4 ±	0.3	1.5 ±	0.1
3	2	256 ±	35	185 ±	14	10 ±	0.0	12 ±	2.5	26 ±	2.0	12 ±	0.0	14 ±	0.7	6 ±	0.2	2.2 ±	0.1	1.4 ±	0.2
4	2	240 ±	12	70 ±	8	10 ±	0.9	5 ±	1.2	13 ±	2.0	16 ±	1.0	13 ±	0.7	9 ±	1.0	3.2 ±	0.3	2.1 ±	0.1
5	2	53 ±	11	44 ±	1	7 ±	0.5	2 ±	0.5	33 ±	1.0	19 ±	2.0	16 ±	0.8	13 ±	1.4	2.2 ±	0.2	1.7 ±	0.2
1	3	535 ±	47	222 ±	7	7 ±	1.2	4 ±	0.2	41 ±	0.2	15 ±	1.7	13 ±	1.2	2 ±	0.2	1.3 ±	0.1	0.6 ±	0.1
2	3	538 ±	3	101 ±	16	17 ±	0.7	15 ±	1.7	24 ±	4.0	20 ±	1.0	13 ±	0.5	8 ±	1.7	2.4 ±	0.3	1.4 ±	0.3
3	3	716 ±	77	359 ±	28	12 ±	1.9	15 ±	0.7	44 ±	2.0	18 ±	4.0	16 ±	2.2	2 ±	0.2	2.1 ±	0.1	1.6 ±	0.1
4	3	347 ±	24	138 ±	4	16 ±	1.2	7 ±	2.0	21 ±	2.0	11 ±	2.0	17 ±	0.3	2 ±	0.7	2.1 ±	0.3	0.7 ±	0.1
5	3	156 ±	14	33 ±	5	23 ±	1.6	6 ±	0.5	12 ±	0.0	17 ±	4.0	11 ±	1.2	11 ±	2.3	2.6 ±	0.0	1.4 ±	0.2
1	4	855 ±	31	504 ±	33	5 ±	0.8	8 ±	1.4	27 ±	1.9	18 ±	0.7	7 ±	0.5	5 ±	1.2	1.4 ±	0.1	0.8 ±	0.2
2	4	768 ±	15	366 ±	21	21 ±	0.7	24 ±	1.2	46 ±	1.0	32 ±	7.0	16 ±	1.2	13 ±	0.7	2.4 ±	0.4	1.6 ±	0.1
3	4	774 ±	5	295 ±	30	8 ±	2.1	8 ±	1.9	24 ±	1.0	13 ±	2.0	12 ±	0.7	4 ±	1.2	1.6 ±	0.1	0.5 ±	0.2
4	4	689 ±	37	415 ±	8	13 ±	1.2	12 ±	0.5	23 ±	2.0	14 ±	2.0	15 ±	1.4	12 ±	1.6	1.9 ±	0.1	1.2 ±	0.2
5	4	416 ±	55	53 ±	3	22 ±	1.7	4 ±	0.7	56 ±	1.0	11 ±	2.0	13 ±	1.2	14 ±	1.2	2.6 ±	0.2	1.1 ±	0.3
Means																					
	1	901 ±	57 *a*	741 ±	40 *a*	20 ±	0.7 *a*	19 ±	1.5 *a*	63 ±	2.5 *a*	54 ±	1.8 *a*	20 ±	0.7 *a*	15 ±	1.1 *a*	3.5 ±	0.2 *a*	2.6 ±	0.2 *a*
	2	210 ±	20 *d*	128 ±	16 *c*	10 ±	0.7 *c*	10 ±	1.8 *b*	20 ±	1.7 *c*	18 ±	1.2 *b*	13 ±	0.7 *bc*	10 ±	0.7 *b*	2.5 ±	0.2 *b*	1.8 ±	0.2 *b*
	3	458 ±	33 *c*	171 ±	12 *bc*	15 ±	1.3 *b*	9 ±	1.0 *b*	28 ±	1.6 *b*	16 ±	2.5 *b*	14 ±	1.1 *c*	5 ±	1.0 *c*	2.1 ±	0.2 *b*	1.1 ±	0.2 *c*
	4	700 ±	29 *b*	327 ±	19 *b*	14 ±	1.3 *bc*	11 ±	1.1 *b*	35 ±	1.4 *b*	18 ±	2.7 *b*	13 ±	1.0 *b*	10 ±	1.2 *a*	2.0 ±	0.2 *b*	1.0 ±	0.2 *c*
LSD		*176*		*161*		*3.5*		*4.2*		*2.5*		*2.1*		*0.8*		*0.8*		*0.50*		*0.47*	

3.3.2 Plant available soil moisture and tuber yield

Figure 3.3 shows the effects of reduced plant available soil moisture (PASM) on tuber yield of all genotypes under the four applied irrigation treatments. Of the thirteen genotypes used in this study, five were tested on both soil types whereas eight were only grown in sand. Thus, the stress severity index (SSI) was developed on the results of five genotypes and then applied to all. The first step in the development of the SSI was to relate the tuber yield to the stress. The stress is here defined as the reduction in available soil moisture and its effect on tuber yield. No clear pattern or relationship was found between the two parameters (Figure 3.3). There seems to be a slight tendency of tuber yield decreasing with decreasing PASM but the correlation is not significant.

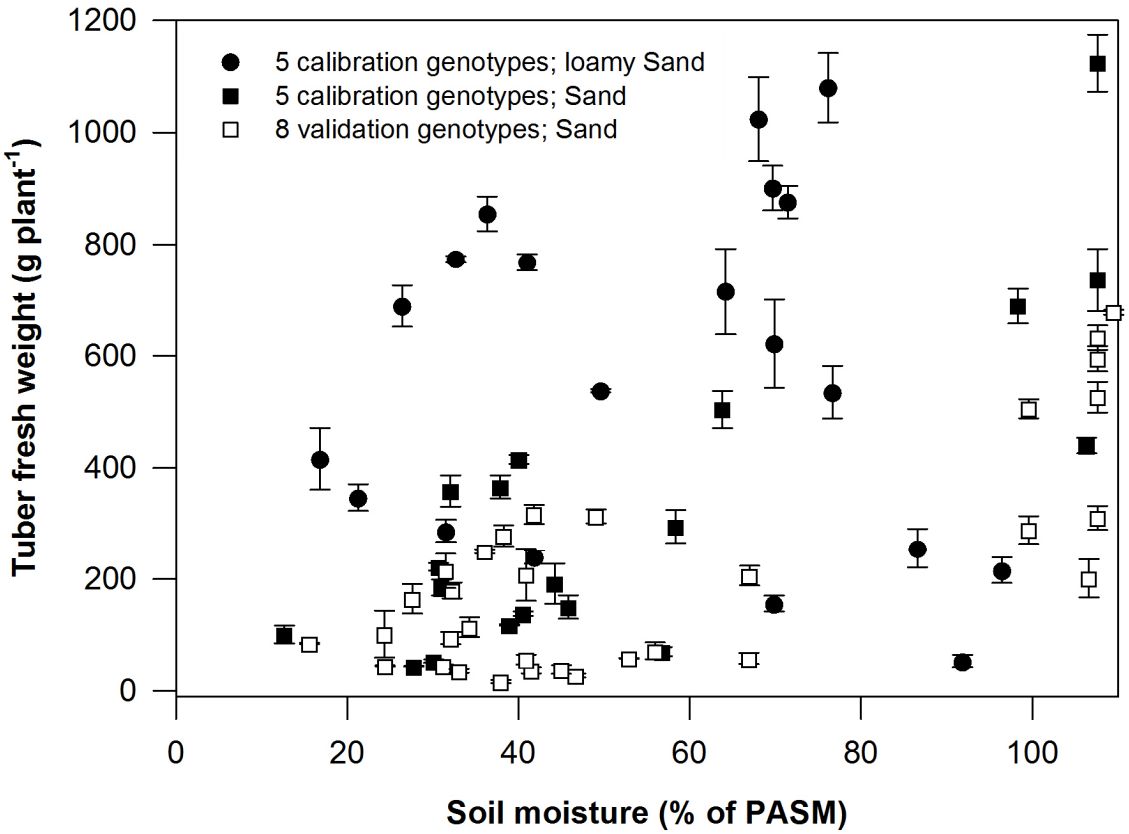


Figure 3.3: Effects of reduced plant available soil moisture (PASM) on tuber yield of all genotypes under the four applied irrigation treatments for both soil types. Calibration genotypes were employed to develop the stress severity index; validation genotypes were used to apply and analyze the stress severity index. Percent of PASM values above 100 indicate irrigation over the irrigation target due to variations in the drip system.

3.3.3 Soil moisture deficit and below-ground development

The increasing deficit in plant available soil moisture after withholding irrigation strongly slowed plant belowground development in the early and medium drought treatments. Because of this, some sensitive development stages (Figure 3.4) were subjected to lower available soil moisture in the early treatments as compared to later treatments. Particularly in sand, soil moisture deficit developed faster and affected sensitive development stages even more severely (Figure 3.4).

3.3.4 Below ground development and tuber fresh weight

Belowground development marks the initiation, filling, and bulking of tubers (Figure 3.2). Water deficit treatments in combination with soil type resulted in genotypic specific changes in phenology and tuber formation (Figure 3.5). Tuber weights in the fully irrigated control increased constantly until maximum yield. In all other treatments, tuber weight development was reduced as compared to the control and final tuber weight was reached earlier with the effect being directly related to the severity of the water deficit in both soils. Initiating soil water deficit early resulted in stagnation of already reached tuber weights (T2) or in an immediate reduction of tuber weights (T3). Initiating the water deficit in the bulking stage (T4) led to a strong reduction in final tuber yield and abortion of already formed tubers. In general, stress effects on tuber weight development were more severe in sand than in loam. In all treatments and for all genotypes, tubers that were not aborted reached physiological maturity, albeit strongly influenced by water deficit resulting in variable final tuber weight.

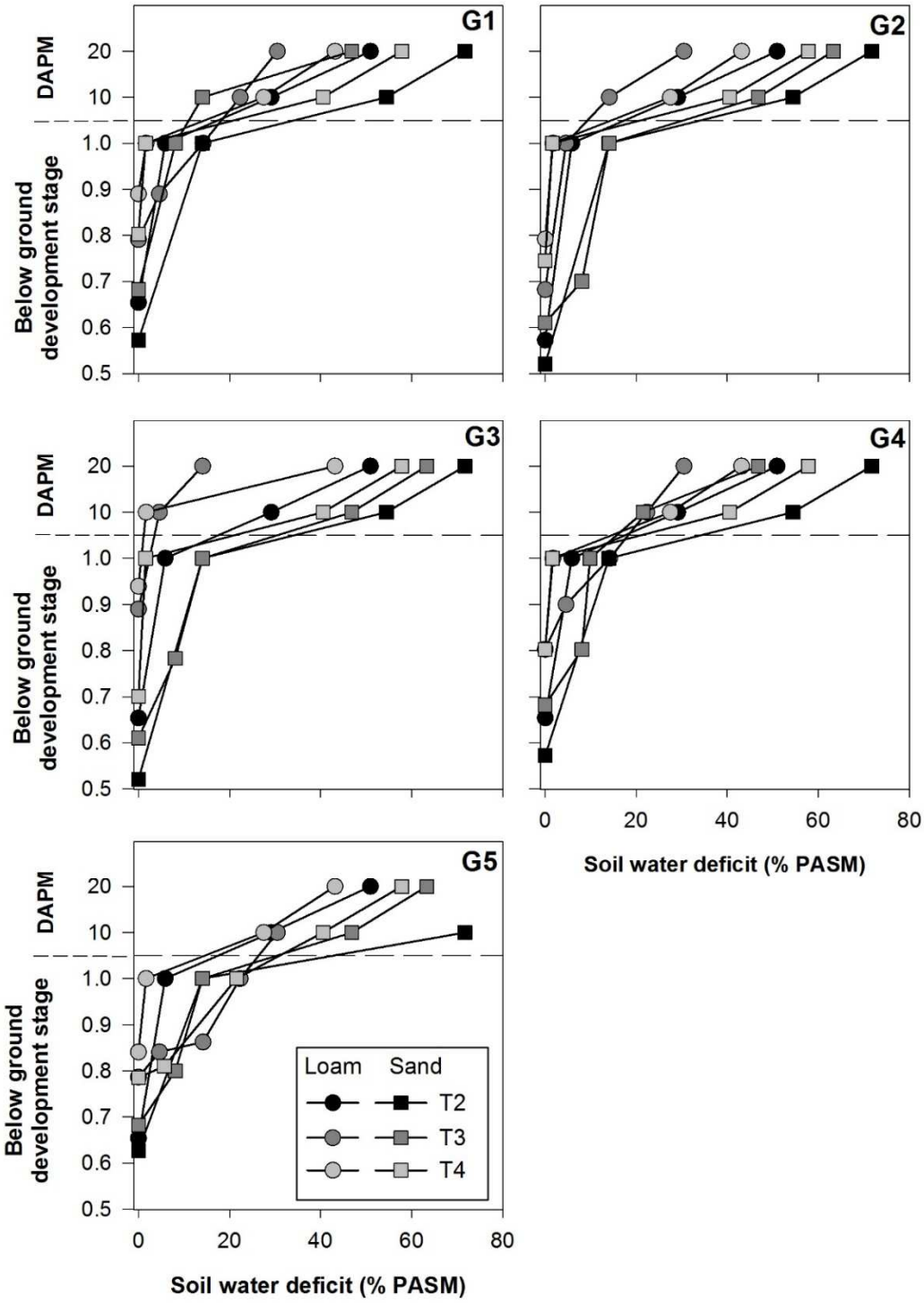


Figure 3.4: Below ground phenology and soil water deficit in the percent of plant available soil moisture (PASM) of five potato clones grown on two soil types (loamy sand: Loam; sandy soil: Sand) under the three drought treatments.

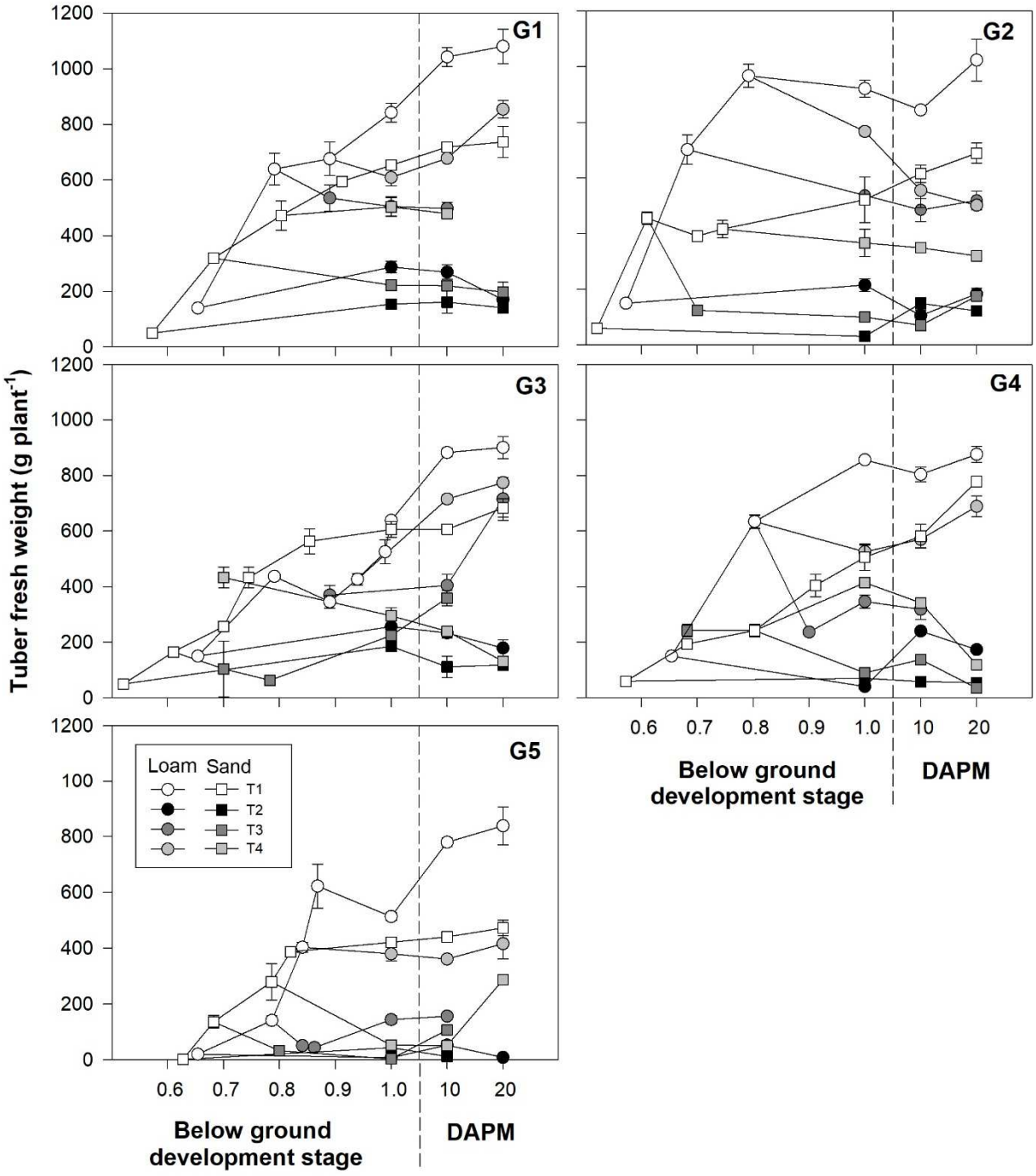


Figure 3.5: Tuber fresh weight dynamics and below ground phenology of five potato clones grown on two soil types under four irrigation treatments. Treatment details are given Table 3.2. Additional destructive samplings 10 or 20 days after the stage of physiological maturity (DAPM) were included where applicable. Error bars = Standard error (n=3).

3.3.5 Stress Severity Index and tuber yield reduction

Combining the stressor (soil moisture deficit and its duration) with the sensitivity of the respective development stage (phenology) to soil moisture deficit, allows calculating a stress severity index that reflects the genotypic response to soil moisture deficit in terms of tuber yield effects. Figure 3.6 shows the log-linear relationship between SSI and the resulting reduction in tuber yield. SSI values beyond 1000 indicate severe drought stress in a range that the plant can maybe survive but cannot be productive anymore. Those genotypes that show relatively little tuber yield reduction at relatively high SSI values (below the regression line for T3 and T4 for SSI between 100 and 1000), may possess interesting traits for drought tolerance. Those above the regression line can be classified as drought sensitive.

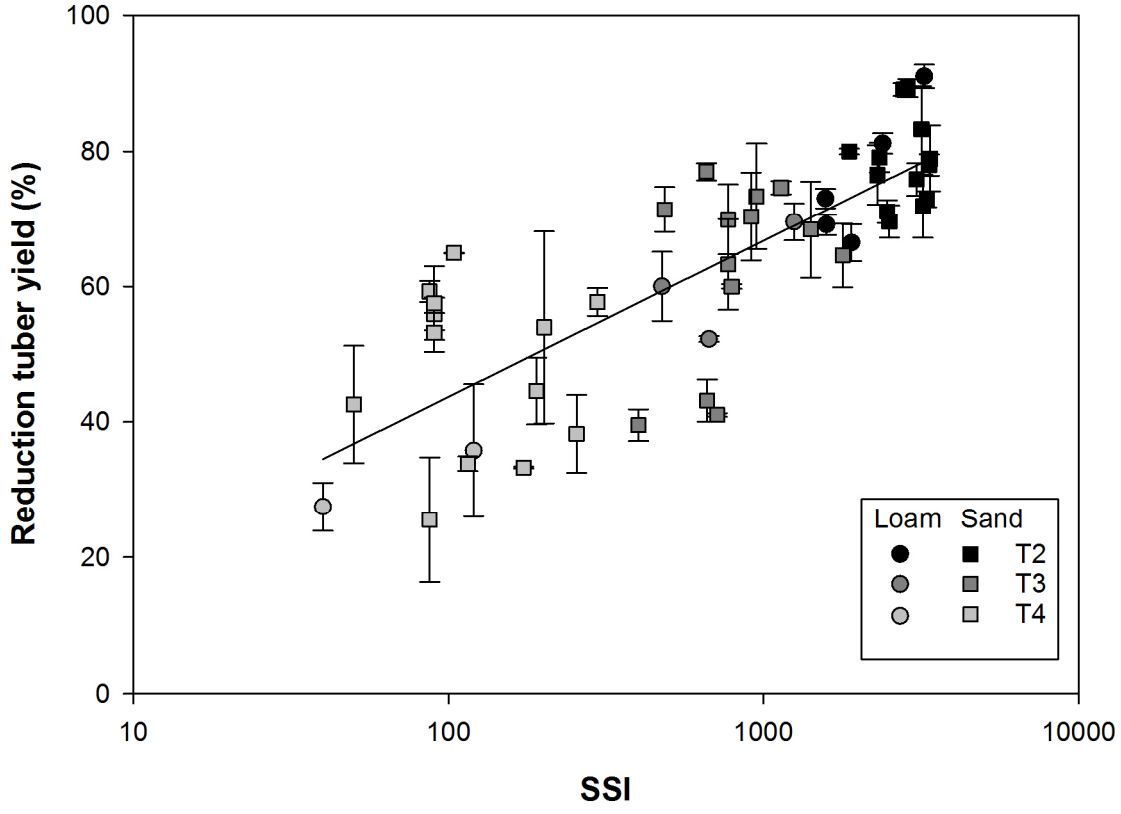


Figure 3.6: Stress severity index and tuber yield reduction relative to fully irrigated yields for all genotypes (Appendix A.2), both soil types (Appendix A.1, and all irrigation treatments (details in Table 3.2). Linear regression on log transformed x values $r^2 = 0.65$.

3.4 Discussion

In this study, the potato clones subjected to different irrigation treatments on two different soil types in general responded to water deficit with a reduction in dry mass, tuber yield, root length, and leaf area (Table 3.4). Genotypes differed in their responses as a function of soil type, stress severity, and development stage during which they were subjected to the treatment. Withholding irrigation at an early stage (T1-tuber filling) triggered the strongest responses, whereas withholding irrigation at later stages (T4 – end tuber filling / tuber bulking) resulted in less severe reductions. Yields on sand were generally lower and drought responses more pronounced. Under full irrigation, highest yields were recorded for genotype 1 and 2 on loam and genotype 3 and 4 on sand. However, in stress conditions such genotypic differentiation between soil types was not observed and yields on sand were always lower than on loam, an effect recently also observed for Dutch potato production systems (Maestrini et al., 2020). The treatments significantly differed in their effects on yield (Table 3.4). Yield and biomass production were most strongly reduced by treatment 2 on sand with no significant differences between the genotypes on either soil type. Many studies on drought tolerance of potato try assessing drought tolerance using above ground indices (e.g. Junhong et al., 2019; Li et al., 2019; Nouri et al., 2016) or below ground indices (e.g. Cabello et al., 2013; Haverkort et al., 1990; Sprenger et al., 2015) but ignore soil type and soil moisture. Assessing genotypic responses to water deficit, based on yield or yield-derived indices varied strongly between locations and years (Cabello et al., 2013) but stress severity was never defined and soil properties were not included in the stress analyses. The importance of including soil moisture and soil matrix potential in the evaluation of stress severity was pointed out by Jensen et al.(Jensen et al. 2010; Jensen, et al. 1998). Jensen et al. showed that different development stages of potato varied in their responses to water deficit.

We evaluated the yield performance of 13 potato clones under varying supply of plant available soil moisture (Figure 3.3) and showed that the total amount of water available to the plant is not directly related to the final tuber yield, which is in line with the arguments of Jensen et al. 1998. We could also show, that the soil moisture deficit developed at different speeds in the two soils (Figure 3.1) which resulted in different water deficit – belowground development stage combinations (Figure 3.4) leading to different stress severities at different development stages and, thus, different effects on tuber yield for the individual genotypes (Figure 3.5). Combining the sensitivity of the individual development stages (Figure 3.2) with the drying effects on the soil matrix potential (Table 3.2) allowed us to calculate a daily stress severity value. Summing

up this value for the duration of the crop until physiological maturity of the tubers resulted in a stress severity index (SSI) describing the intensity the individual genotypes were subjected to. Values of the stress severity index varied between 25 for T4 on loam and 3500 for T2 on sand. Highest SSI was calculated for early and intermediate drought. On loam and sand under early drought, G1 and G9, respectively, showed the highest SSI and the highest tuber yield reductions. SSI values above 1000 did not distinguish the individual responses of the varieties anymore as in all cases yield reductions of more than 60% technically rendered all genotypes susceptible. The SSI we calculated here allows assessing the actual severity of the stress the plant is subjected to, independent of the duration of the stress. Since it is based on soil functions and the level of water loss in these soils, it is location, year, and genotype independent as an index. Combining it with physiological traits such as chlorophyll concentration (Ramírez et al., 2014) or remote sensing-based indices (Ray et al., 2006) would increase the accuracy in assessing drought resistance and tolerance traits in large numbers of genotypes non water losses. In this study we focused on relatively late development stages and still found a good relationship between soil moisture losses (calculated as changes in soil tension) and the sensitivity of the individual development stage, to come to a fair assessment of the water deficit effects on yield. In future we will concentrate on earlier development stages in order to evaluate to what extend existing indices can benefit from our stress severity approach.

3.5 Conclusion

The SSI is not exact, but sufficient to separate sensitive genotypes from more resistant genotypes at low stress levels. The SSI indicates drought stress responses across genotypes and environments as seen by the coinciding results of yield reductions at similar SSI values in sand and in loam. The SSI allows comparing results from drought treatments across sites and environments since it provides an independent indicator for the stress a plant is subjected to which allows evaluating the responses on a site independent basis. To identify drought tolerant potato genotypes under field conditions is one of the major tasks to ensure food security in the future. However, the more environments and drought scenarios are tested, the more complicated becomes the data comparison. The results of this study showed that same drought conditions resulted in different drought stress severities for various potato genotypes. Phenological differences and varying soil water content are the driving factors of the differences in drought stress experienced by plants. Simply comparing tuber yield or tuber yield reductions does not allow identifying drought tolerant genotypes. Since yield is built in phases that coincide with development stages, the sensitivity of the respective phenological phase as well as the soil

tension experienced during this phase determine the impact of the water deficit on yield. SSI allows cumulating stress severity and thus, the higher the yield at a high SSI the stronger are the plants defense and adaptation mechanisms. Therefore, other indices that have looked into stay-green syndrome, rooting depth adaptations, leaf surface temperature, or canopy reflectance indices with only medium success, may benefit from including SSI in their indices to identify the underlying mechanisms of drought tolerance in potato.

Author Contributions: Conceptualization, J. H. and F. A.; methodology, J. H. and F.A.; formal analysis, J. H.; investigation, J. H., L. K. and J. Z.; resources, CIP, D; data curation, J. H.; writing—original draft preparation, J. H and F.A..; writing— review and editing, J. H. and F.A.; visualization, J. H. and F. A.; supervision, F. A.; project administration, J. H.; funding acquisition, M. B. and Team.

All authors have read and agreed to the published version of the manuscript.

Funding: Financial support by the German Ministry for Collaboration and Development (GIZ No. 11.7860.9-001.00). **Data Availability Statement**: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: The authors thanks INIA-Arequipa for providing facilities. We are grateful to Jesus Zumaran and Leah Kuppinger for their support during the field trials. Competent technical assistance by Jorge Vega, Anthony Quello, Elisabeth Torreblanca and Trinidad Unda is gratefully acknowledged.

4 Suitability of the Stress Severity Index combined with remote-sensing data as a tool to evaluate drought resistance traits in potato

This chapter is submitted as:

Hoelle, J., Asch, F., Khan, A., Bonierbale, M. 2023. Suitability of the Stress Severity Index combined with remote-sensing data as a tool to evaluate drought resistance traits in potato. Journal of Agronomy and Crops Science.

Keywords: stress severity, phenology, drought, *Solanum tuberosum* L., crop reflectance, thermography

Abstract: Potato is a drought susceptible crop and even short drought spells reduce tuber yields notably. In an earlier study we developed a stress severity index (SSI) based on the development stage of a genotype at onset of drought and the soil water deficit based on the soil water tension. Here, we test the suitability of the SSI to be combined with remotely sensed data as screening tool. Normalized vegetation index (NDVI) and the photochemical reflectance index (PRI) were obtained from reflectance measurements and thermography was used to estimate the transpirational cooling of the leaves. Via cluster analysis including SSI, tuber yield reduction, NDVI, PRI and thermography, three groups were distinguished: 1. SSI<1000 with fast decreasing NDVI, PRI and temperature difference, 2. SSI 1000-2000 with almost constant NDVI and temperature deficit and 3. SSI>2000 described by small changes of NDVI, PRI and temperature deficit. For SSI < 1000, ΔT, PRI and NDVI showed to be good indicators of genotypic performance under drought. Potential strategies for drought resistance in potato detectable through remote sensing are discussed.

4.1 Introduction

Global staple yields need to be doubled by 2050 to ensure food security for a rising population and a changing global diet (Ray et a., 2013). An increasing demand for potato or potato products will need to be met by increasing tuber yields per hectare. An efficient and rapid development of new varieties is needed to ensure future food security. Drought is among the most important abiotic stress factors limiting yields in potato. Due to its shallow root system, potato has been classified as being sensitive to even minor drought spells. All development stages of the potato have been described to be drought sensitive (Spitters & Schapendonk, 1990).

In general, genotypic performance is modified by environmental conditions such as soil type, air temperature, radiation intercepted, water availability, air humidity, or wind. In different

environments, genotypes may perform differently due to genotype*environment interactions rendering comparisons across environments difficult. Earlier studies often based, drought treatments on changes in soil water potential (Haverkort et al., 1990; Lahlou and Ledent 2005) or on the effect of certain irrigation management. For example, drought can be initiated at a fixed date before harvest (Hoelle et al., 2020; Lefèvre et al., 2012; Luitel et al., 2015) or may comprise rewatering after a drought spell of varying length (Chang et al., 2018; Mane et al., 2008) with different methods of intermittent droughts being employed (Anithakumari et al., 2012; Deblonde & Ledent, 2001). In all studies mentioned above, the drought period was specified as a time period and the severity of the water deficit as changes in soil water potential without considering the specific sensitivity of the respective phenological stage. We have shown in an earlier study that drought stress severity depends on the duration and magnitude of the water deficit, which are strongly depending on soil type and climatic conditions, and the sensitivity of the phenological stage (Hoelle et al., 2020). We propose a combination of absolute tuber yield under drought and tuber yield reduction relative to a well-watered control to be suitable traits in identifying genotypes tolerant to drought. Testing a large number of genotypes under well-watered and water deficit conditions based on specific phenological stages is an enormous experimental effort. Thus linking tuber yield reductions to a relatively simple way of calculating an environmentally robust stress severity index has already increased the predictive power for genotype selection. It would be even faster and less laborious if easily and remotely sensed, phenology specific proxies could be employed to predict a potential yield loss early during water deficits. Phenological stages in potato are usually identified via the above ground development, which can be assessed easily remotely, however, affects the synchrony in development between the aboveground and below ground development (Hoelle et al., 2017), which in turn affects the accuracy of remotely sensed data on the detrimental effects of water deficit on potato yield. Several studies addressed remotely sensed data and its relation to drought effects on yield via various physiological responses related to underlying tolerance strategies. The normalized difference vegetation index (NDVI) is a proxy for canopy density and total aboveground biomass (Cabrera-Bosquet et al., 2011) and the photochemical reflectance index (PRI) measures the xanthophyll cycle activity, which is related to photosynthetic light-use efficiency in plants (Coops et al., 2010). NDVI is strongly correlated with biomass production and leaf area in potato plants (Monneveux et al., 2013). PRI has been used to investigate the photosynthetic activity of potato under drought stress conditions (Gerhards et al., 2016; Romero et al., 2017). Hyperspectral remote sensing is a powerful tool to

screen for drought tolerance, as it is fast and provides a continuous spectrum. Continuous sampling and easy selection of crop-specific wavebands render evaluations widely applicable.

Thermal imaging of crop canopies has been proposed as a proxy for stomatal control over transpirational water losses (Jones et al., 2009), allowing studying plant-water kinetics, with a focus on stomatal conductance (Grant et al., 2012; Merlot et al., 2002). Potato plants grown under soil water deficit close their stomata, reduce transpiration, and, thereby, leaf temperature increases. These leaf temperature changes in comparison to a well-watered control can be detected via thermal imaging (Idso, 1982; Jones, 1999).

As drought tolerance comprises a number of traits representing different strategies, various parameters need to be monitored to allow identifying drought tolerant potato genotypes. Albeit, without a clear indication of the severity of the stress the individual plants were subjected to, datasets will have little value across studies. Hill et al. (2021) reviewed 82 primary research articles and concluded that the implementation of drought has never been standardized. With the introduction of the stress severity index (SSI), we developed the first tool to describe stress severity of individual genotypes based on the individual phenology and soil water potential (Hoelle et al., 2020). In this study, we investigate to what extend combing the SSI with remote sensing methods improves identifying strategies of drought tolerance in potato. Drought is among the most important abiotic stress factors limiting yields in potato. Due to its shallow root system, potato has been classified as being sensitive to even minor drought spells. All development stages of the potato have been described to be drought sensitive (Spitters & Schapendonk, 1990). In general, genotypic performance is modified by environmental conditions such as soil type, air temperature, radiation intercepted, water availability, air humidity, or wind. In different environments, genotypes may perform differently due to genotype*environment interactions rendering comparisons across environments difficult. Earlier studies often based, drought treatments on changes in soil water potential (Haverkort et al., 1990; Lahlou and Ledent 2005) or on the effect of certain irrigation management. For example, drought can be initiated at a fixed date before harvest (Hoelle et al., 2020; Lefèvre et al., 2012; Luitel et al., 2015) or may comprise rewatering after a drought spell of varying length (Chang et al., 2018; Mane et al., 2008) with different methods of intermittent droughts being employed (Anithakumari et al., 2012; Deblonde & Ledent, 2001). In all studies mentioned above, the drought period was specified as a time period and the severity of the water deficit as changes in soil water potential without considering the specific sensitivity of the respective phenological stage. We have shown in an earlier study that drought stress severity depends on

the duration and magnitude of the water deficit, which are strongly depending on soil type and climatic conditions, and the sensitivity of the phenological stage (Hoelle et al., 2020). We propose a combination of absolute tuber yield under drought and tuber yield reduction relative to a well-watered control to be suitable traits in identifying genotypes tolerant to drought. Testing a large number of genotypes under well-watered and water deficit conditions based on specific phenological stages is an enormous experimental effort. Thus linking tuber yield reductions to a relatively simple way of calculating an environmentally robust stress severity index has already increased the predictive power for genotype selection. It would be even faster and less laborious if easily and remotely sensed, phenology specific proxies could be employed to predict a potential yield loss early during water deficits. Phenological stages in potato are usually identified via the above ground development, which can be assessed easily remotely, however, affects the synchrony in development between the aboveground and below ground development (Hoelle et al., 2017), which in turn affects the accuracy of remotely sensed data on the detrimental effects of water deficit on potato yield. Several studies addressed remotely sensed data and its relation to drought effects on yield via various physiological responses related to underlying tolerance strategies. The normalized difference vegetation index (NDVI) is a proxy for canopy density and total aboveground biomass (Cabrera-Bosquet et al., 2011) and the photochemical reflectance index (PRI) measures the xanthophyll cycle activity, which is related to photosynthetic light-use efficiency in plants (Coops et al., 2010). NDVI is strongly correlated with biomass production and leaf area in potato plants (Monneveux et al., 2013). PRI has been used to investigate the photosynthetic activity of potato under drought stress conditions (Gerhards et al., 2016; Romero et al., 2017). Hyperspectral remote sensing is a powerful tool to screen for drought tolerance, as it is fast and provides a continuous spectrum. Continuous sampling and easy selection of crop-specific wavebands render evaluations widely applicable.

Thermal imaging of crop canopies has been proposed as a proxy for stomatal control over transpirational water losses (Jones et al., 2009), allowing studying plant-water kinetics, with a focus on stomatal conductance (Grant et al., 2012; Merlot et al., 2002). Potato plants grown under soil water deficit close their stomata, reduce transpiration, and, thereby, leaf temperature increases. These leaf temperature changes in comparison to a well-watered control can be detected via thermal imaging (Idso, 1982; Jones, 1999).

As drought tolerance comprises a number of traits representing different strategies, various parameters need to be monitored to allow identifying drought tolerant potato genotypes. Albeit,

without a clear indication of the severity of the stress the individual plants were subjected to, datasets will have little value across studies. Hill et al. (2021) reviewed 82 primary research articles and concluded that the implementation of drought has never been standardized. With the introduction of the stress severity index (SSI), we developed the first tool to describe stress severity of individual genotypes based on the individual phenology and soil water potential (Hoelle et al., 2020). In this study, we investigate to what extend combing the SSI with remote sensing methods improves identifying strategies of drought tolerance in potato.

4.2 Materials and Methods

4.2.1 Site description

Field trials were conducted over two years at an experimental station of the "Instituto Nacional de Innovacion Agraria" in St. Rita de Siguas (16°28'35"S; 72°6'18"W), Peru, from July to November 2013 and from August to December 2014.

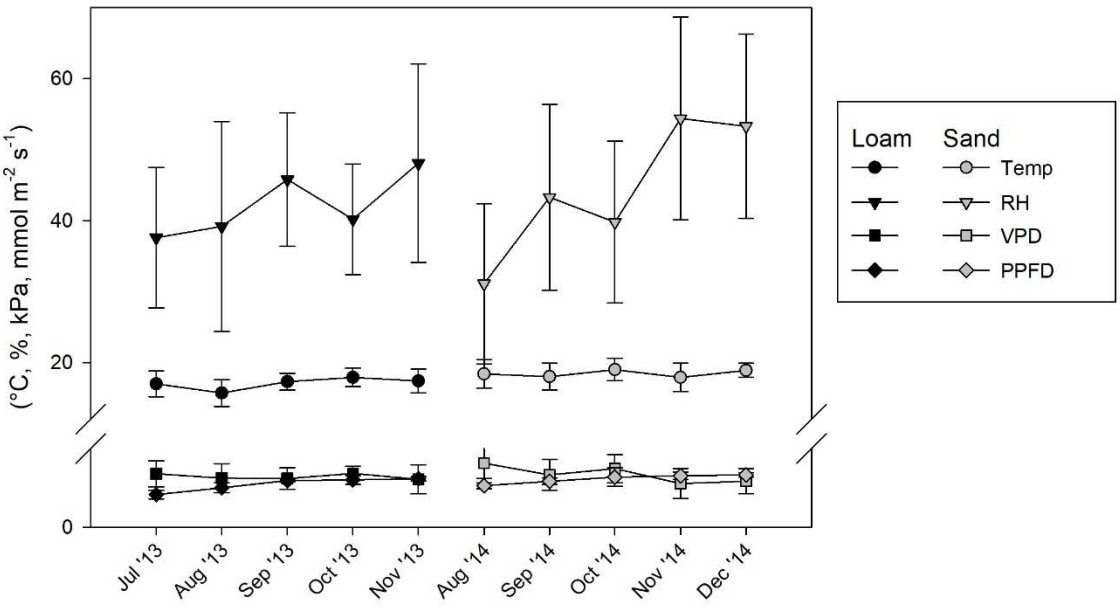


Figure 4.1: Weather conditions during the experimental periods in 2013 and 2014 in St. Rita de Siguas, Arequipa, Peru. Data are shown as monthly averages of daily mean values. Temp=Temperature (°C), RH=relative air humidity (%), VPD = vapor pressure deficit, (kPa) and PPFD = photosynthetic photon flux density (mmol m^{-2} s^{-1}). The error bars represent the standard deviation.

The experimental site has an arid climate with little interannual variation. Air temperature, air humidity, wind speed, and photosynthetically active radiation at 2 m height were recorded in 15 min intervals with a HOBO® Weather station close to the experimental plots (Figure 4.1). No rainfall occurred during the field trials. Two neighboring fields differing in soil texture were

selected. Soil samples were taken with a cylindrical auger (Delta T-Device) as bulk samples from 0-15 cm and 15-30 cm along a diagonal transect with five replications for each field and depth before planting. Soil samples were analyzed at the soil laboratory at the Universidad Agraria La Molina, Lima, Peru. Soil texture, pH, and organic matter content are given in the Appendix.

4.2.2 Plant materials

Five genotypes from the International Potato Center (CIP) breeding program were planted on 17.07.2013 and 13.08.2014 loamy sand and sand, respectively. For reasons of simplicity, genotypes are named G1-G5 in the text. A list of all genotypes and CIP identification codes is given in Appendix A.2**.** Before planting, seed tubers were disinfected with Homai (BASF) and afterwards with Decis (Bayer) against potato beetle (Leptinotarsa decemlineata). Experiments were laid out in a strip plot design with three replications. The size of the experimental subplots was 8 m^2 (3 m x 2.7 m). Plants were arranged in three rows of 11 plants each with 0.9 m between and 0.3 m within the rows for all genotypes. Observations, measurements, and samplings were conducted in the middle row and the neighboring rows served as border plants. Before planting, 1000 kg ha-1 Guano was applied into the furrows and pre-sprouted seed tubers were placed by hand with the sprouts upside. Mineral fertilizer mixture of 160 kg ha-1 potassium sulfate (50 % K2O, 18 % S, INTI), 80 kg ha-1 stabilized ammonium nitrate (33% N – 3% P2O5 – 0% K2O, MISTI S.A.) and 250 kg ha-1 Fertiphos®-Plus (20 % P2O5; 36 % CaO; 6 % S, 17 % SiO2; 1.08 % Fe2O3; 0.9 % MgO; Micronutrients Zn, Mn, Cu, B) was placed manually between the seed tubers. A second nitrogen dose was top-dressed manually as ammonium nitrate (120 kg ha-1) during hilling. Fungicides and insecticides were applied in approximately 20-day intervals according to the instructions of the suppliers. Following products were used: Sorba 50 EC (Syngenta), Ultra Pegasol (Farmagro S.A), Rover (Sipcam Pacific), Pentacloro Farmex, Cipermex (Farmex), Confidor 350 SC Fitoraz (Bayer), Evisect 50 SP (Arysta). Insecticides with changing functional groups were applied to avoid build-up of resistances in the field. Manual weeding was done in 14-day intervals.

4.2.3 Irrigation treatments and soil moisture measurements

Irrigation of the experimental plots was established via drip irrigation with 0.3 m distance between individual drips and one dripline per row until hilling and two driplines per row thereafter. The full irrigation treatments were targeted to 85 % field capacity of the respective fields (T1). Irrigation was withheld at 50 days after planting (DAP) for T2, at 65 DAP for T3, and at 80 DAP for T4.

Soil moisture was measured in the plots planted with G1-G5 for each treatment and replication in 3 to 5 day intervals via frequency domain reflectometry (FDR, PR2 Soil Moisture Profile Probe, Delta T-Device). The four sensors of the profile probe measure in 10 cm increments in 0-40 cm depth via access tubes made of fiberglass. For each value, three measurements were taken with the probe rotated by approximately 120 degrees for each measurement to account for suboptimal soil contact of the access tube and the gap in the sensor ring. The upper 10 cm were excluded in further presentation, as the soil dried down very fast in this horizon and the FDR probe did not measure adequately at soil moisture content under 5 vol. %. Further details are given in Hoelle et al. (2020).

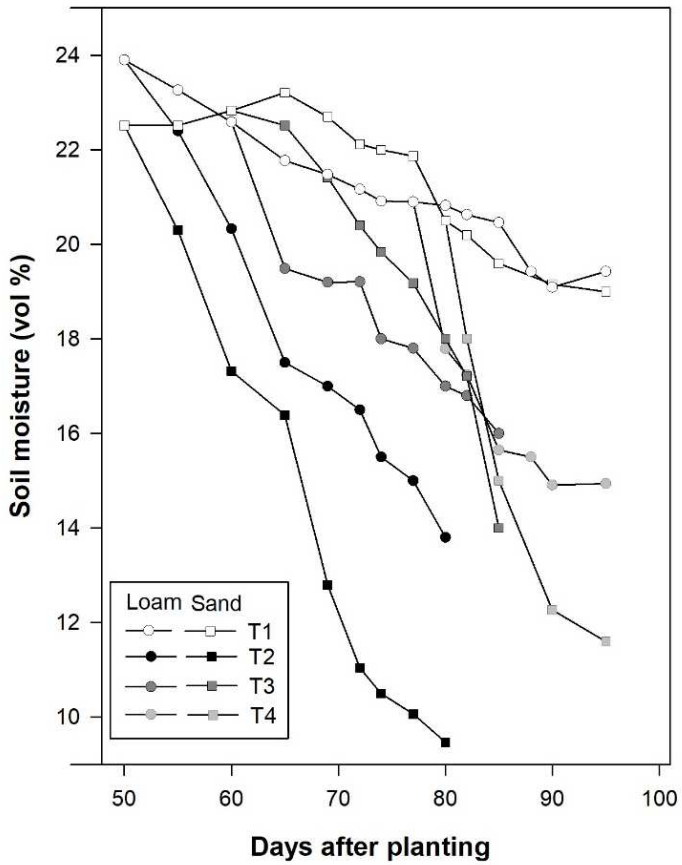


Figure 4.2: Depletion of soil moisture in vol. % at days after planting for the four irrigation treatments (T1-T4) in loamy sand (Loam) and sandy soil (Sand). Measurements were taken in 5-day intervals per genotype, treatment, and replication. Each data point represents a mean of 15 measurements of the average soil moisture from 10-40 cm depth. Error bars have been omitted for readability.

4.2.4 Harvest, yield and yield components

One randomly selected plant per genotype, replication, and treatment was sampled destructively at 10, 20, and 30 days after withholding water (DAWW). Care was taken that each sampled plant was in the center of eight neighboring plants to avoid border effects. Roots and tubers were carefully excavated, adhering soil removed, average root length was measured, and tubers were counted. Leaves, stems, and roots were separated and dried in paper bags for 3 days at 80 °C until constant weight. Fresh tuber weight (TFW) was determined with a fine balance (Kern und Sohn, Type 440). The tuber yield reduction (TubRed, %) relative to the fully watered treatment (FI) were calculated as:

$$\mathrm{TubRed}(\%) = 100 - \left(\frac{\mathrm{TFW_{TD}} * 100}{\mathrm{TFW_{FI}}}\right)$$

with TFW_{TD} for fresh tuber yield in grams per plant under water deficit and TFW_{FI} for fresh tuber yield in grams per plant under fully irrigated control.

Remote sensing

Crop canopy reflectance was measured with a field spectrometer (FieldSpec HandHeld 2, ASD). The measuring lens's angle is 45°, the spectrometer was held 10 to 15 cm above canopy, to avoid soil reflection measurements. After each block, the spectrometer was calibrated with the white reference plate. NDVI was calculated as follows:

$$NDVI = \frac{(\mathrm{pNIR} - \mathrm{pRed})}{(\mathrm{pNIR} + \mathrm{pRed})}$$

with 900 nm for the near infrared (NIR) and 680 nm for the red waveband (pRed, Rouse, Haas, Schell, & Deering, 1974).

The other remote sensing parameter was the photochemical reflectance index (PRI, Gamon, Serrano, & Surfus, 1997). The PRI is calculated as follows:

$$\mathrm{PRI} = \frac{(\mathrm{R531} - \mathrm{R570})}{(\mathrm{R531} + \mathrm{R570})}$$

The spectra at 531 and 570 nm gives measurements of the xanthophyll cycle and the photochemical efficiency of the photosystem II (PSII) as well as the carotenoid: chlorophyll pigment ratio.

Leaf temperature was measured with an infrared camera (FLIR™ B335, 320*240 Pixel) between 9 am to 3 pm for each genotype in each replication. The emissivity factor was set at 0.98 (Chen, 2015; Jones, Archer, Rotenberg, & Casa, 2003). Actual air temperature and air

humidity was actualized in 30 min intervals. The analysis of the picture was done with FLIR QuickReport® software provided by FLIR Instruments. Three analysis points in the upper third of 3 plants per genotype and replication was selected and analyzed. Minimum, maximum, and average leaf temperature was evaluated. The transpirational cooling of each genotype was calculated as:

$$\Delta T = T_{air} - T_{leaf}$$

With temperature of the air (T_{air}, °C) and temperature of the leaf (T_{leaf}, °C). Patches of bare ground were avoided. For identification of shaded foliage and dead biomass, a digital picture was taken simultaneously.

4.2.5 Irrigation and Stress Severity Index

Irrigation was targeted to 0.85 * field capacity, however, since irrigation was based on time and not volume, variability in the drip points resulted in a varying moisture level for irrigated plots for both soils (Figure 4.1, Figure 4.2). Withholding irrigation resulted in all treatments in rapid soil drying and, depending on the treatment and the soil type, resulted in a loss of plant available water of 30 to 80 %, thus, creating relatively severe stress levels for the plants. Taking into account the varying sensitivity to water deficit of the different development stages a stress severity index was calculated.

The stress severity index (SSI) comprises of the soil water tension experienced by the plant weighted by the relative genotypic sensitivity of the respective phenological stage, cumulated for the duration of the water deficit treatment. For detailed description of the stress severity index and the calculations of the SSI used in this study, please refer to Hoelle et al. (2020).

4.2.6 Data analysis

Statistical analyses were performed with R Statistical Program (R Foundation for Statistical Computing, Vienna, Austria, 2008). All data were tested for normal distribution and homogeneity of variances using the Bartlett's test and outliers were removed. We used the one-way ANOVA with the Fisher's least significant difference test as post-hoc test and Bonferroni correction for tuber yield analysis. All statistical analyses used a nominal alpha of $p < 0.05$. For cluster analysis the objects in k-means were calculated with the Euclidean distance. In the cluster analysis fresh tuber yield, tuber yield reduction and the SSI were included. Graphs and regressions were generated with SigmaPlot 12.5, Systat Software, Inc., Erkrath, Germany.

4.3 Results

4.3.1 Identification of drought tolerance via tuber yield information and remote-sensing methods

In general, withholding irrigation, in both, loamy sand and sand, resulted in significantly lower tuber yields and high tuber yield reductions (Table 4.1). On both soil types, significantly highest yields were measured under full irrigation whereas under terminal drought tuber yields differed significantly between soil types. Yields were generally higher for plants grown in loamy sand while drought induced reductions in tuber yield were similar across soil types. Tuber yield was most reduced by the early drought treatment, followed by the intermediate drought and least affected by the drought initiated late in the cycle.

Figure 4.3 shows the relationship between tuber yield reduction and remotely sensed NDVI, PRI and ΔT for all three drought treatments at 10,20 and 30 DAWW.

Table 4.1: Average maximum tuber fresh weight in gram per plant (max. TFW) and maximum tuber yield reduction in percent per plant (max. TubRed) for each treatment. ANOVA analysis with the Fisher's least significant difference test and Bonferroni correction at significant level p=0.05 (n=45). Irrigation was withheld at 50 days after planting (DAP) for T2, at 65 DAP for T3, and at 80 DAP for T4. T1 is the well irrigated control.

	Loam		**Sand**	
Treatment	**max. TFW (g pl^{-1})**	**max. TubRed (%)**	**max. TFW (g pl^{-1})**	**max. TubRed (%)**
1	1016 ± 299 a		617 ± 322 a	
2	202 ± 96 d	-74 ± 10 c	93 ± 73 d	-78 ± 6 c
3	402 ± 150 c	-53 ± 20 b	151 ± 68 c	-62 ± 13 b
4	631 ± 300 b	-46 ± 21 a	305 ± 129 b	-58 ± 23 a
LSD	*68*	*8*	*45*	*10*

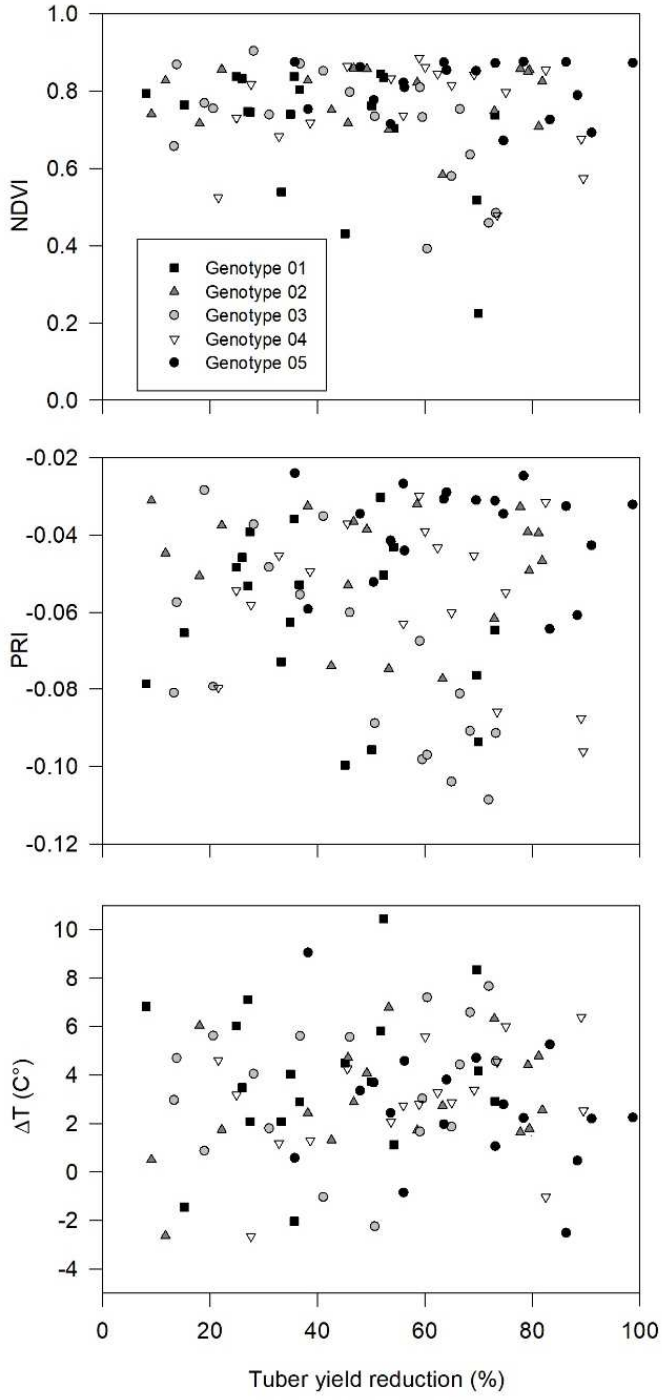


Figure 4.3: The tuber yield reduction (%) and days after planting (DAP) in relation to normalized vegetation index (NDVI), photochemical reflectance index (PRI) and transpirational cooling of the leaves (ΔT, °C). The five genotypes were tested in three drought treatments: T2, early drought, initiated at 50 DAP, T3, intermediate drought, initiated at 75 DAP and late drought with drought initiation at 90 DAP. The sampling after 30 days without water in loamy sand and sandy soil are presented.

Although large variations were observed between genotypes and within genotypes for both, the remotely sensed variables and the tuber yield reductions, no significant correlation was found for any of the remotely sensed parameters with tuber yield reduction in neither treatment.

4.3.2 Identification of drought tolerant genotypes by combining remote sensing with SSI

The stress severity index was calculated for each genotype and drought treatment on either soil type and grouped into 3 intensity levels, SSI<1000, SSI 1000-2000 and SSI>2000. These were related to tuber yield reduction, NDVI, PRI and ΔT at 30 DAWW as shown in Figure 4.4. The first group (SSI < 1000) consists of three data points representing tuber yield reduction ranged between 52 % to 70 % and including the genotypes with the smallest tuber yield reductions under intermediate drought, namely CIP 392797.22, CIP 397078.12 and CIP 397073.16. In the second group (SSI 1000 -2000) tuber yield reductions were severe, ranging between 65% up to 75%. This group is comprised plants grown under early and intermediate drought. A SSI above 2000 represents such a strong stress that tuber yield reductions as well as any of the remotely sensed parameters were not clearly related to SSI any more.

In the third cluster with SSI<1000, NDVI was strongly negatively correlated with SSI (r = 0.85) as well as with PRI (r = 0.73), indicating an increased development rate in order to quickly complete the phenological cycle under moderate drought stress (Table 4.2.) This correlation weakened with increasing SSI in the other two groups. Tuber yield reduction (r = 0.83) and NDVI was correlated within the second SSI cluster in the group with SSI from 1000 to 2000. For ΔT in the group SSI<1000 a negative correlation was found with SSI however, in contrast to PRI and NDVI this was weak (r=0.3) and SSI and tuber yield reduction was weakly correlated in the other two groups of SSI.

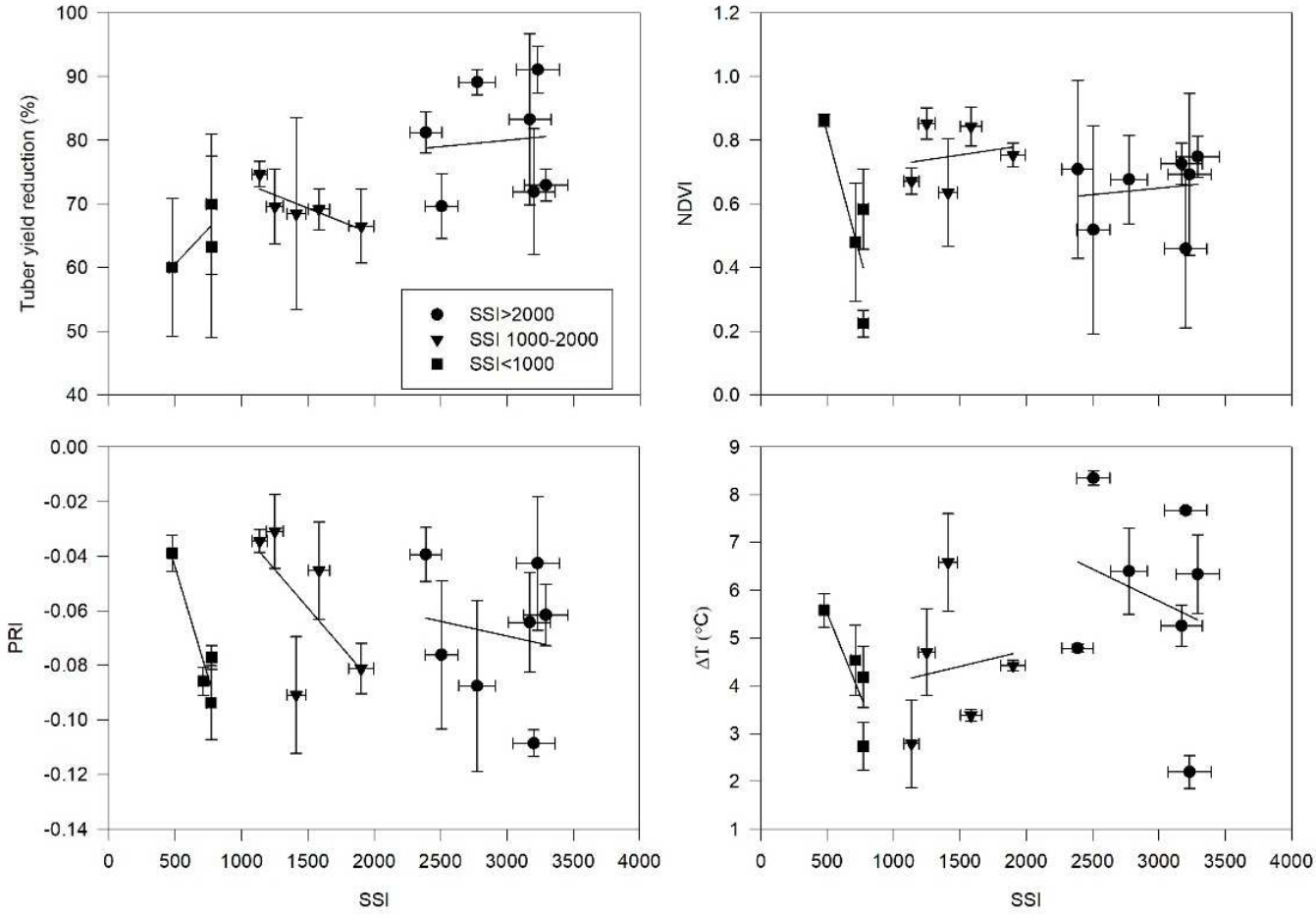


Figure 4.4: Stress severity index (SSI) cluster in three SSI groups: SSI<1000, SSI 1000-2000, SSI>2000, in relation to tuber yield reduction (%), normalized vegetation index (NDVI), photochemical reflectance (PRI) and transpirational cooling of the leaves (ΔT) at 30 days after withholding water grown in Sand and loamy Sand.

Table 4.2: Regression equations for the correlation between the SSI cluster (SSI<1000, SSI 1000-2000, SSI >2000) to the tuber yield reduction (%), the normalized vegetation index (NDVI), photochemical reflectance index (PRI) and transpirational cooling of the leaves (ΔT, °C) with correlation coefficient (r).

Tuber yield reduction (%)	r	NDVI	r	PRI	r	ΔT (°C)	r
y = -0.004x + 68.056	0.28	y = -6E-06x - 0.00529	0.17	y = -3E-05x + 0.7405	0.14	y = -0.0013x + 9.7964	0.24
y = -0.0083x + 81.752	0.83	y = - 6E-05x - 0.0255	0.62	y = - 6E-05x + 0.6602	0.17	y = 0.00073x +3.7284	0.05
y = 0.0111x + 49.76	0.14	y = -0.0002x + 0.0431	0.85	y = -0.0016x + 1.684	0.73	y = -0.0078x + 10.815	0.32

Figure 4.5 indicates the relationship between the different parameters and how they are affected by SSI in form of a principle component analysis with a biplot of the parameters involved, explaining about 76% of the variance in the data. PC2 is strongly negatively correlated with tuber yield reduction and strongly positively correlated with ΔT whereas PC1 is strongly positively correlated with NDVI and PRI. This indicates genotypes with a small reduction in tuber yield could be identified by a large ΔT, a high NDVI or a large PRI value. The scatter in the PCA suggests that this should be possible across all SSI classes indicating a large ΔT to PC 2.

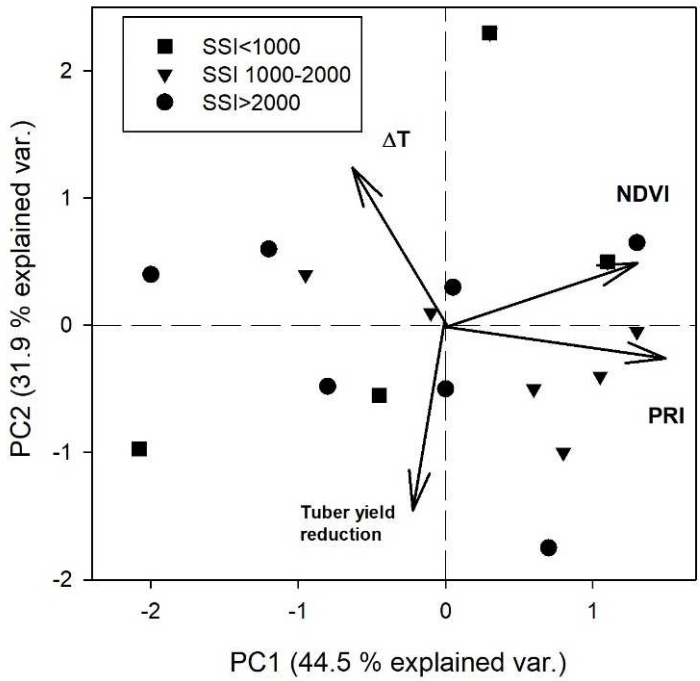


Figure 4.5: Principal components analysis of the 4 traits, tuber yield reduction, NDVI, PRI and ΔT. The two principal components together accounted for 76.4% of the total variation in these four parameters.

4.4 Discussion

Responses of potato genotypes to drought have been investigated for yield (Jefferies & Mackerron, 1989; Levy, 1986), root growth (Lahlou & Ledent, 2005; Tourneux et al., 2003) and a variety of morphophysiological parameters (Aliche et al., 2018; Michel et al., 2019). However, modern screening methods and technologies make scarcely use of the available knowledge by, for example, linking it to remote sensing or multispectral imaging (Gerhards et

al., 2016; Panigada et al., 2014). Most of the combinations between morphophysiological parameters (e.g. chlorophyll content, greenness, leaf area, leaf area index or water content) and spectral indices have been tested and validated under glasshouse conditions (Rolando et al., 2015; Romero et al., 2017). However, when applied in a field trial in this study, no relationship between reduction in tuber yield and remotely sensed physiological parameters was found. For all five genotypes tested in this study, data on tuber yield reduction as well as on NDVI, PRI and ΔT scattered across the entire data range (Figure 4.3). This is in strong contrast to an earlier outdoor pot study by Gerhards et al. (2016) who showed NDVI and PRI to be indicative of genotypic sensitivity to water deficit stress and were even employed to predict tuber yields in potato. However, the study of Gerhards et al. (2016) comprised of one genotype, one soil type, a moderate water deficit treatment for only 9 days after stress initiation at only one development stage under temperate climatic conditions. Thus, transferability of the results to a tropical, multi-genotype study with multiple levels of stress severity as we report on here, is low. Nonetheless, our results show that linking remotely sensed physiological data with tuber yield reduction alone does not encompass sufficiently the complexity of genotype*environment interactions to allow identifying promising genotypes. The sensitivity of a parameter may depend more on stress severity than genotype (Handayani & Watanabe, 2020), which in turn may be an expression of genotype differing in sensitivity to water deficit from one phenological stage to the next. Therefore, the magnitude of change in a given parameter required to affect yield may vary with genotype and stress severity. Luitel et al. (2015), which needs to be taken into account when using proxies for drought-induced yield reduction based on remotely sensed data.

A number of yield-derived drought resistance indexes have been formulated and tested in different environments (Fischer & Maurer, 1978; Moosavi et al., 2008), however, studies allowing to evaluate plant responses to soil water deficit across phenological stages and growing environments are scarce (Hill et al., 2021; Hoelle et al., 2020). Some studies report the phenological stages at treatment initiation, but very few additionally include soil borne stress intensity in the same study (Chang et al., 2018; Deblonde & Ledent, 2001a). The SSI (Hoelle et al., 2020) normalizes stress responses across genotypes, soil type and phenological stages. In the present study, NDVI, PRI and ΔT decreased rapidly at SSI <1000 and a moderately severe increase in yield reductions (Figure 4.4), which supports the findings of Gerhards et al. (2016) for mild early stress conditions. For SSI values higher 1000, the predictive value for yield reductions decreases rapidly and above 2000 yield reductions in most cases exceed 80% and are at that level not correlated to any of the physiological parameters anymore. In the principal

component analysis (Figure 4.5), tuber yield reduction and ΔT are negatively correlated on the y-axis which explains about 32% of the variation in the dataset. This indicates the importance of an early stomatal stress response as a strategy to conserve water within the plant (Dahal et a., 2019) as was seen for SSI < 1000 in Figure 4.4. At the same time, it underlines the potential for deep rooting varieties with better access to water that may be able to maintain leaf cooling longer than shallow rooting varieties (Puértolas et al. 2014, Stalham and Allen 2001). On the x-axis, explaining about 45% of the variation within the dataset, NDVI and PRI are negatively correlated to tuber yield reduction indicating the importance of the stay green mechanism, quantum yield, and xanthophyll cycle for genotypic drought resistance (Deblonde et a., 1999; Rolando et al., 2015).

Overall, the analysis of potential genotypic traits promising for enhanced drought resistance through remote sensing shows that early responses and magnitudes of changes in physiological characteristics are more likely to reveal resistance strategies than when applied to later drought responses in later phenological stages where plant often just accelerate development to complete their cycle (Aliche et al. 2018; Deblonde and Ledent 2001; Lahlou and Ledent 2005). For SSI < 1000, even in this relative small but contrasting set of genotypes, ΔT, PRI and NDVI showed to be good indicators of genotypic performance under drought. Thus, combining these indicators with SSI and tuber yield reduction proved to be a first promising step for a new screening method for drought tolerance in a wider genotypic range. Whereas reflectance data can be recommended for assessing responses under mild to moderate stress severity, thermal imaging should rather be used to screen under mild or early drought stress. More research is needed to identify the combination of environmental conditions and phenological stage of the plants that most explicitly allows evaluating yield responses to water deficit at an early stage using remotely sensed data.

Author Contributions: Conceptualization, J. H. and F. A.; methodology, J. H. and F.A.; formal analysis, J. H.; investigation, J. H., L. K. and J. Z.; resources, CIP, D; data curation, J. H.; writing—original draft preparation, J. H and F.A..; writing— review and editing, J. H. and F.A.; visualization, J. H. and F. A.; supervision, F. A.; project administration, J. H.; funding acquisition, M. B. and Team.

All authors have read and agreed to the published version of the manuscript.

Funding: Financial support by the German Ministry for Collaboration and Development (GIZ No. 11.7860.9-001.00)

Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: The authors thanks INIA-Arequipa for providing facilities. We are grateful to Jesus Zumaran and Leah Kuppinger for their support during the field trials. Competent technical assistance by Jorge Vega, Anthony Quello, Elisabeth Torreblanca and Trinidad Unda is gratefully acknowledged.

5 General Discussion

As drought tolerance is linked to multiple traits, the measure of drought tolerance includes a broad range of morphophysiological parameters. To develop and select drought tolerant potato genotypes and adapt them to changing climate and agriculture, breeding strategies have to be intensified and selection processes accelerated, such as through non-destructive measurements of critical physiological processes via remote sensing. Tuber yield is a function of aboveground biomass, the source, and belowground development, the sink. The synchrony of the above and belowground development reflects the response of the phenology to drought. Vice versa, the sensitivity of the potato to drought changing according to its phenology. Only a handful of studies focus on drought initiation at a specific phenological stage and its impact on final yield or tuber number, but none did investigated the synchrony of the above and belowground phenology under drought (Lahlou et al., 2003; Luitel et al., 2015).

The growth stages of the potato were first described in by Meier (2001). The belowground and aboveground development has been described as linearly correlated.

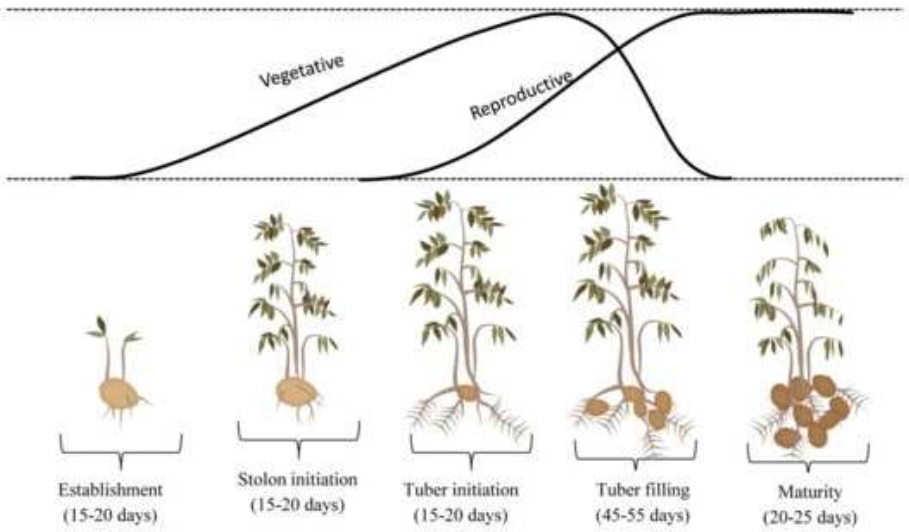


Figure 5.1: Phenological development of potato, modified after Obidiegwu et al. (2015).

During the initial development phases the sprouts and roots are grow out of the planted tuber. This is followed by aboveground growth in terms of leaf area and stolon branching, while belowground, root growth, and the formation of basal side shoots, which also coincides with the stolon initiation. In the next growth step, the main stem elongates and further leaf area increase occurs in parallel with tuber initiation. During flowering, aboveground biomass

reaches its maximum, as the tuber forms and fills. Finally, during the aboveground senescence process, development and ripening of the fruits, the bulking phase is finished.

In our field experiment we tested 13 genotypes under field conditions at four different irrigation regimes. The well-watered control, early terminal drought, initiated at 50 DAP during flowering and early tuber-filling stage, intermediate terminal drought (65 DAP), started at tuber filling and finally the late drought treatment with the beginning at late tuber filling stage at 80 DAP. In our study, under early drought, during the flowering and early tuber-filling stage, the aboveground development was accelerated while the belowground development slowed down. In all experiments, stolon initiation was not affected as the drought treatments as they started at stolon initiation, earliest at 50 days after planting). Tuber filling lasted up to 10 days longer than when under irrigation, whereas flowering and senescence was five to ten days earlier. Many studies take the previously mentioned positive correlation of the above and belowground development as a given (Aliche et al., 2020; Rodriguez & Sadras, 2005; Tuberosa, 2012). Therefore, it is often accepted to take the aboveground phenological stage to estimate the belowground development. But the sensitivity of different phenological stages to water deficit changes within the development stage (Aien et al., 2017; Lizana et al., 2017; Rodríguez et al., 2016). Plants at tuberization reduced their phenological cycle due to drought and high temperatures, which minimized the final tuber yield. In accordance to this study, withholding irrigation at an early phenological stage like flowering and stolon initiation, triggered the strongest responses (Kumar et al., 2020). At later phenological stage like the late- flowering or tuber-bulking stage, water deficit resulted in less severe reductions. Drought during tuber initiation and tuber filling lead to high reductions in tuber yield in terms of reduced tuber size and fresh tuber weight (Boguszewska-Mańkowska et al., 2017). Potato plants are able to use escape mechanisms during water deficit (Rodríguez et al. 2016). For example, the plants in this study reduced the duration of the phenological stages by adjusting their metabolism to accelerate the completion of their life cycle. Another possibility is avoidance, which might involve the reduction of water loss by closing the stomata, preventing dehydration and increasing drought tolerance (Levitt, 1980). This strategy leads to longer life cycles, even under drought. Strategies might be combined or exclusively used by a plant under drought stress. However, not all drought is made equal, and drought intensity changes with soil type and drought duration. The differences in soil texture leads to different soil water potential at the same water content and consequently varying soil water availability.

The potato genotypes were tested in Arenosol with different soil textures: sandy soil and loamy sand. The changes in phenology were more pronounced in the sandy soil compared to the loamy sand, due to the faster depletion of soil moisture. In general, drought increased the relative tuber filling phase and senescence while the relative time to flowering was shortened. Including soil moisture and soil matrix potential in the evaluation of stress severity was suggested by Jensen et al. (2010) and Nasir (2022). Both soil moisture and soil matrix potential induce hydraulic and chemical changes in the root system, which then regulates the aboveground response, in the form of stomatal closure or changes in photosynthesis. However, the total amount of plant available water is not directly related to the final potato tuber yield (Jensen et al. 1998). The important factor is soil water potential, which determines plant growth. Our investigation of the above and belowground synchrony will help to identify phenological stages, in which drought should be avoided, thereby diminishing high tuber yield losses. Therefore, under drought stress, we cannot assume the aboveground reflects to the belowground development stage. Consecutive harvests of the whole plant and detailed evaluation of the belowground development is additionally needed.

As the different phenological stages showed different sensitivity to drought, the stress severity as a function of drought duration and magnitude needed to also be included in the selection process. Combining changes in the soil matrix potential during water deficit, the sensitivity of the respective phenological stage, and the duration of the stress, allows the comparison of genotypic performance over a range of climatic conditions, soil types, and water deficit intensities. The results of this study showed that the same drought conditions resulted in different drought stress severities for various potato genotypes. Differences in the phenological stage and varying soil water tension were the driving factors of the differences in drought stress experienced by the plants. A sensitivity score, describing the sensitivity of different phenological stages to drought, was first published by Doorenbos and Kassam (1979). Boguszewska-Mańkowska et al. (2017) developed a visual sensitivity score. This score ranges from 1 (highly sensitive) to 9 (no sensitive). In our study we used this sensitivity score but reciprocally, resulting in a score of 1 for not sensitive and 9 for highly sensitive plants. This conversion of the score was necessary to model the positive relationship between phenology and stress levels. Our score lead to tuber initiation and tuber filling being defined as the most sensitive development stages (Figure 3.2). To calculate the daily stress severity value and ultimately the magnitude of stress, we combined the sensitivity of the individual development stages with the drying effects on the soil matrix potential, resulting in the stress severity index (SSI). Summing up this value for the duration of the crop until physiological maturity, the SSI

described the intensity of drought the individual genotypes at each day during the drought treatment. For each genotype, the individual SSI can be calculated and combined with the corresponding yield information. Under early drought, such as drought initiation at tuber filling, the SSI ranged from 2000 up to 3500. In the intermediate drought treatment, at early tuber filling, SSI values were lower, but still ranging from 1000 up to 2000. The SSI can be used to compare drought stress responses across genotypes and environments as tuber yield reductions in both loam and loamy sand were represented. Therefore, SSI provides an independent indicator for the stress a plant is subjected to, which allows for the evaluation of plant responses on a site independent basis. SSI reflects cumulative stress severity and thus, the higher the yield at a high SSI, the stronger are the plant's defense and adaptation mechanisms. A plant's defense and adaptation mechanisms are based on various physiological parameters and their response to drought.

The status of a plant can be measured by a range of physiological parameters. Thermal imaging, the reflectance of a plant's leaves, and phenology are useful and nondestructive. Remote sensing in combination with the SSI would allow to fill the genotype-phenotype gap, which means faster selection in plant breeding. Additionally, the combination of an individual's stress severity with remotely sensed parameters will allow assessing a large number of genotypes simultaneously. The stress severity could be evaluated by the combination of the SSI with the changes of remotely sensed parameters, like the greenness of leaves (NDVI), changes in the xanthophyll (PRI) and transpirational cooling of the leaves (Luitel et al. 2015). The relationship of morphophysiological parameters (chlorophyll, greenness, concentration, foliar area and water content) with spectral indices has been demonstrated (Gerhards et al., 2016; Rolando et al., 2015; Romero et al., 2017). Leaf reflectance measurements in the red, green and near-infrared spectra allow statement/estimations of the biomass development and actual status of the plant. The NDVI can be used to evaluate water content, nitrogen status and vegetation cover (Lukina et al., 1999). Additionally, the radiation changes in the red and near-infrared region are correlated with water stress in various crops like potato and maize (Mistele & Schmidhalter, 2008; Ober et al., 2005; Ray et al., 2006).

Drought during tuber initiation led to the lowest NDVI values. With ongoing drought, the reflectance in the red spectra decreased and the infrared emission increased. The NDVI is sensitive enough to detect changes in the water status due to drought treatment in the potato plants, however, this parameter cannot distinguish between single genotypes. Further field experiments should be implemented following data sets to find genotypic responses: 1. Start

drought at earlier phenological stage. In this experiment, the drought started at 50 days after planting, at early tuber filling stage. Drought initiation at an earlier phenological stage may fill data gaps between germination and tuber initiation. 2. The evaluation takes place every 10 days, which leads to data gaps. If the data collection is organized in a 2 to 3 days' interval more critical data points will be caught. 3. The terminal drought, lasting up to 70 days until final harvest, lead to dramatic drought stress on all three drought treatments. Eventually a point was reached at which no genotypic differences were observed as all plants struggled too much. Generally, plant stress can be detected with changes in PRI. The differentiation of the PRI in the drought treatments started at 20 days after withholding water. However, the PRI is affected by other parameters like pigment composition and canopy structure (Kohzuma, Tamaki, & Hikosaka, 2021)**.** Remotely sensed PRI is advantageous as in comparison to leaf or plant-based evaluations it can be measured remotely, rapidly on plant-, row- and even on field-level. However, soil and its heat reflection may influence reading as at advanced senescence. Beside the greenness of the leaves, the efficiency of the photosystem is another important parameter for tuber building. To fill the tubers, the plants need to allocate carbon or rather sugar which is built via photosynthesis. To maintain photosynthesis, the plants need to need to allow for CO_2 uptake via stomatal respiration. The evaporation of water at the leaf's surface is also cooling the leaf. As long as the plants photosynthesize they are transpiring and therefore losing water. The stomatal closure under drought helps the plants to maintain the leaf water potential but adversely it reduces CO_2 uptake, which diminishes photosynthesis and therefore growth. Consequently, CO_2 uptake is dependent on the leaf's temperature. In our experiments, changes in the leaf temperature were already measured under early drought stress. High temperatures in combination with drought stress led to high tuber yield losses due to closed stomata and therefore reduced CO_2 uptake. However, the regulation of stomatal transpiration is one important strategy to cope with drought through minimal transpirational water loss (Boguszewska, Zarzy, & Wasilewska-Nascimento, 2022; Dahal et al., 2019). This corresponds with the transpirational behavior in our study, where potato genotypes with lower tuber yield reduction were able to maintain the ΔT ($= T_{air} - T_{leaf}$) at 6.5 °C. These genotypes were in contrast to genotypes with high tuber losses and increased ΔT (rapidly up to 8.2 °C), indicating the closure of the stomata and reduced transpiration and thus smaller/lower carbon allocation.

We were able to cluster genotypes using the SSI values, dividing them into three groups and then combining them with the corresponding physiological measurements (Figure 4.4). The grouping into different groups helped to identify physiological responses in contrast to many studies, where the grouping is based on tuber yield or tuber yield reduction (Kebede, Firew,

Tesfaye, & Asrat, 2019; Nouri et al., 2016). The first group had a SSI from 0 to 1000, the second group ranged between 1000-2000 and the third group included SSI values above 2000. Lower SSI values were paired with lower tuber yield reductions, fast declining NDVI, PRI and ΔT. Both groups with higher SSI (>1000), can be sorted to the treatments with early drought initiation at early phenological stages with high tuber yield reductions. On one hand, these SSI groups were characterized by stay-green mechanisms, identified by slowly reduced NDVI and PRI values and at the other hand by very high ΔT values. These plants were not able to maintain transpirational cooling via stomatal transpiration, ergo photosynthesis was disrupted. With the help of a principal component analysis (PCA) we identified the validity of specific physiological parameters. In accordance to the first findings in previous chapters the SSI, and therefore the stress intensity plays a crucial role in the screening diagnosis. Tuber yield reduction and ΔT were oppositely scored to each other, while NDVI and PRI are grouped together. At SSI>2000 either NDVI, PRI, nor ΔT were able to identify drought tolerant potato genotypes. The plants with maximum stress reduced or completely halted all life-supporting processes. Fast ripening of the belowground tuber as well as aboveground senescence are the predominant mechanisms. At an SSI from 1000 to 2000 the NDVI, PRI and ΔT still have some prediction power, however, as the NDVI and PRI include information about stay-green mechanisms, quantum yield and the xanthophyll cycle, these parameters are more meaningful as ΔT.

Even in the latest publications of potato cultivars tested under different drought scenarios, the experimental setup included soil moisture measurements instead of soil water tension (Zaki & Radwan, 2022). Additionally, in this study low tuber weights coincided with lower transpiration rates, which is most probably reflected in higher leaf temperatures in our experiments. With the current understanding we propose replacing the time-consuming measurements of stomatal conductance and plants transpiration with thermal imaging. Thermal imaging is faster and can be used as a proxy for tranpirational behave of the plants. Diaz-Valencia et al. (2021) summarized, that the yield-component variables more powerfully distinguished between the tolerant and susceptible genotypes than the physiological parameters due to their high variance. We think especially in trials with many different genotypes, like 104 genotypes in the previous mentioned study, a genotypic stress level in combination with physiological measurements will help to segregate the genotypes into tolerant or susceptible ones. The comparability of field collected data is difficult due to the high variation in soil types, different phenological development and soil borne drought stress. However, a screening tool need to be consistent in the validity and repeatability. The SSI allows us to compare the physiological responses over

years, season, soil type effects and different drought treatments. With the combination of the SSI and physiological parameters, we identified important strategies of the plants to cope with drought. Additionally, NDVI, PRI and the differences in temperature can be used under mild stress scenarios to predict plants performance under drought.

6 Concluding Remarks and Final Recommendations

The methodologies for undertaking screening trials to identify drought tolerant potato genotypes, particularly under repeatable and representative growing conditions in the field, is lagging and need to be implemented, improved and speeded up. In conventional breeding trials the aboveground phenology is evaluated to assess the belowground development, without harvesting the plants. In literature a linear correlation of the above and belowground development is described. However, in dependence on the phenological stage at onset of drought and stress severity and soil texture the above and below ground development changed from a linear to a nonlinear correlation. Further research is needed to validate the synchrony of the above and belowground phenology under drought for other soil types. Additional experiment including rewatering and earlier drought initiation should be implemented to complete the data sets. In actual studies it should be considered, that under drought conditions it cannot be concluded from the aboveground to the belowground development and harvests of the whole plant have to be implemented.

Drought affects plant growth in multiple ways depending upon the duration and intensity of drought and plant developmental stage. To compare the datasets from different environments, we need a stress severity index under consideration of the phenological stage of potato and soil water tension and drought duration. For potato plants grown in sandy soil higher stress intensities were calculated as for plants grown in loamy sand. Early drought events during early tuber filling lead to highest SSI values. Further research is needed to specific the influence of different soil types on the SSI under different drought scenarios. First, we recommend to test same genotypes in soils with different soil texture compositions of from sand, loam and clay. Secondly, the drought scenarios should be implemented at staggered date, starting at 20 or 30 days after plating. This experimental setup helps to capture stress responses at stolon initiation stage.

We found a screening tool, which combines the phenology, drought stress and drought duration in combination with tuber yield reductions. Additionally, we found an approach to combine this multivariable stress severity index with remote sensing (NDVI, PRI, thermography). With this aggregation we are able to identify drought tolerant and susceptible potato genotypes under

mild stress. To include standard drought tolerance indices, like tolerance index, mean productivity, geometric mean productivity, it can be tested, how the SSI is correlated with to speed up the selection process. Additionally, further specification of a certain SSI values, like

point of no return in terms of no tuber yield recover can defined. The SSI can be tested to estimate water requirement in potato production. With the SSI we know the sensitive and less sensitive phenological stage of the potato plants and in combination with actual soil water measurements we could calculate the actual stress severity to organize time-phased irrigation as water saving strategy.

7 Appendix

Appendix A.1. Chemical soil analysis.

Texture	Depth (cm)	E.C. (1:1, dS/m)	$CaCO_3$ (%)	P (ppm)	K (ppm)
Loam	0-15	0.84	0.14	16.88	499.20
	15-30	0.62	0.12	3.52	321.40
Sand	0-15	2.81	0	19.82	447.40
	15-30	1.01	0	11.66	325.80

		Exchangeable Cations (meg/100g)				
		CEC	Ca^{2+}	Mg^{2+}	K^{+}	Na^{+}
Loam	0-15	6.79	3.36	1.67	1.31	0.44
	15-30	6.08	3.29	1.42	0.91	0.46
Sand	0-15	4.86	2.58	1.33	0.72	0.23
	15-30	3.84	1.81	1.13	0.67	0.24

Appendix A.2. The Breeders code, variety name, grouping of the genotype according to target region and the duration to physiological maturity of the tested potato genotypes. The duration to physiological maturity as determined in Majes is classified as follows: very early <70 days, early 70-80 days, intermediate 80-90 days and late >90 days.

No.	CIP number	Group	Duration - Majes	Variety name
G1	CIP 392797.22	Lowland tropic virus-resistant	Early	Unica
G2	CIP 397078.12	Lowland tropic virus-resistant	Intermediate	
G3	CIP 392025.7	Lowland tropic virus-resistant	Intermediate	
G4	CIP 397073.16		Early	
G5	CIP 301040.63	Lowland tropic virus & late blight resistant	Late	

8 References

Aien, A., Chaturvedi, A. K., Bahuguna, R. N., & Pal, M. (2017). Phenological sensitivity to high temperature stress determines dry matter partitioning and yield in potato. *Indian Journal of Plant Physiology*, *22*(1), 63–69. https://doi.org/10.1007/s40502-016-0270-z

Albiski, F., Najla, S., Sanoubar, R., Alkabani, N., & Murshed, R. (2012). In vitro screening of potato lines for drought tolerance. *Physiology and Molecular Biology of Plants*, *18*(4), 315–321. https://doi.org/10.1007/s12298-012-0127-5

Ali, M., Jensen, C. R., Mogensen, V. O., & Bahrun, A. (1999). Drought adaptation of fleld grown wheat in relation to soil physical conditions. *Plant and Soil*, *208*, 149–159. https://doi.org/https://doi.org/10.1023/A:1004535819197

Aliche, E. B., Oortwijn, M., Theeuwen, T. P. J. M., Bachem, C. W. B., Visser, R. G. F., & van der Linden, C. G. (2018). Drought response in fi eld grown potatoes and the interactions between canopy growth and yield. *Agricultural Water Management*, *206*(October 2017), 20–30. https://doi.org/10.1016/j.agwat.2018.04.013

Aliche, Ernest B., Theeuwen, T. P. J. M., Oortwijn, M., Visser, R. G. F., & van der Linden, C. G. (2020). Carbon partitioning mechanisms in POTATO under drought stress. *Plant Physiology and Biochemistry*, *146*, 211–219. https://doi.org/10.1016/j.plaphy.2019.11.019

Aliche, Ernest B, Oortwijn, M., Theeuwen, T. P. J. M., Bachem, C. W. B., Visser, R. G. F., & Linden, C. G. Van Der. (2018). Drought response in field grown potatoes and the interactions between canopy growth and yield. *Agricultural Water Management*, *206*, 20–30. https://doi.org/10.1016/j.agwat.2018.04.013

Anithakumari, A. M., Nataraja, K. N., Visser, R. G. F., & van der Linden, C. G. (2012). Genetic dissection of drought tolerance and recovery potential by quantitative trait locus mapping of a diploid potato population. *Molecular Breeding : New Strategies in Plant Improvement*, *30*(3), 1413–1429. https://doi.org/10.1007/s11032-012-9728-5

Araus, J. L., & Cairns, J. E. (2014). Field high-throughput phenotyping: The new crop breeding frontier. *Trends in Plant Science*. https://doi.org/10.1016/j.tplants.2013.09.008

Asch, F., Bahrun, A., & Jensen, C. R. (2009). Root-shoot communication of field-grown maize drought-stressed at different rates as modified by atmospheric conditions. *Journal of Plant Nutrition and Soil Science*, *172*(5), 678–687. https://doi.org/10.1002/jpln.200800214

Auber, J., Khan, M. A., Farfan, E., Bonierbale, M., & Asch, F. (2014). Does combining canopy reflectance and canopy temperature allow identifying drought resistance strategies in potato? In *Tropentag: International Research on Food Security, Natural Resource Management and Rural Development*. Prague.

Banika, P., Zengb, W., Taic, H., Bizimunguc, B., & Tanino, K. (2016). Effects of drought acclimation on drought stress resistance in three potato (*Solanum tuberosum* L .) genotypes. *Environment, Development and Botany*, *126*, 76–89. https://doi.org/10.1016/j.envexpbot.2016.01.008

Beyene, Z. K., Mekbib, F., Abebe, T., & Asfaw, A. (2019). Drought Resistance Indices for Screening of Potato (*Solanum tuberosum* L.) Genotypes. *Turkish Journal of Agriculture - Food Science and Technology*, *7*(8), 1118–1124. https://doi.org/10.24925/turjaf.v7i8.1118-1124.2226

Blum, A. (2005). Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? *Australian Journal of Agricultural Research*, *56*, 1159–1168. https://doi.org/10.1071/AR05069

Boguszewska-Mańkowska, D., Pieczyński, M., Wyrzykowska, A., Kalaji, H. M., Sieczko, L., Szweykowska-Kulińska, Z., & Zagdańska, B. (2017). Divergent strategies displayed by potato (*Solanum tuberosum* L.) cultivars to cope with soil drought. *Journal of Agronomy and Crop Science*, *204*(1), 13–30. https://doi.org/10.1111/jac.12245

Boguszewska-Mańkowska, D., Zarzyńska, K., & Nosalewicz, A. (2020). Drought Differentially Affects Root System Size and Architecture of Potato Cultivars with Differing Drought Tolerance. *American Journal of Potato Research*, *97*(1), 54–62. https://doi.org/10.1007/s12230-019-09755-2

Boguszewska, D., Zarzy, K., & Wasilewska-Nascimento, B. (2022). Potato (*Solanum tuberosum* L .) Plant Shoot and Root Changes under Abiotic Stresses — Yield Response. *Plants*, *11*(3568), 1–13. https://doi.org/10.3390/plants11243568

Breidenbach, R. W., Saxton, M. J., Hansen, L. D., & Criddle, R. S. (1997). Heat generation and dissipation in plants: can the alternative oxidative phosphorylation pathway serve a thermoregulatory role in plant tissues other than specialized organs? *Plant Physiology*, *114*(4), 1137–1140. https://doi.org/10.1104/pp.114.4.1137

Broge, N. H., & Mortensen, J. V. (2002). Deriving green crop area index and canopy chlorophyll density of winter wheat from spectral reflectance data. *Remote Sensing of Environment*, *81*(1), 45–57. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S0034425701003327

Cabello, R., De Mendiburu, F., Bonierbale, M., Monneveux, P., Roca, W., & Chujoy, E. (2012). Large-Scale Evaluation on Potato Improved Varieties. Genetic Stocks and Landraces for Drought Tolerance. *American Journal of Potato Research*, *89*, 400–410. https://doi.org/10.1007/s12230-012-9260-5

Cabello, Rolando, Monneveux, P., Mendiburu, F., & Bonierbale, M. (2013). Comparison of yield based drought tolerance indices in improved varieties, genetic stocks and landraces of potato (*Solanum tuberosum* L.). *Euphytica*, *193*(2), 147–156. https://doi.org/10.1016/j.eja.2005.05.004

Cabrera-Bosquet, L., Molero, G., Stellacci, A., Bort, J., Nogués, S., & Araus, J. (2011). NDVI as a potential tool for predicting biomass, plant nitrogen content and growth in wheat genotypes subjected to different water and nitrogen conditions. *Cereal Research Communications*, *39*(1), 147–159. https://doi.org/10.1556/CRC.39.2011.1.15

Carli, C., Yuldashev, F., Khalikov, D., Condori, B., Mares, V., & Monneveux, P. (2014). Effect of different irrigation regimes on yield, water use efficiency and quality of potato (*Solanum tuberosum* L.) in the lowlands of Tashkent, Uzbekistan: A field and modeling perspective. *Field Crops Research*, *163*, 90–99. https://doi.org/10.1016/j.fcr.2014.03.021

Celis-Gamboa, C., Struik, P. C., Jacobsen, E., & Visser, R. G. F. (2003). Temporal dynamics of tuber formation and related processes in a crossing population of potato (*Solanum tuberosum*). *Annals of Applied Biology*, *143*, 175–186. https://doi.org/10.1111/j.1744-7348.2003.tb00284.x

Chang, D. C., Jin, Y. I., Nam, J. H., Cheon, C. G., Cho, J. H., Kim, S. J., & Yu, H.-S. (2018). Early drought effect on canopy development and tuber growth of potato cultivars with different maturities. *Field Crops Research*, *215*, 156–162. https://doi.org/https://doi.org/10.1016/j.fcr.2017.10.008

Chen, C. (2015). Determining the leaf emissivity of three crops by infrared thermometry. *Sensors (Switzerland)*, *15*(5), 11387–11401. https://doi.org/10.3390/s150511387

Coops, N. C., Hilker, T., Hall, F. G., Nichol, C. J., & Drolet, G. G. (2010). Estimation of light-use efficiency of terrestrial ecosystems from space: A status report. *BioScience*, *60*(10), 788–797. https://doi.org/10.1525/bio.2010.60.10.5

Dahal, K., Li, X.-Q., Tai, H., Creelman, A., & Bizimungu, B. (2019). Improving potato stress tolerance and tuber yield under a climate change scenario – a current overview. *Frontiers in Plant Science*, *10*, 1–16. https://doi.org/10.3389/fpls.2019.00563

Dalla Costa, L., Delle Vedove, G. Gianquintoi, G., Giovanardi, R., & Peressotti, A. (1997). Yield, water use efficiency and nitrogen uptake in potato: influence of drought stress. *Potato Research*, *40*, 19–34. https://doi.org/10.1007/BF02407559

Deblonde, P. M. K., Haverkort, A. J., & Ledent, J. F. (1999). Responses of early and late potato cultivars to moderate drought conditions: agronomic parameters and carbon isotope discrimination. *European Journal of Agronomy*, *11*(2), 91–105. https://doi.org/https://doi.org/10.1016/S1161-0301(99)00019-2

Deblonde, P. M. K., & Ledent, J. F. (2001a). Effects of moderate drought conditions on green leaf number, stem height, leaf length and tuber yield of potato cultivars. *European Journal of Agronomy*, *14*(1), 31–41. https://doi.org/10.1016/S1161-0301(00)00081-2

Deblonde, P. M. K., & Ledent, J. F. (2001b). Effects of moderate drought conditions on green leaf number, stem height, leaf length and tuber yield of potato cultivars. *European Journal of Agronomy*, *14*(1), 31–41. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S1161030100000812

Diaz-Valencia, P., Melgarejo, L. M., Arcila, I., & Mosquera-Vásquez, T. (2021). Physiological, biochemical and yield-component responses of *solanum tuberosum* L. Group phureja genotypes to a water deficit. *Plants*, *10*(638), 1–13. https://doi.org/10.3390/plants10040638

Doorenbos, J., & Kassam, A. H. (1979). Yield response to water. *FAO Irrigation and Drainage Papers*, *33*. https://doi.org/10.1016/B978-0-08-025675-7.50021-2

Ewing, E. E., & Struik, P. C. (1992). Tuber formation in potato: induction, initiation, and growth I. In J. D. Ivins & E. L. Milthorpe (Eds.), *Horticultural Reviews* (Vol. 14, pp. 89–198). https://doi.org/https://doi.org/10.1002/9780470650523.ch3

FAO. (2008). International Year of the Potato 2008. Potato and water resources.URL https://www.fao.org/agriculture/crops/thematic-sitemap/theme/hort-indust-crops/international-year-of-the-potato/en/

FAOSTAT. (2018). FAOSTAT. URL https://www.fao.org/faostat/en/

Ferrio, J. P., Villegas, D., Zarco, J., Aparicio, N., Araus, J. L., & Royo, C. (2005). Assessment of durum wheat yield using visible and near-infrared reflectance spectra of canopies. *Field Crops Research*, *94*(2–3), 126–148. https://doi.org/10.1016/j.fcr.2004.12.002

Fischer, R., & Maurer, R. (1978). Drought resistance in spring wheat cultivars. I. Grain yield responses. *Crop and Pasture Science*, *29*, 897–912. https://doi.org/https://doi.org/10.1071/AR9780897

Food and Agriculture Organization of the United Nations. (2015). Crop Water Information: Potato. URL http://www.fao.org/nr/water/cropinfo_potato.html (13/07/2020)

Gamon, J. A., Serrano, L., & Surfus, J. S. (1997). The photochemical reflectance index: An optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia*, *112*(4), 492–501. https://doi.org/10.1007/s004420050337

Geremew, E. B., Steyn, J. M., & Annandale, J. G. (2007). Evaluation of growth performance and dry matter partitioning of four processing potato (*Solanum tuberosum*) cultivars. *New Zealand Journal of Crop and Horticultural Science*, *35*(3), 385–393. https://doi.org/10.1080/01140670709510204

Gerhards, M., Rock, G., Schlerf, M., & Udelhoven, T. (2016). Water stress detection in potato plants using leaf temperature, emissivity, and reflectance. *International Journal of Applied Earth Observation and Geoinformation*, *53*, 27–39. https://doi.org/10.1016/j.jag.2016.08.004

Grant, O. M., Davies, M. J., James, C. M., Johnson, A. W., Leinonen, I., & Simpson, D. W. (2012). Thermal imaging and carbon isotope composition indicate variation amongst strawberry (Fragaria×ananassa) cultivars in stomatal conductance and water use efficiency. *Environmental and Experimental Botany*, *76*, 7–15. https://doi.org/10.1016/j.envexpbot.2011.09.013

Gratani, L. (2014). Plant Phenotypic Plasticity in Response to Environmental Factors. *Advances in Botany*, *2014*, 1–17. https://doi.org/10.1155/2014/208747

Halterman, D., Guenthner, J., Collinge, S., Butler, N., & Douches, D. (2015). Biotech Potatoes in the 21st Century: 20 Years Since the First Biotech Potato. *American Journal of Potato Research*, *93*(1), 1–20. https://doi.org/10.1007/s12230-015-9485-1

Handayani, T., & Watanabe, K. (2020). The combination of drought and heat stress has a greater effect on potato plants than single stresses. *Plant, Soil and Environment*, *66*(4), 175–182. https://doi.org/10.17221/126/2020-PSE

Harris, D. R., & Hillmann, G. C. (2014). *Foraging and Farming: The Evolution of Plant Exploitation*. (D. R. Harris, Ed.) (1st Editio). London: Routledge.

Haverkort, A. J., Van De Waart, M., & Bodlaender, K. B. A. (1990). The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions. *Potato Research*, *33*(1), 89–96. https://doi.org/10.1007/BF02358133

Hijmans, R. J. (2003). The effect of climate change on global potato production. *American Journal of Potato Research*, *80*, 271–280. Retrieved from http://www.springerlink.com/index/N87N1L247271269X.pdf

Hill, D., Nelson, D., Hammond, J., & Bell, L. (2021). Morphophysiology of Potato (*Solanum tuberosum*) in Response to Drought Stress: Paving the Way Forward. *Agronomie*, *11*, 257–268. https://doi.org/doi: 10.1051/agro:2002089

Hoelle, J., Asch, F., Khan, A., & Bonierbale, M. (2020). Phenology-adjusted stress severity index to assess genotypic responses to terminal drought in field grown potato. *Agronomy*, *10*(9), 1–17. https://doi.org/10.3390/agronomy10091298

Hoelle, J., Kuppinger, L., Zumaran, J., Farfan, E., Khan, M. A., Bonierbale, M., & Asch, F. (2017). Drought effects on the synchrony of above and belowground phenology of five

potato clones. In *Tropentag: Future Agriculture: Social-ecological transitions and bio-cultural shifts*. Bonn.

Hughes, J. C. (1974). Factors influencing the quality of ware potatoes. 2. Environmental factors. *Potato Research*, *17*, 512–547. https://doi.org/https://doi.org/10.1007/BF02362168

Idso, S. B. (1982). Non-water-stressed baselines: a key to measuring and interpreting plant water stress. *Agricultural Meteorology*, *27*, 59–70. https://doi.org/10.1016/0002-1571(82)90020-6

Idso, S. B., Jackson, R. D., Pinter Jr., P. J., Reginato, R. J., & Hatfield, J. L. (1981). Normalizing the stress-degree-day parameter for environmental variability. *Agricultural Meteorology*, *24*, 45–55. Retrieved from http://www.sciencedirect.com/science/article/pii/0002157181900327

Ihuoma, S. O., & Madramootoo, C. A. (2019). Sensitivity of spectral vegetation indices for monitoring water stress in tomato plants. *Computers and Electronics in Agriculture*, *163*, 104860. https://doi.org/10.1016/j.compag.2019.104860

Ivins, J. D., & Bremner, P. M. (1965). Growth, Development and Yield in the Potato. *Outlook on Agriculture*, *4*, 211–217. https://doi.org/https://doi.org/10.1177/003072706500400503

Iwama, K. (2008). Physiology of the Potato: New Insights into Root System and Repercussions for Crop Management. *Potato Research*, *51*(3–4), 333–353. https://doi.org/10.1007/s11540-008-9120-3

Jefferies, R. A. (1993). Cultivar responses to water stress in potato: effects of shoot and roots. *New Phytologist*, *123*(3), 491–498. https://doi.org/10.1111/j.1469-8137.1993.tb03761.x

Jefferies, R. A., & Lawson, H. M. (1991). A key for the stages of development of potato (Solatnum tuberosum L.). *Annals of Applied Biology*, *119*, 387–399. https://doi.org/DOI: 10.1111/j.1744-7348.1991.tb04879.x

Jefferies, R. a., & Mackerron, D. K. L. (1989). Radiation interception and growth of irrigated and droughted potato (*Solanum tuberosum*). *Field Crops Research*, *22*(2), 101–112. https://doi.org/10.1016/0378-4290(89)90061-0

Jefferies, R. A., & Mackerron, D. K. L. (1987). Aspects of the physiological basis of cultivar differences in yield of potato under droughted and irrigated conditions. *Potato Research*, *30*(2), 201–217. https://doi.org/10.1007/BF02357663

Jefferies, R. A., & Mackerron, D. K. L. (1993). Responses of potato genotypes to drought. II. Leaf area index, growth and yield. *Annals of Applied Biology*, *122*(122), 105–112. https://doi.org/10.1111/j.1744-7348.1993.tb04018.x

Jensen, C. R., Mogensen, V. O., Mortensen, G., Fieldsend, J. K., Milford, G. F. J., Andersen, M. N., & Thage, J. H. (1996). Seed glucosinolate, oil and protein contents of field-grown rape (Brassica napus L.) affected by soil drying and evaporative demand. *Field Crops Research*, *47*(2–3), 93–105. https://doi.org/10.1016/0378-4290(96)00026-3

Jensen, C. R., Mogensen, V. O., Poulsen, H.-H., Henson, I. E., Aagot, S., Hansen, E., Ali, M., Wollenweber, B. (1998a). Soil water matric potential rather than water content determines drought responses in field-grown lupin (Lupinus angustifolius). *Australian Journal of Agricultural Research*, *25*, 353–363. https://doi.org/10.1071/PP97072

Jensen, Ch. R., Battilani, A., Plauborg, F., Psarras, G., Chartzoulakis, K., Janowiak, F., Stikic, R., Jovanovic, Z., Li, G., Qi, X., Liu, F., Jacobsen, S. E., Andersen, M. N. (2010). Deficit irrigation based on drought tolerance and root signalling in potatoes and tomatoes. *Agricultural Water Management*, *98*(3), 403–413. https://doi.org/10.1016/j.agwat.2010.10.018

Jones, H. G. (1999). Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant, Cell and Environment*, *22*(9), 1043–1055. https://doi.org/10.1046/j.1365-3040.1999.00468.x

Jones, H. G. (2002). Use of infrared thermography for monitoring stomatal closure in the field: application to grapevine. *Journal of Experimental Botany*, *53*(378), 2249–2260. https://doi.org/10.1093/jxb/erf083

Jones, H. G., Archer, N., Rotenberg, E., & Casa, R. (2003). Radiation measurement for plant ecophysiology. *Journal of Experimental Botany*, *54*(384), 879–889. https://doi.org/10.1093/jxb/erg116

Jones, H. G., Serraj, R., Loveys, B. R., Xiong, L., Wheaton, A., & Price, A. H. (2009). Thermal infrared imaging of crop canopies for the remote diagnosis and quantification of

plant responses to water stress in the field. *Functional Plant Biology*, *36*(11), 978. https://doi.org/10.1071/FP09123

Junhong, Q., Bian, C., Jiangang, L., Zhang, J., & Liping, J. (2019). An efficient greenhouse method to screen potato genotypes for drought tolerance. *Scientia Horticulturae*, *253*, 61–69. https://doi.org/10.1111/jac.12119

Kebede, Z., Firew, M., Tesfaye, D., & Asrat, A. (2019). Drought Resistance Indices for Screening of Potato (*Solanum tuberosum* L.) Genotypes. *Turkish Journal of Agriculture - Food Science and Technology*, *7*(8), 1118. https://doi.org/10.24925/turjaf.v7i8.1118-1124.2226

Khan, M. A., Saravia, D., Munive, S., Lozano, F., Farfan, E., Eyzaguirre, R., & Bonierbale, M. (2015). Multiple QTLs Linked to Agro-Morphological and Physiological Traits Related to Drought Tolerance in Potato. *Plant Molecular Biology Reporter*, *33*(5), 1286–1298. https://doi.org/10.1007/s11105-014-0824-z

Kohzuma, K., Tamaki, M., & Hikosaka, K. (2021). Corrected photochemical reflectance index (PRI) is an effective tool for detecting environmental stresses in agricultural crops under light conditions. *Journal of Plant Research*, *134*(4), 683–694. https://doi.org/10.1007/s10265-021-01316-1

Kumar, S., Kumar, D., Singh, Y. P., Singh, P., Kumar, A., & Kumar, A. (2020). Determination of assimilate partitioning at different growth stages of potato plant under water stress conditions. *Annals of Horticulture*, *13*(2), 174–177. https://doi.org/10.5958/0976-4623.2020.00030.4

Kuppinger, L., Auber, J., Farfan, E., Khan, M. A., Bonierbale, M., & Asch, F. (2014). Effects of Drought Stress on Crop Development, Growth and Chlorophyll Fluorescence in Five Potato Clones. In E. Tielkes (Ed.), *Tropentag: Bridging the gap between increasing knowledge and decreasing resources*. Prague, Czech Republic.

Lahlou, O., & Ledent, J.-F. (2005). Root mass and depth, stolons and roots formed on stolons in four cultivars of potato under water stress. *European Journal of Agronomy*, *22*(2), 159–173. https://doi.org/https://doi.org/10.1016/j.eja.2004.02.004

Lahlou, O., Ouattar, S., & Ledent, J.-F. (2003). The effect of drought and cultivar on growth parameters, yield and yield components of potato. *Agronomie, EDP Science*, *23*(3), 257–

268. https://doi.org/10.1051/agro:2002089

Lefèvre, I., Ziebel, J., Guignard, C., Hausman, J.-F., Gutiérrez Rosales, R. O., Bonierbale, M., Hoffmann, L., Schafleitner, R., Evers, D. (2012). Drought Impacts Mineral Contents in Andean Potato Cultivars. *Journal of Agronomy and Crop Science*, *198*(3), 196–206. https://doi.org/10.1111/j.1439-037X.2011.00499.x

Levitt, J. (1980). Responses of plants to environmental stresses. In *Responses of plants to environmental stresses* (Vol. 2;2, pp. 213–228). New York: Academic Press.

Levy, D. (1986). Tuber yield and tuber quality of several potato cultivars as affected by seasonal high temperatures and by water deficit in a semi-arid environment. *Potato Research*, *29*(1), 95–107. https://doi.org/10.1007/BF02361984

Levy, David, & Veilleux, R. E. (2007). Adaptation of potato to high temperatures and salinity-a review. *American Journal of Potato Research*, *84*(6), 487–506. https://doi.org/10.1007/BF02987885

Li, X., Ramírez, D. A., Qin, J., Dormatey, R., Bi, Z., Sun, C., Wan, H., Bai, J. (2019). Water restriction scenarios and their effects on traits in potato with different degrees of drought tolerance. *Scientia Horticulturae*, *256*(108525), 1–9. https://doi.org/10568/101472

Lizana, X. C., Avila, A., Tolaba, A., & Martinez, J. P. (2017). Field responses of potato to increased temperature during tuber bulking: Projection for climate change scenarios, at high-yield environments of Southern Chile. *Agricultural and Forest Meteorology*, *239*, 192–201. https://doi.org/https://doi.org/10.1016/j.agrformet.2017.03.012

Luitel, B. P., Khatri, B. B., Choudhary, D., Paudel, B. P., Jung-Sook, S., Hur, O.-S., Baek, H. J., Cheol, K. H., Yul, R. K. (2015). Growth and Yield Characters of Potato Genotypes Grown in Drought and Irrigated Conditions of Nepal. *International Journal of Applied Sciences and Biotechnology*, *3*(3), 513–519. https://doi.org/10.3126/ijasbt.v3i3.13347

Lukina, E. V., Stone, M. L., & Raun, W. R. (1999). Estimating vegetation coverage in wheat using digital images. *Journal of Plant Nutrition*, *22*(2), 341–350. https://doi.org/10.1080/01904169909365631

Lutaladio, N., & Castaldi, L. (2009). Potato: The hidden treasure. *Journal of Food Composition and Analysis*, *22*(6), 491–493. https://doi.org/10.1016/j.jfca.2009.05.002

MacKerron, D. K. L., & Jefferies, R. A. (1986). The influence of early soil moisture stress on tuber numbers in potato. *Potato Research*, *29*(3), 299–312. https://doi.org/10.1007/BF02359959

Maestrini, B., Matthijs, B., Thomas, B., & Lambertus A. P., L. (2020). Can We Use the Relationship Between Within-Field Elevation and NDVI as an Indicator of Drought-Stress? In *Environmental Software Systems. Data Science in Action, 13th IFIP WG 5.11 International Symposium, Wageningen, The Netherlands, February 5–7, 2020, Proceedings* (pp. 122–131). https://doi.org/10.1007/978-3-030-39815-6_12

Mane, S. P., Robinet, C. V., Ulanov, A., Schafleitner, R., Tincopa, L., Gaudin, A., Nomberto, G., Alvarado, C., Solis, C., Bolivar, L. A., Blas, R., Ortega, O., Solis, J., Panta, A., Rivera, C., Samolski, I., Carbajulca, D. H., Bonierbale, M., Pati, A., Heath, L. S., Bohnert, H. J., Grene, R. (2008). Molecular and physiological adaptation to prolonged drought stress in the leaves of two Andean potato genotypes. *Functional Plant Biology*, *35*(8), 669–688. https://doi.org/10.1071/FP07293

Martin, R. J., Jamieson, P. D., Wilson, D. R., & Francis, G. S. (1992). Effects of soil moisture deficits on yield and quality of 'russet burbank' potatoes. *New Zealand Journal of Crop and Horticultural Science*, *20*(1), 1–9. https://doi.org/10.1080/01140671.1992.10422319

Meier, U. (1997). *Growth stages of mono- and dicotyledonous plants.* (M. U, Ed.). Blackwell, Berlin. https://doi.org/10.5073/20180906-074619

Meier, U. (2001). *Growth stages of mono-and dicotyledonous plants BBCH Monograph* (2nd ed.). Braunschweig: Federal Biological Research Centre for Agriculture and Forestry. https://doi.org/10.5073/20180906-074619

Merlot, S., Mustilli, A. C., Genty, B., North, H., Lefebvre, V., Sotta, B., Vavasseur, A., Giraudat, J. (2002). Use of infrared thermal imaging to isolate Arabidopsis mutants defective in stomatal regulation. *Plant Journal*, *30*(5), 601–609. https://doi.org/10.1046/j.1365-313X.2002.01322.x

Michel, A. J., Teixeira, E. I., Brown, H. E., Dellow, S. J., Maley, S., Gillespie, R. N., & Richards, K. K. (2019). Water stress responses of three potato cultivars. *Agronomy New Zealand*, *49*, 25–37. https://doi.org/10.1111/j.1469-8137.1993.tb03761.x

Minhas, J. S., & Bansal, K. C. (1991). Tuber yield in relation to water stress at different stages

of growth in potato (*Solanum tuberosum* L.). *Journal Indian Potato Association*, *18*(1–2), 1–8. https://doi.org/10.1080/1343943X.2021.1963293

Mistele, B., & Schmidhalter, U. (2008). Spectral measurements of the total aerial N and biomass dry weight in maize using a quadrilateral-view optic. *Field Crops Research*, *106*(1), 94–103. https://doi.org/10.1016/j.fcr.2007.11.002

Monneveux, P., Ramírez, D., & Pino, M.-T. (2013). Drought tolerance in potato (S. tuberosum L.): Can we learn from drought tolerance research in cereals? *Plant Science : An International Journal of Experimental Plant Biology*, *205–206*, 76–86. https://doi.org/10.1016/j.plantsci.2013.01.011

Moosavi, S. S., Samadib, B. Y., Naghavic, M. R., Zalib, A. A., Dashtid, H., & Pourshahbazie, A. (2008). Introduction of new indices to identify relative drought tolerance and resistance in wheat genotypes. *Desert*, *5*(12), 165–178. https://doi.org/10.22059/JDESERT.2008.27115

Mould, R. D., & Rutherfoord, R. J. (1980). The effect of moisture stress during consecutive growth stages on tuber yield and quality of BP1 potatoes (*Solanum tuberosum* L.). *Crop Prod*, *9*, 89–92. https://doi.org/10.1007/BF02849334

Muthoni, J., & Kabira, J. N. (2016). Potato Production under Drought Conditions: Identification of Adaptive Traits. *International Journal of Horticulture*, *6*(12), 1–10. https://doi.org/10.5376/ijh.2016.06.0012

Muthoni, J., & Shimelis, H. (2020). Heat and drought stress and their implications on potato production under dry African tropics. *Australian Journal of Crop Science*, *14*(9), 1405–1414. https://doi.org/10.21475/ajcs.20.14.09.p2402

Nasir, M. W. (2022). Effect of Drought Stress on Potato Production : A Review. *Agronomy*, *12*(635), 1–22. https://doi.org/https://doi.org/10.3390/agronomy12030635

Nouri, A., Nezami, A., Kafi, M., & Hassanpanah, D. (2016). Growth and yield response of potato genotypes to deficit irrigation. *International Journal of Plant Production*, *10*(April), 139–158. https://doi.org/10.22069/ijpp.2016.2785

Ober, E. S., Bloa, M. Le, Clark, C. J. a., Royal, A., Jaggard, K. W., & Pidgeon, J. D. (2005). Evaluation of physiological traits as indirect selection criteria for drought tolerance in

sugar beet. *Field Crops Research*, *91*(2–3), 231–249. https://doi.org/10.1016/j.fcr.2004.07.012

Obidiegwu, J. E., Bryan, G. J., Jones, H. G., & Prashar, A. (2015). Coping with drought: stress and adaptive responses in potato and perspectives for improvement. *Frontiers in Plant Science*, *6*(542), 1–23. https://doi.org/10.3389/fpls.2015.00542

Onder, S., Caliskan, M. E., Onder, D., & Caliskan, S. (2005). Different irrigation methods and water stress effects on potato yield and yield components. *Agricultural Water Management*, *73*(1), 73–86. https://doi.org/10.1016/j.agwat.2004.09.023

Panigada, C., Rossini, M., Meroni, M., Cilia, C., Busetto, L., & Amaducci, S. (2014). International Journal of Applied Earth Observation and Geoinformation Fluorescence , PRI and canopy temperature for water stress detection in cereal crops. *International Journal of Applied Earth Observations and Geoinformation*, *30*, 167–178. https://doi.org/10.1016/j.jag.2014.02.002

Peñuelas, J., & Filella, I. (1998). Visible and near-infrared reflectance techniques for diagnosing plant physiological status. *Trends in Plant Science*, *3*(4), 151–156. Retrieved from http://www.sciencedirect.com/science/article/pii/S1360138598012138

Puértolas, J., Ballester, C., Elphinstone, E. D., & Dodd, I. C. (2014). Two potato (*Solanum tuberosum*) varieties differ in drought tolerance due to differences in root growth at depth. *Functional Plant Biology*, *41*(11), 1107–1118. https://doi.org/10.1071/FP14105

Rahaman, M. M., Chen, D., Gillani, Z., Klukas, C., & Chen, M. (2015). Advanced phenotyping and phenotype data analysis for the study of plant growth and development. *Frontiers in Plant Science*, *6*(August), 1–15. https://doi.org/10.3389/fpls.2015.00619

Ramírez, D. a., Yactayo, W., Gutiérrez, R., Mares, V., De Mendiburu, F., Posadas, A., & Quiroz, R. (2014). Chlorophyll concentration in leaves is an indicator of potato tuber yield in water-shortage conditions. *Scientia Horticulturae*, *168*, 202–209. https://doi.org/10.1016/j.scienta.2014.01.036

Ramírez, D. A., Yactayo, W., Rens, L. R., Rolando, J. L., Palacios, S., De Mendiburu, F., Mares, V., Barreda, C., Loayza, H., Monneveux, P., Zotarelli, L., Khan, A., Quiroz, R. (2016). Defining biological thresholds associated to plant water status for monitoring water restriction effects: Stomatal conductance and photosynthesis recovery as key

indicators in potato. *Agricultural Water Management*, *177*, 369–378. https://doi.org/10.1016/j.agwat.2016.08.028

Ranjbar, M., Esfahani, M. N., Esfahani, M. N., & Salehi, S. (2012). Phenology and Morphological Diversity of the Main Potato Cultivars in Iran. *Journal of Ornamental and Horticultural Plants*, *2*(3), 201–212. https://doi.org/10.1007 › 978-3-030-30343-3_4

Rauf, S., Al-Khayri, J. M., Zaharieva, M., Monneveux, P., & Khalil, F. (2016). Breeding strategies to enhance drought tolerance in crops. *Advances in Plant Breeding Strategies: Agronomic, Abiotic and Biotic Stress Traits*, *2*, 397–445.

Ray, D. K., Mueller, N. D., West, P. C., & Foley, J. A. (2013). Yield Trends Are Insufficient to Double Global Crop Production by 2050. *PLoS ONE*, *8*(6). https://doi.org/10.1371/journal.pone.0066428

Ray, S. S., Das, G., Singh, J. P., & Panigrahy, S. (2006). Evaluation of hyperspectral indices for LAI estimation and discrimination of potato crop under different irrigation treatments. *International Journal of Remote Sensing*, *27*(24), 5373–5387. https://doi.org/10.1080/01431160600763006

Reddy, J. M., Jumaboev, K., Bobojonov, I., Carli, C., & Eshmuratov, D. (2016). Yield and water use efficiency of potato varieties under different soil-moisture stress conditions in the Fergana Valley of Central Asia. *Agroecology and Sustainable Food Systems*, *40*(5), 407–431. https://doi.org/10.1016/j.agwat.2012.03.008

Rivera-Hernández, B., Carrillo-Ávila, E., Obrador-Olán, J. J., Juárez-López, J. F., Aceves-Navarro, L. A., & García-López, E. (2009). Soil moisture tension and phosphate fertilization on yield components of A-7573 sweet corn (Zea mays L.) hybrid, in Campeche, Mexico. *Agricultural Water Management*, *96*(9), 1285–1292. https://doi.org/10.1016/j.agwat.2009.03.020

Rodriguez, D., & Sadras, V. (2005). Spatial assessment of the physiological status of wheat crops as affected by water and nitrogen supply using infrared thermal imagery. *Australian Journal of Agricultural Research*, *56*, 983–993. https://doi.org/10.1071/AR05035

Rodríguez, P. L., Sanjuanelo, C., D., Ñústez L., C. E., & Moreno-Fonseca, L. P. (2016). Growth and phenology of three Andean potato varieties (*Solanum tuberosum* L.) under

water stress. *Agronomía Colombiana*, *34*(2), 141–154. https://doi.org/10.15446/agron.colomb.v34n2.55279

Rolando, J. L., Ramírez, D. A., Yactayo, W., Monneveux, P., & Quiroz, R. (2015). Leaf greenness as a drought tolerance related trait in potato (*Solanum tuberosum* L.). *Environmental and Experimental Botany*, *110*, 27–35. https://doi.org/10.1016/j.envexpbot.2014.09.006

Romano, G., Zia, S., Spreer, W., Sanchez, C., Cairns, J., Araus, J. L., & Müller, J. (2011). Use of thermography for high throughput phenotyping of tropical maize adaptation in water stress. *Computers and Electronics in Agriculture*, *79*(1), 67–74. https://doi.org/10.1016/j.compag.2011.08.011

Romero, A. P., Alarcón, A., Valbuena, R. I., & Galeano, C. H. (2017). Physiological assessment of water stress in potato using spectral information. *Frontiers in Plant Science*, *8*, 1–17. https://doi.org/10.3389/fpls.2017.01608

Rouse, J., Haas, R. H., Schell, J. A., & Deering, D. W. (1974). Monitoring vegetation systems in the great plains with ERTS. In *Third Earth Resources Technology Satellite-1 Symposium* (pp. 301–317). Greenbel: NAS ASP-351.

Salaman, R. N. (1985). *The history and social influence of the potato*. (U. of B. J. G. Hawkes, Ed.) (2nd ed.). Birmingham: University of Birmingham.

Santini, M., Noce, S., Antonelli, M., & Caporaso, L. (2022). Complex drought patterns robustly explain global yield loss for major crops. *Scientific Reports*. https://doi.org/10.1038/s41598-022-09611-0

Saravia, D., Farfán-Vignolo, E. R., Gutiérrez, R., De Mendiburu, F., Schafleitner, R., Bonierbale, M., & Khan, M. A. (2016). Yield and Physiological Response of Potatoes Indicate Different Strategies to Cope with Drought Stress and Nitrogen Fertilization. *American Journal of Potato Research*, *93*(3), 288–295. https://doi.org/10.1007/s12230-016-9505-9

Schafleitner, R., Gaudin, A., Gutierrez Rosales, R. O., Aliaga Alvarado, C. A., & Bonierbale, M. (2006). Proline accumulation and real time PCR expression analysis of genes encoding enzymes of proline metabolism in relation to drought tolerance in Andean potato. *Acta Physiologiae Plantarum*, *29*(1), 19–26. https://doi.org/10.1007/s11738-006-

0003-4

Schafleitner, R., Gutierrez, R., Espino, R., Gaudin, A., Pérez, J., Martínez, M., Domínguez, A., Tincopa, L., Alvarado, C., Numberto, G., Bonierbale, M. (2007). Field Screening for Variation of Drought Tolerance in *Solanum tuberosum* L. by Agronomical, Physiological and Genetic Analysis. *Potato Research*, *50*(1), 71–85. https://doi.org/10.1007/s11540-007-9030-9 Field

Schafleitner, R., Gutierrez Rosales, R. O., Gaudin, A., Alvarado Aliaga, C. A., Nomberto Martinez, G., Tincopa Marca, L. R., Bolivar, L. A., Mendiburu Delgado, F., Simon, R., Bonierbale, M. (2007). Capturing candidate drought tolerance traits in two native Andean potato clones by transcription profiling of field grown plants under water stress. *Plant Physiology and Biochemistry : PPB / Société Française de Physiologie Végétale*, *45*(9), 673–690. https://doi.org/10.1016/j.plaphy.2007.06.003

Schittenhelm, S., Sourell, H., & Löpmeier, F. J. (2006). Drought resistance of potato cultivars with contrasting canopy architecture. *European Journal of Agronomy*, *24*(3), 193–202. https://doi.org/10.1016/j.eja.2005.05.004

Sellers, P. J. (1985). Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing*, *6*(8), 1335–1372. https://doi.org/10.1080/01431168508948283

Sellers, P. J. (1987). Canopy reflectance, photosynthesis, and transpiration, II. The role of biophysics in the linearity of their interdependence. *Remote Sensing of Environment*, *21*(2), 143–183. https://doi.org/10.1016/0034-4257(87)90051-4

Sims, D. A., & Gamon, J. A. (2003). Estimation of vegetation water content and photosynthetic tissue area from spectral reflectance: a comparison of indices based on liquid water and chlorophyll absorption features. *Remote Sensing of Environment*, *84*(4), 526–537. Retrieved from http://linkinghub.elsevier.com/retrieve/pii/S0034425702001517

Simunek, J., Sejna, M., & van Genuchten, M. T. (2008). Hydrus-1D, Version 4.17. Prague, Czech Republic: PC-Progress s.r.o. Retrieved from https://www.pc-progress.com/en/Default.aspx?H1d-downloads

Slater, J. W. (1963). Mechanisms of tuber initiation. In J. D. Ivins & F. L. Milthorpe (Eds.), *In*

The Growth of the Potato (pp. 27–34). Nottingham.

Spitters, C. J. T., & Schapendonk, A. (1990). Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. *Plant and Soil*, *123*, 193–203. https://doi.org/10.1007/BF00011268

Sprenger, H., Rudack, K., Schudoma, C., Neumann, A., Seddig, S., Peters, R., Zuther, E., Kopka, J., Hincha, D. K., Walther, D., Köhl, K. (2015). Assessment of drought tolerance and its potential yield penalty in potato. *Functional Plant Biology*, *42*(7), 655–667. https://doi.org/10.1071/FP15013

Stalham, M. A., & Allen, E. J. (2001). Effect of variety, irrigation regime and planting date on depth, rate, duration and density of root growth in the potato (*Solanum tuberosum*) crop. *Journal of Agricultural Science*, *137*(3), 251–270. https://doi.org/10.1017/s0021859601001332

Stark, J. C., Love, S. L., King, B. A., Marshall, J. M., Bohl, W. H., & Salaiz, T. (2013). Potato Cultivar Response to Seasonal Drought Patterns. *American Journal of Potato Research*, *90*(3), 207–216. https://doi.org/10.1007/s12230-012-9285-9

Steckel, J. R. A., & Gray, D. (1979). Drought tolerance in potatoes. *The Journal of Agricultural Science*, *92*(2), 375–381. https://doi.org/10.1017/S0021859600062900

Suárez, L., Zarco-Tejada, P. J., Sepulcre-Cantó, G., Pérez-Priego, O., Miller, J. R., Jiménez-Muñoz, J. C., & Sobrino, J. (2008). Assessing canopy PRI for water stress detection with diurnal airborne imagery. *Remote Sensing of Environment*, *112*(2), 560–575. https://doi.org/10.1016/j.rse.2007.05.009

Tourneux, C., Devaux, A., Camacho, M., Mamani, P., & Ledent, J.-F. (2003a). Agronomy for sustainable development. *Agronomie*, *23*, 169–179. https://doi.org/10.1051/agro

Tourneux, C., Devaux, A., Camacho, M. R., Mamani, P., & Ledent, J. F. (2003b). Effect of water shortage on six potato genotypes in the highlands of Bolivia (II): Water relations, physiological parameters. *Agronomie*, *23*(2), 181–190. https://doi.org/10.1051/agro:2002080

Tuberosa, R. (2012). Phenotyping for drought tolerance of crops in the genomics era. *Frontiers in Physiology*, *3*, 1–5.

van Loon, C. (1981). The effect of water stress on potato growth, development, and yield. *American Journal of Potato Research*, *58*, 51–69. https://doi.org/10.1007/BF02855380

Verhulst, N., & Govaerts, B. (2010). *The normalized difference vegetation index (NDVI) GreenSeeker TM handheld sensor: Toward the integrated evaluation of crop management Part A: Concepts and case studies*. Mexico. Retrieved from https://repository.cimmyt.org/bitstream/handle/10883/550/94192.pdf?sequence=1&isAllowed=y

Viola, R. (2000). Tuber filling and starch synthesis in potato. *Developments in Crops Science*, *26*, 169–194. https://doi.org/https://doi.org/10.1016/S0378-519X(00)80009-4

Vitasse, Y., Bresson, C. C., Kremer, A., Michalet, R., & Delzon, S. (2010). Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology*, *24*(6), 1211–1218. https://doi.org/10.1111/j.1365-2435.2010.01748.x

Vos, J., & Haverkort, A. J. (2007). Water availability and potato crop performance. In *Potato Biology and Biotechnology: Advances and Perspectives* (pp. 333–351). Amsterdam, Netherlands: Elsevier. https://doi.org/10.1016/B978-044451018-1/50058-0

Wang, X., Cai, J., Jiang, D., Liu, F., Dai, T., & Cao, W. (2011). Pre-anthesis high-temperature acclimation alleviates damage to the flag leaf caused by post-anthesis heat stress in wheat. *Journal of Plant Physiology*, *168*(6), 585–593. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21247658

Weisz, R., Kaminski, J., & Smilowitz, Z. (1994). Water deficit effects on potato leaf growth and transpiration: Utilizing fraction extractable soil water for comparison with other crops. *American Potato Journal*, *71*(12), 829–840. https://doi.org/10.1007/BF02849378

Wishart, J., George, T. S., Brown, L. K., White, P. J., Ramsay, G., Jones, H., & Gregory, P. J. (2014). Field phenotyping of potato to assess root and shoot characteristics associated with drought tolerance. *Plant and Soil*, *378*(1–2), 351–363. https://doi.org/10.1007/s11104-014-2029-5

Wurr, D. C. E., Fellows, J. R., & Allen, E. J. (1992). Determination of optimum tuber planting density in th< potato varieties Pentland Squire. *Journal of Agricultural Science*, *119*, 35–44. https://doi.org/10.1017/S0021859600071525

Zaki, H. E. M., & Radwan, K. S. A. (2022). Response of potato (*Solanum tuberosum* L.) cultivars to drought stress under in vitro and field conditions. *Chemical and Biological Technologies in Agriculture*, *9*(1), 1–19. https://doi.org/10.1186/s40538-021-00266-z