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GENOTYPIC VARIATION IN TRANSPIRATION RESPONSE TO PROGRESSIVE SOIL DRYING IN A SET OF POTATO (*Solanum tuberosum*) CULTIVARS

Masterthesis

from

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Declaration of Originality

I hereby certify that this work was written entirely by me. I verify that informationand data derived from other work, published or unpublished, are fully acknowledged inthe text and references are listed in the corresponding section.
I declare that this thesis has not been submitted for an academic degree at another university or institution.

Tulln, March 2017 Stefan Peter Ryall BSc

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Abstract

Water scarcity is one of the major limitations to crop production at the global scale. Improving transpiration efficiency (TE; i.e. ratio of produced biomass to water transpired; g l^{-1}) is widely considered as an avenue for improving crop adaptation to water-stress conditions. Plants generally experience water-stress when their transpiration rate exceeds the rate of water supply. Restricting the rate of transpiration in response to increasing atmospheric vapour pressure deficit (VPD) and exhibiting higher sensitivity to soil drying by initiating decreased stomatal conductance at higher soil water contents are among the promising traits for enhancing TE in crop plants. The underlying hypothesis of this research work was that cultivars exhibiting an earlier reduction in transpiration rate in response to the fraction of transpirable soil water (FTSW) would conserve water and use it more efficiently later at yield-forming stages. Thus reducing the rate of transpiration at higher levels of FTSW would result in higher TE. Hereby the relative change in yield formation must be considered, due to the fact that a higher TE is mostly affiliated with lower biomass production.

The objective of this research was to investigate genotypic variation in TE among a set of potato cultivars. Hereby, seven cultivars were grown under well-watered (WW) and water-stressed (WS) conditions in a glasshouse pot experiment and their daily rates of transpiration and final dry biomass production were recorded. The imposed WS-treatment simulated a progressive soil drying condition.

In line with the research hypothesis, all potato cultivars responded to progressive soil drying by restricting their transpiration rate (-51 %). The observed thresholds for decline in the rate of transpiration in response to FTSW ranged from 0.25 (cultivars Diamant and Mondial) to 0.32 (cultivar Spunta). The average TE of WW plants was 7.13 g l^{-1} plant^{-1}, while under WS-conditions the average TE was increased by 20 %. There were no significant differences between the potato cultivars in their TE under WS-conditions (average 7.84 g l^{-1} plant^{-1}), except for Caesar, which had a TE that was roughly 25 % higher than the average value. The underlying hypothesis that cultivars with higher FTSW-thresholds would exhibit lower TE was rejected, as no correlation between the parameters was found. Furthermore, WS-conditions reduced the dry mass of stems (-27 %), leaves (-24 %) and tubers (-49 %) in all cultivars. However, the relative reduction in biomass production was lowest in Caesar, as this cultivar managed to maintain its leaf canopy expansion under WS-conditions. Caesar also exhibited the highest harvest index (HI) under WS-conditions. Furthermore, the less vigorous cultivars (e.g. cultivars Caesar and Diamant) survived longer under WS-conditions. The results of this research suggest that intrinsic vigour plays an essential role in plant response to water-deficit as less vigorous genotypes can exhibit lower FTSW-thresholds despite having a higher TE at the cost of reduced biomass production.

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1 Introduction

Production volumes and importance of potato as a staple crop are elaborated. Furthermore, the biological and agronomical aspects are viewed.

1.1 Global and regional potato production

On a global scale, potatoes are the fourth most important staple crop (in 2013) according to production volume. It is subordinate only to maize, rice and wheat. In 2013 potatoes were the twelfth most important crop regarding net production value (FAOSTAT, 2015c).

Table 1: The 2013 production volume [t], average yield [tkg^{-1}] and net production value [international $] of the most important potato producers in the world and Europe respectively, as well as of three selected countries (FAOSTAT, 2013; FAOSTAT, 2015a; FAOSTAT, 2015c; FAOSTAT, 2015d).

Producing countries 2013	Production volume [t]	Average yield [tha^{-1}]	Net production value [int. $]
Global	374 463 885	19.5	49 460 870.90
China (Mainland)	95 941 504	17.1	11 928 850.35
India	45 343 600	22.7	7 106 557.76
Russian Federation	30 199 126	14.4	2 992 286.11
Ukraine	22 258 600	15.9	1 509 966.81
U.S.A.	19 715 480	46.3	3 115 008.46
Europe	112 980 347	20.1	-------------
Ukraine	22 258 600	15.9	1 509 966.81
Germany	9 669 700	39.8	1 538 388.18
Poland	7 290 427	21.0	621 822.96
France	6 953 300	43.2	745 168.12
Netherlands	6 576 860	42.2	1 014 880.15
Bangladesh	8 603 000	19.3	1 377 095.32
Algeria	4 886 538	30.3	802 826.19
Austria	604 100	28.6	91 664.96

Since 1961 the production volume and yield of potato have steadily increased, whereas the total potato cultivation area has declined. Thereby the average yield increased from roughly 12 t ha^{-1} (in 1961) to circa 19.5 t ha^{-1} (in 2013) (Table 1). In 2013 the highest yields were produced in New Zealand, U.S.A., Belgium and France, with around 45 t ha^{-1} respectively (FAOSTAT, 2015d). In 2013 the global production was roughly 374 million t. In 2013 Asia accounted for 50 % of the total production, Europe 41 %, North and South America (combined) 11.5 %, Africa 7.5 % and Oceania 0.5 %. China has by far become the largest potato producer with a total production volume of roughly 96 million t in 2014 (FAOSTAT, 2015d).

1.1.1 Importance for food security

Since its domestication, the potato has spread around the world and features as an important staple crop in many countries, especially as a subsistence crop in highlands (Berger *et al.*, 2006, CIP, 2015b, Messer, 2000). In the 16th century the Spanish first introduced the South-American tuber to Europe (Berger *et al.*, 2006) where it was initially used as an anti-famine food but eventually became a staple crop (Messer, 2000). It was not until the 19th century that the potato became a national food in Austria (Berger *et al.*, 2006).
The potato crop achieves outstanding performances regarding its nutritional productivity. According to Renault & Wallender (2000) potato crops can produce the most calories per unit of water input compared to other staple crops such as wheat, rice or maize.

1.1.2 Utilisation

The potato is a resourceful staple food with high biological significance and can furthermore pose as raw material for many products (Berger *et al.*, 2006). The AGES (2014) segregate the varieties according to their substance of content into different utilization categories. In compliance with this, Berger *et al.* (2006) distinguishes between five clusters: (i) table potato, (ii) food-industry-potato, (iii) starch-industry-potato, (iv) fodder potato and (v) seed tuber.
The FAO (2008c) clusters the applications into the following segments:

- Food uses: table potatoes, value-added or processed potatoes (food-industry, starch)
- Non-food uses: starch, fuel-grade alcohol, animal feed
- Seed potato production

The importance of potatoes as a fodder crop has been decreasing due to cheap cereal substitutes (Berger *et al.*, 2006; FAO, 2008a).

1.2 Potato biology

The potato (*Solanum tuberosum* ssp. *tuberosum*) is a member of the *Solanaceae* family of flowering plants (Berger *et al.*, 2006) and is believed to have originated in the high valleys of the Andean mountains of South-America. The modern potato (*Solanum tuberosum* ssp. *tuberosum* Hawks; hereby further referred to as potato or *Solanum tuberosum*) was domesticated first by natives of the Andean region from its progenitors *S. tuberosum* ssp. *andigena* (Hawks) and *S. tuberosum* ssp. *tuberosum* approximately 4000 years ago (Berger *et al.*, 2006; CIP, 2015b). There are over 4000 edible varieties of potato, most of which are found in the Andean region of South America (CIP, 2015a). Furthermore, there are many wild species of potato. Not all of them are suitable for human consumption but they carry an array of genetic potential and increase the local biodiversity. Their genetic traits include natural resistance to pests and diseases as well as an ability to cope with various climatic conditions (Berger *et al.*, 2006; CIP, 2015b, Vasquez-Robinet *et al.*, 2008). Ploidy levels among these South American species, or landraces, range from diploid (2n = 24) and triploid (2n = 36) to tetraploid (2n = 48) and pentaploid (2n = 60). The wild progenitors comprise an estimated 180 to 196 species (Spooner & Hijams, 2001; Spooner *et al.*, 2004). Potentially these wild species possess all ploidy levels of the cultivated landraces as well as hexaploidy (2n = 72) (Spooner *et al.*, 2005).

Primitive indigenous cultivated (landraces) potatoes are broadly spread across the Andes region of South America (Spooner *et al*., 2005). The taxonomy is quite dynamic as past studies indicate (Bukasov, 1971; Ochoa, 1990; Hawks, 1990). Potato landraces have been classified into 21 species (Bukasov, 1971), 9 species (Ochoa, 1990), 7 species (Hawks, 1990) or even a single species (*S. tuberosum*) with eight different cultivar groups.
The potato is an annual herbaceous plant which can grow to a height of about 100 cm (CIP, 2015c). As mentioned before, *S. tuberosum* is part of the *Solanaceae*, or nightshade, family and, therefore, all fresh plant tissues contain the toxic glycoalkaloid solanine (AGES, 2014; Berger *et al.*, 2006). The highest alkaloid concentrations are measured in the herbaceous shoots (Berger *et al.*, 2006).

The stems are angular and covered with a coat of fine hairs (Berger *et al.*, 2006; CFIA, 2013). According to Berger *et al.* (2006), the number of main stems (Figure 1) depends on the genotype and normally ranges between five and 20. The angular stems possess protruding ridges, or so-called ‘wings’, running along them (CFIA, 2013). The internodes of the stems are considered by the CFIA (2013) to be hollow in most cultivars.

The whole leaf of a potato plant is defined as an imparipinnate compound leaf (Figure 1) (Berger *et al.*, 2006). A leaf is typically composed of two to four pairs of large primary leaflets, various smaller secondary and tertiary leaflets as well as of a terminal leaflet which are all arranged on the midrib (Figure 1). The exact arrangement and number of leaflets varies according to the cultivar (CFIA, 2013). Furthermore, these versatile leaves display genotypic variations in regard of their growth habits (Berger *et al.*, 2006; CFIA, 2013). Environmental factors (soil condition, weather, etc.) affect foliage characteristics development similarly, in almost all potato varieties (CFIA, 2013).

The inflorescence is combined to cymes (Berger *et al.*, 2006) and is composed of a peduncle, pedicle and bud (CFIA, 2013). The flowers may be faint blue, white or purple, depending on the floral pigments produced by a genotype. Autogamy has proven to be the primary pollination-pathway although also allogamy is possible. The resulting fruit is a berry, from the botanical stance, which may contain up to about 150 seeds (true potato seeds, TPS). The berries are not edible as they contain the toxin solanine (Berger *et al*., 2006).

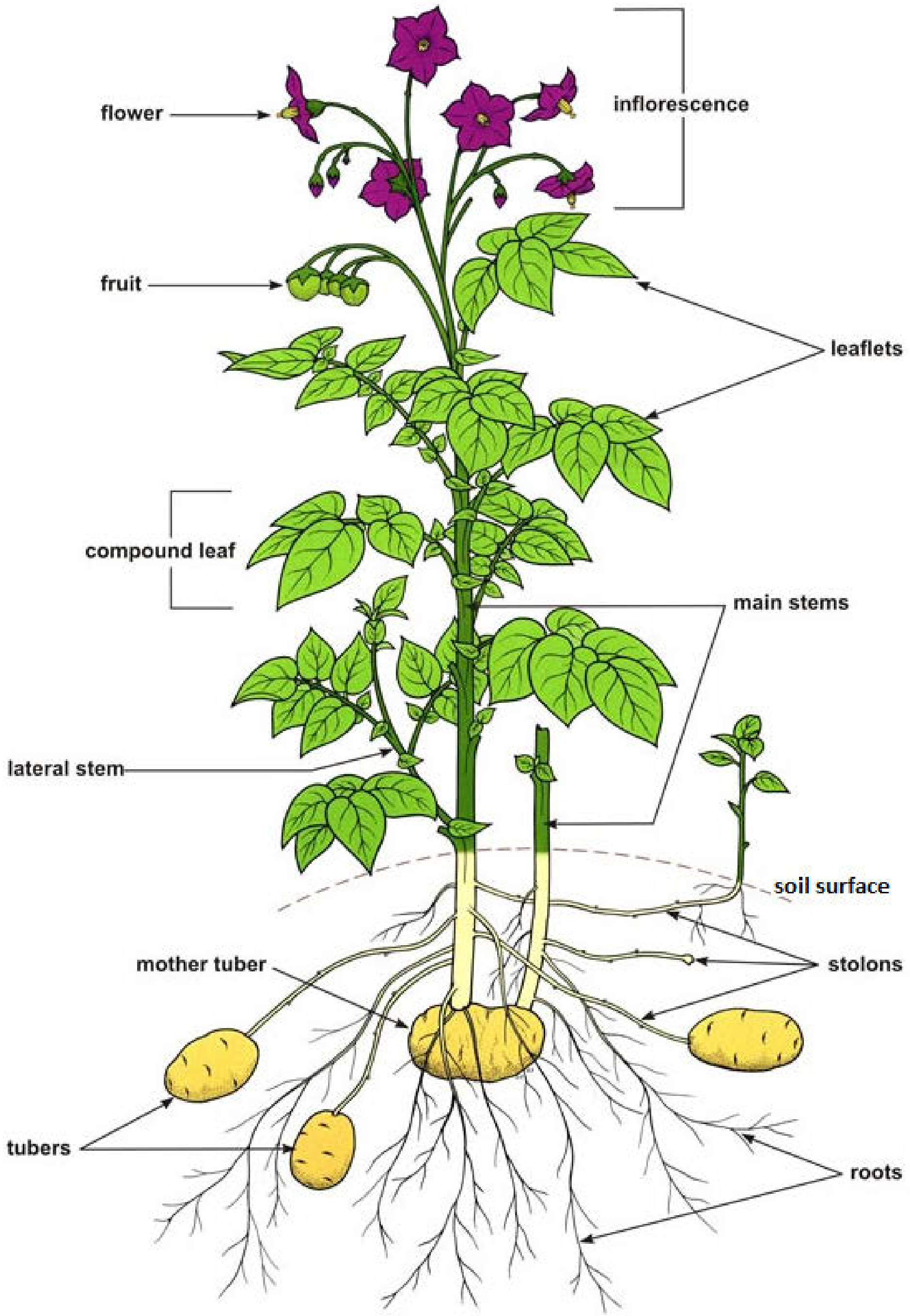

Figure 1: Schematic illustration of various organs of a potato plant (modified after CIP, 2015c).

Under favourable growth conditions potatoes can develop a far-reaching and wide-spread shallow rooting system which is concentrated in the top soil layer (Berger *et al.*, 2006).

1.3 The tuber

In the soil, special runners, so-called stolons, emerge from the basal nodes close to the soil surface. The potato tuber is a thickened tip of such a subsoil stolon (Berger *et al.*, 2006). Berger *et al.* (2006) proclaim that two facts prove that stolons are thickened subsoil shoots: (1) if tubers are exposed to sunlight they start greening and (2) tubers possess eyes out of which foliage shoots or further stolons may emerge. Furthermore, the greening is accompanied by the synthesis and accumulation of *solanum*-alkaloids such as solanine and chaconine (AGES, 2014).

The compound leaves synthesize starch which is transported via the phloem to the apical tissue of the stolons where it accumulates (FAO, 2008b). Hereby the outer internodes of a subterranean shoot thicken to form a sprout-nodule, the so-called tuber (Dahlgren *et al.*, 1987). The exact number of tubers produced depends on the genotype and the available resources and growth conditions (FAO, 2008b). Not all tubers from the same plant will display identical features, though they are all genetic clones of the mother tuber (CFIA, 2013). Towards maturation the tubers are more apt to be true to genotype.

Tubers have two ends: (i) the so called stem end is attached by a stolon to the rest of the plant, and (ii) the bud end, in contrast, contains clustered eyes out of which new stolons might emerge (CFIA, 2013).

The flesh colour ranges from white and yellow to pink, blue and purple (AGES, 2014; Berger *et al.*, 2006;). According to the AGES (2014) as well as the CFIA (2013) tuber skin colour variations are dependent on the genotype and comprise of cream, red, pink, blue, white and yellow pigments. All tubers turn green when they are exposed to light as they are submerged bloated shoots (Berger *et al.*, 2006). The tubers can be pigmented uniformly or partially. The skin texture may vary according to environmental conditions or plant physiology and is identified as smooth, russet or feathered (CFIA, 2013).

The fresh tuber consists primarily of water (~ 77 %) (Figure 2) (Berger *et al.*, 2006). The dry mass is mainly made up of sugars and starch (78 %), as well as of proteins (10 %), mineral nutrients (6 %) and fibre (5 %) (Table 2). Furthermore, potato tubers contain trace amounts of vitamins, especially Vitamin C (Berger *et al.*, 2006).

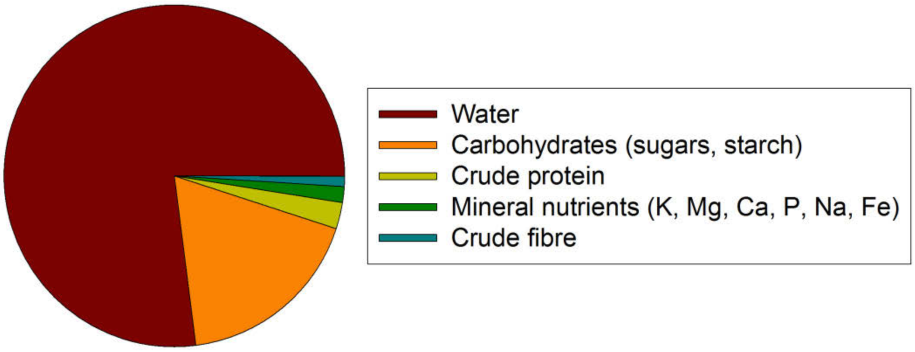

Figure 2: The main components of a fresh potato (*Solanum tuberosum*) tuber are depicted and listed according to their average composition (modified after Berger *et al.*, 2006).

Table 2: Average nutrient composition per 100 g fresh potato tubers (modified after USDA, 2016).

Minerals	Values	Vitamins	Values	Lipids	Values
Potassium	413.0 mg	**Vitamin C (total)**	11.4 mg	**Fatty acids (total polyunsaturated)**	43 µg
Phosphorus	38.0 mg	**Niacin**	1.0 mg	**Fatty acids (total saturated)**	26 µg
Calcium	30.0 mg	**Pantothenic acid**	0.3 mg	**Fatty acids (monounsaturated)**	2 µg
Magnesium	23.0 mg	**Vitamin B-6**	0.2 mg		
Sodium	10.0 mg	**Riboflavin**	40 µg		
Iron	3.2 mg	**Thiamin**	20 µg		
Manganese	0.6 mg	**Folate (total)**	17.0 µg		
Copper	0.4 mg				
Zinc	0.3 mg				
Selenium	0.3 µg				

1.4 Genotypes

Varieties are commonly grouped according to their specific growth habits. Potato genotypes differ greatly in the time required to reach maturity (CFIA, 2013). Hereby four maturity groups can be distinguished, ranging from early (circa 100 days) to late varieties (circa 170 days) (Berger *et al*., 2006). Early maturing varieties are considered by the CFIA (2013) to be mostly low-growing, spreading or busting. Main crop varieties (commonly late maturation), on the other hand, display commonly tall, upright growth characteristics (CFIA, 2013). All varieties are unified by the fact that they lose their distinctive growth habits towards maturation. The CFIA (2013) proclaims that different potato varieties can be identified by their specific growth patterns in combination with their foliar and floral characteristics.

The BBCH-scale can aid their management concerning fertilisation, plant-protection as well as other cultivation requirements such as irrigation. The most critical developmental stages are marked in Table 3, as they require preceding nutrient and water supply (Berger *et al.*, 2006).

Table 3: Phenological development (BBCH) stages of *Solanum tuberosum* ssp. *tuberosum*. The stages marked with *** are considered as most critical and susceptible to stresses (Berger *et al.*, 2006; *Hack et al.*, 1993).

BBCH-code	Above ground development	Below ground development
00 (01-09)	----------	germination; root formation
10 (11-15)	emergence; leaf development	root formation
20 (21-25)	basal side shoot and leaf formation ***	basal side shoot elongation ***
30 (31-39)	main stem elongation	
40 (41-49)	canopy closing	stolon formation
50 (51-59)	inflorescence emergence ***	tuberisation ***
60 (61-69)	full blossom ***	tuber growth ***
70 (71-79)	fruit development ***	main tuber growth ***
80 (81-89)	fruit and seed maturation; discoloration	maturation
90 (91-99)	senescence	tuber ripening until harvest

The varietal catalogue of the European Union (EU) contains more than 1500 varieties which are registered and permitted to be cultivated, whereas the Austrian varietal catalogue only permits the cultivation of 42 genotypes (AGES, 2014).

1.5 Cultivation

Due to the limitations imposed by temperature, potatoes are planted in early spring in temperate climates (e.g. Austria) or in late winter in warmer regions (e.g. Bangladesh) (FAO, 2008a). The FAO (2008a) estimates that in some sub-tropical countries potatoes can be cultivated the whole year round due to a mild climate and high solar irradiation.

In temperate climates pre-sprouted mother tubers can be planted in March while low temperatures still prevail (4 to 6 °C) whereas pre-germinated seed tubers require 6 to 8 °C (mid-April) at the time of planting. The required amount of seed tubers is determined by the intended purpose of the tubers as well as the mother tuber size (Berger *et al.*, 2006). The cropping density for consumption, starch and processing potato is denoted by Berger *et al.* (2006) to be between 40,000 and 42,000 mother tubers per hectare, whereas the plant density for seed tuber production can reach up to 55,000 plants per hectare (Berger *et al.*, 2006).

Potatoes are commonly grown on flat soil or on ridges, which are built up subsequent to planting (FAO WATER, 2015). Rain-fed potato crops in dry areas are commonly grown on a flat soil surface due to the fact that this management practice conserves soil water better and therefore allows higher yields (FAO, 2008a). Ridges can help to provide optimum growth conditions but also increase the unproductive evaporation due to the relative higher soil surface. Ridging can also aid to prevent greening of tubers (FAO WATER, 2015).

Plant spacing is mentioned by the FAO WATER (2015) to be roughly 75 x 30 cm for crops under irrigation and 100 x 50 cm for rain-fed cropping systems. Berger *et al*. (2006) recommend the distance between rows to be approx. 70 to 75 cm. The distance between two mother tubers within a row depends on the genotype, the tuber size as well as the intended use, and ranges between 25 - 40 cm (even less in seed tuber production) (Berger *et al.*, 2006). The mother tubers are planted five to ten centimetres deep under the soil depending on the tuber size (FAO, 2008a). Berger *et al*. (2006) suggest that the tubers should be planted as deep as they are thick (approx. 4 to 5 cm) (Berger *et al*., 2006).

- **Maturity and harvest**

The senescing and dying off of the foliage and shoots indicates that the tubers have matured and are ready for harvest (Berger *et al*., 2006; CFIA, 2013). Harvest maturity is also noticeable on the tubers as their skin becomes very firm and they detach readily from the stolons (Berger *et al*., 2006). Crops intended for direct further processing or direct consumption are removed from the soil, whereas tubers intended to be stored are left buried under the soil in order for their skin to thicken. The thicker skin limits water loss (e.g.: shrinkage) and the susceptibility towards storage diseases. The shoots must be separated from the root system and stolons approx. two to three weeks prior to excavation of the tubers (FAO, 2008a). The actual harvest is commonly completed by mechanised harvester. Hereby tuber damage ranges between 5 and 80 % depending on the harvest conditions, genotypic susceptibility as well as the driving skills of the operator (Berger *et al*., 2006).

- **Plant protection**

An abundance of harmful organisms are able to colonise potato plants and cause economically relevant damage (Table 4). Therefore the control of weeds, pests and pathogens should be founded on the concept of integrated plant protection, and all preventative and cultural measures must be applied and executed on time. Additional subsequent chemical treatments must be oriented on the respective damage thresholds (Berger *et al*., 2006).

Table 4: Potentially harmful organisms and quality reducing occurrences (Berger *et al*., 2006; CIP, 2015d).

Harmful source	Examples
Pathogenic fungi	*Phytophthora infestans*; *Fusarium spp.; Botrytis cinerea*
Pathogenic bacteria	*Pseudomonas solanacearum; Dickeyasolani; Streptomyces scabies*
Pathogenic virus	Leaf-roll-virus; acuba mosaic virus; mop-top virus, stem mottle
Pests	*Leptinotarsa decemlineata*; *Elateridae* larvae; aphids
Non-parasitic damages	aftershoot; greening; growth cracks; cold-damages

The most important plant protection measure is commonly seen in the maintenance of a generous cropping cycle (Berger *et al*., 2006; FAO, 2008a). Potatoes should be grown in a rotation of at least three years, alternating with other, dissimilar crops (e.g.: maize, beans, cereals, etc.) (FAO, 2008a). Within the rotation cycle all cereal crops have proven to be suitable intermediate crops, mostly due to the fact that *S. tuberosum* does not demand high requirements from its prior crop (Berger *et al*., 2006). Frequently repeated cultivation of potato crops may lead to a strong increase in the occurrence of pests and diseases, especially nematodes and fungi like potato wart. Adequate crop rotation offers the possibility to reduce production risks such as pathogens and pests as well as marketing and price-risks. The rotation cycle furthermore aims at maintaining or enhancing soil fertility (Berger *et al*., 2006; FAO, 2008a).

If potatoes are harvested from a dry soil they will leave a loosened and tilthed field behind (Berger *et al*., 2006). This optimum soil condition is very favourable for all cereals as a latter crop in the rotation cycle (Berger *et al*., 2006).

1.6 Environmental requirements

The habitat requirements for potato cultivation as well as typical production environments are explained.

1.6.1 Soil

Potato can generally be cultivated in a wide range of different soils (Berger *et al.*, 2006). Well-drained, well-aerated, porous soils provide a buffer for fluctuations in the water supply and provide sufficient oxygen for the stolon and tuber formation and are therefore seen as very favourable (FAO WATER, 2015). Yields of highest quality and volume are produced on humus-rich loamy-sandy-soils and on sandy loam (Berger *et al.*, 2006).

Potatoes can be grown in almost any type of soil, except alkaline and saline soils (FAO, 2008a). The soils can range within a pH-level of 4.5 and 7.5 without seriously influencing the yield (BMLFUW, 2006). The susceptibility towards potato-scab increases with the soil pH-level and, therefore, the soil-alkalinity (BMLFUW, 2006; Berger *et al.*, 2006).

The soil must undergo intensive preparation measures before potatoes can be planted (FAO, 2008a). A loose soil structure should be achieved by cultivating the soil early in the growing season as well as after the harvest (Berger *et al.*, 2006; FAO, 2008a). These measures include frequent harrowing and rolling as well as multiple ploughings (FAO, 2008a).

1.6.2 Nutrition and fertilisation

The amount and quality of fertilizer is chiefly determined by the intended use of the tubers (Berger *et al.*, 2006), the expected yield as well as the yield potential of the genotype (FAO, 2008a) (Table 5). In order to attain the desired tuber quality and yield the adequate fertilizers must be crop-available at the right time, in the right form and quantity (Berger *et al.*, 2006, FAO, 2008a). Hereby the two production goals, quality and volume, diverge. Furthermore, the amount of nutrients released by soil, as well as the crop residues remaining on the field, must be considered (Berger *et al.*, 2006).

Table 5: Nutrient requirements [kg ha^{-1}] of *Solanum tuberosum* according to their intended application (Berger *et al.*, 2006; BMLFUW, 2006).

Nutrient	Tubers for human consumption and industrial purposes [kg ha^{-1}]	Early varieties and seed tuber production [kg ha^{-1}]
Nitrogen	110 – 130	90 – 110
Phosphorus	65	60
Potassium	200	180
Sulphur	10 – 20	10 – 20

Berger *et al.* (2006) suggest that nitrogen-acquisition-efficiency depends on the genotype. *S. tuberosum* species generally prefer laggard N-fertilizers such as ammonium sulphate. A nitrogen surplus results in reduced starch-production, worsened tuber shelf-life, disease susceptibility and delayed maturation. Phosphorus is a very important macronutrient as it affects essential yield-forming stages such as seed tuber emergence, tuber initialization, tuber growth and tuber maturation. Potassium, on the other hand, enhances the yield and the storage capability and prevents discoloration. Magnesium-rich fertilizers can be applied if demanded and influence the starch concentration in the tubers (Berger *et al.*, 2006).

Application of lime must be adapted into the cropping cycle as far away from the potato production as possible, due to the increased risk of common potato scab (Berger *et al.*, 2006).

In addition to the macronutrients mentioned above, potatoes also require some micronutrients. According to Berger *et al.* (2006) as well as the Austrian ministry of agriculture (BMLFUW, 2006) potatoes have a medium demand for boron, manganese and zinc and a low requirement of copper and molybdenum.

1.6.3 Climatic requirements

Potatoes are grown in more than 100 countries worldwide under temperate, sub-tropical and tropical climatic conditions (FAO, 2008a). The broad potential cultivation area extends from around the equator to approx. 70° N and S (Dahlgren *et al.*, 1987).

According to Franke *et al.* (2013) elevated atmospheric CO_2 levels will benefit crop yields and limit crop water use if the seed tubers are planted at appropriate times of the year; e.g. earlier in the season to avoid late spring or summer heat, as the yield is affected by the prevailing atmosphere and soil temperatures (FAO WATER, 2015; Franke *et al.*, 2013). According to Berger *et al.* (2006) potatoes thrive in cool temperate climates as they are frequently described as cool-season crops (FAO, 2008a). Their cultivation area is geographically limited through the tissue-susceptibility to very low as well as to hot temperatures. The lower temperature threshold for germination is considered to be 8 to 10 °C, whereas root development already starts at 5 °C (Berger *et al.*, 2006). The optimum temperature for tuber formation is denoted by the FAO WATER (2015) to be 18 - 20 °C. Night temperatures below 15 °C generally favour tuber initiation (FAO WATER, 2015). Temperatures above 30 °C and below 10 °C arrest or inhibit the tuber formation as well as whole plant physiology (Berger *et al.*, 2006; FAO, 2008a). The potato is furthermore very susceptible to frost and brief exposure to temperatures hovering around -1 °C can cause damage to all plant tissues (Berger *et al.*, 2006).

Potatoes are commonly grown in three main environments:

(1) Fully-irrigated areas which decrease the importance of natural climates and water regimes, as well as genotypic variations in water use efficiency. Irrigation is most efficient if the application system, timing and depth are adjusted to local field situations. Furrow or sprinkler irrigation is estimated to be the most common irrigation method applied. Frequent irrigation schedules are beneficial due to the high water demand and the shallow root system (FAO WATER, 2015).

    Example: El Oued, Algeria, has profiled itself as a major potato producer in Africa since the mid-1800's. In 2013 Algeria was the largest potato producer in Africa (FAOSTAT, 2015d). In such dry and poor environments (see figure 3) irrigation and crop management are essential for yield formation (Islam, 2016). Therefore potatoes are commonly grown in irrigated pivots (FAO, 2008d). The main fresh potato growing areas are in proximity of the Mediterranean coastline, where a mild climate permits year-round production and harvest (FAO, 2008d).

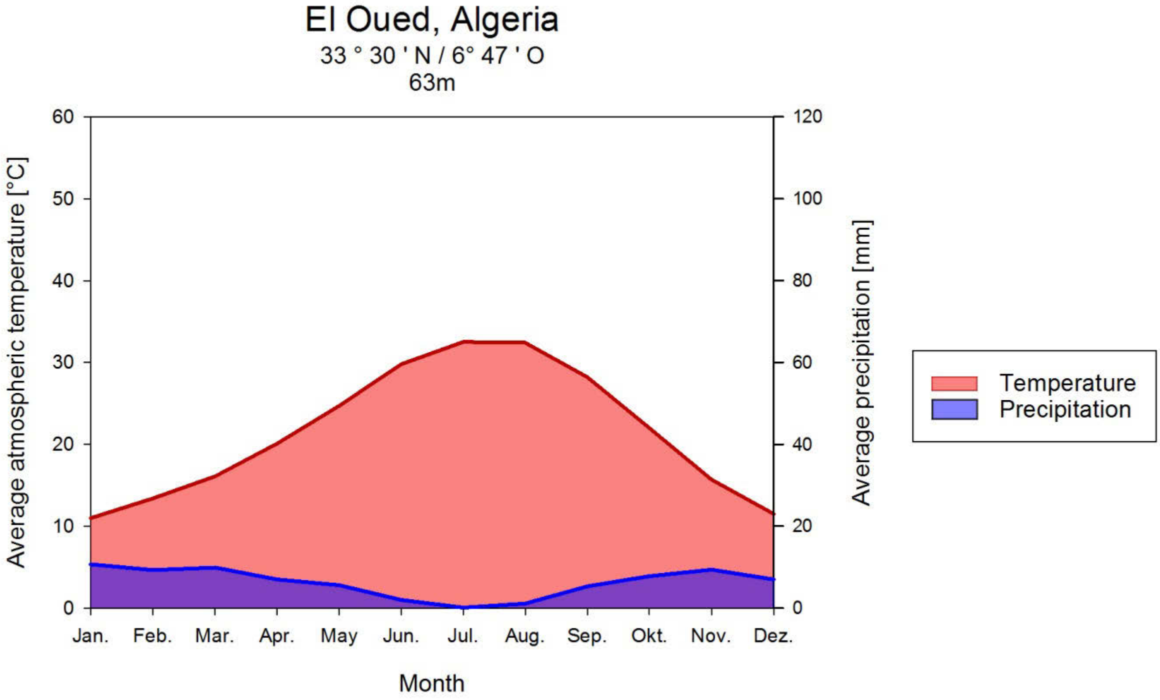

Figure 3: Climate diagram of El Oued, Algeria (modified after DWD, 2016).

Irrigation is necessary to achieve economic yields with early varieties in rather dry regions. Due to the shallow root system of *S. tuberosum* the optimum irrigation technique must replenish evapo-transpired water from the top soil layer every few days, according to demand (Berger *et al.*, 2006). In order to supply sufficient water, Berger *et al.* (2006) suggest that the utilizable field capacity circles around 40 %. Late maturing crops require an estimated 500 to 700 mm of water (FAO, 2008a). The FAO WATER (2015) denotes the water requirement (total evapo-transpiration) for irrigated high yielding crops (120-150 days to maturity) to be approx. 700 to 1000 mm (FAO WATER, 2015).

(2) Areas with sufficient precipitation throughout the growing season and adequate water supply for crop growth and yield formation. In these temperate climates water is very unlikely to be the limiting factor in production and crop irrigation is unnecessary to achieve high yields. In such environments the transpiration primarily depends on the prevailing vapour pressure deficit (VPD) as the soil water content remains at sufficient levels. Genetic traits related to contrasting sensitivities towards fluctuating VPDs result in differing yields.

Example: Oberleis in Austria is a typical potato growing site in a humid continental climate. Potato as a main crop is planted mid-April to mid-May in Austria (Berger *et al.*, 2006). The time of planting primarily depends on the prevailing soil and atmospheric temperatures (Figure 4). Cold spells are typical for April in this climate and may affect seedlings or juvenile plants aversely and initially retard their growth, thus resulting in a later canopy closure and therefore an increased weed-presence(Berger *et al.*, 2006).

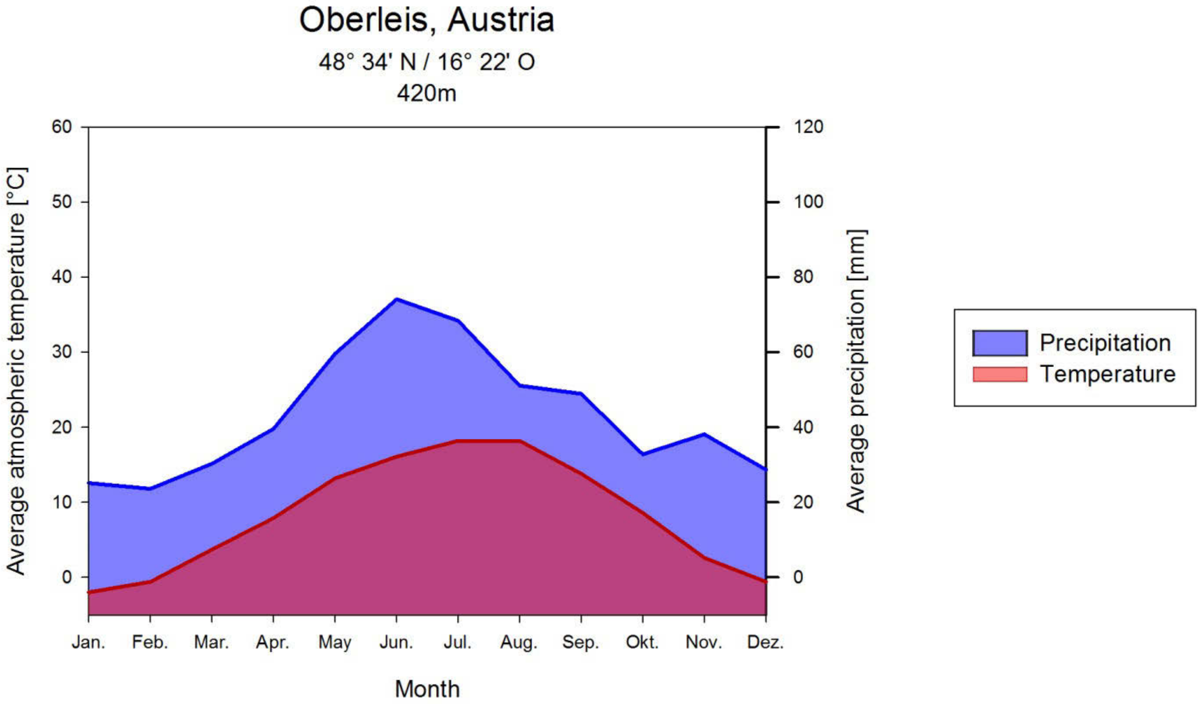

Figure 4: Climate diagram of Oberleis, Austria (modified after ZAMG, 2016).

(3) Locations with periodically very limited or insufficient precipitation which are managed without irrigation. In such environments it is of greatest importance to harvest or sequestrate as much precipitation water in the soil as possible. The amount of stored soil moisture determines the amount of plant available water throughout the growing season. The transpiration depends on both the VPD and the soil water content. Therefore, genotypes with high stomatal sensitivity towards soil drying, adjusting their transpiration rates rapidly to changing environmental conditions, may perform better under such conditions.

Example: Rajshahi in Bangladesh, a typical potato growing site in a tropical monsoon climate. In northern Bangladesh the potato growing season commonly starts around mid-October to mid-November, towards the end of the rainy-season. The season in the southern part of the country starts roughly two weeks later. The time of planting can be seen as a trade-off between too high temperatures and too low soil water content (Figure 5). Early planting may cause heat stress but also results in an earlier canopy closure and therefore less unproductive evaporation. The comparably low night temperatures of northern cultivation areas benefit the productivity in comparison to growing sites in the South of Bangladesh (Islam, 2016).

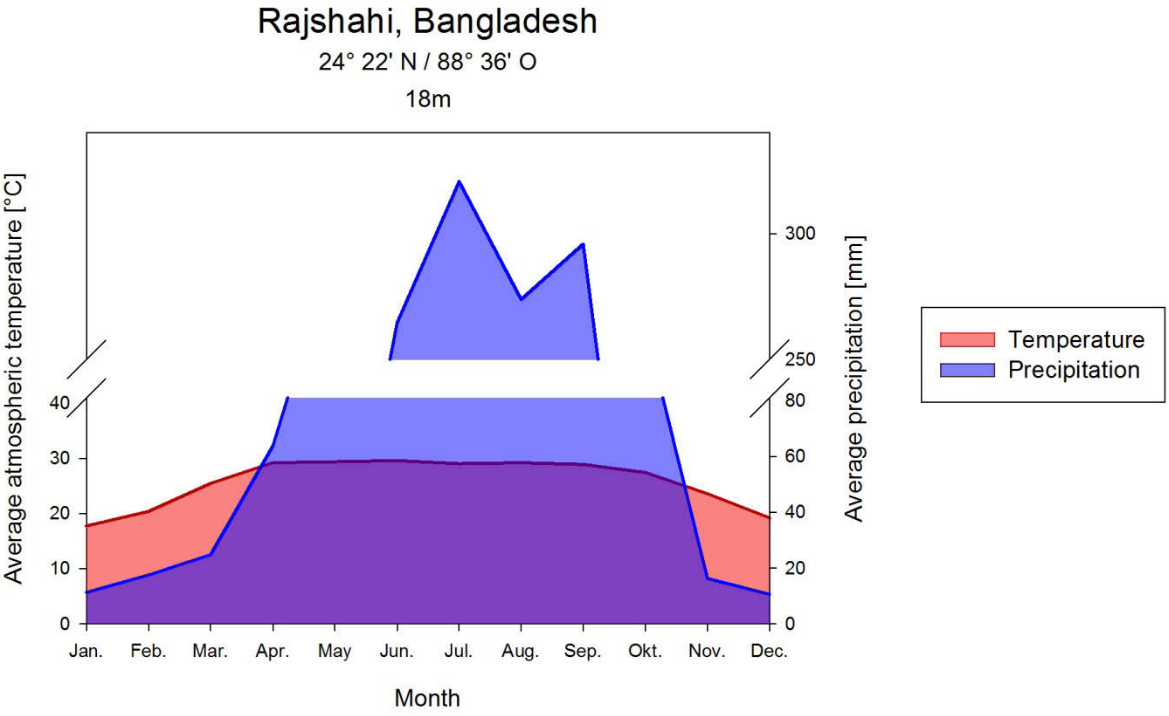

Figure 5: Climate diagram of Rajshahi, Bangladesh (modified after BMD, 2014a, 2014b, 2014c).

1.7 Water requirement

Water management is the key influencing factor determining not only the volume but also the quality of potato yield (Berger *et al*., 2006; FAO, 2008a). The total water requirement can be seen as relatively high (Berger *et al.*, 2006). Due to high sensitivities towards soil water deficits, the soil water content must be kept at a relatively high level to achieve optimum yields, as suggested by the FAO (2008a) as well as the FAO WATER (2015). The hydraulic regime in the top soil layers is of greatest importance because *S. tuberosum* does not root very deep (Berger *et al.*, 2006). Due to the shallow root system the water uptake from the soil occurs to 70 % from the upper 30 cm and to 100 % from the upper 40 to 60 cm. Soil texture and structure as well as genotypic characteristics further influence the water uptake pattern (FAO WATER, 2015).Potatoes require roughly between 300 and 700 mm of water, depending on the environment, soil, year and characteristic crop genotypic growth (Shock & Feibert, 2002; Sood & Singh, 2003; Wright & Stark, 1990).

Kumar *et al*. (2003) estimate water to be the main limiting factor in potato production. They further believe that the global average yield (circa 20 t ha^{-1}) could be increased by roughly 50%, solely by optimising the water supply to the crop. Low volume but high frequency watering must be well planned and applied in order to achieve optimum yields (Vayda, 1994; Wright & Stark, 1990).

Tuber development is commonly seen as the period which is most critical to water deficit. Optimum yields require adequate water supply from tuber initiation to maturity (Egúsquiza, 2000; Jensen *et al*., 2000). Water stress imposed during tuber initiation until end of tuber bulking stage has the greatest impact on biomass and yield formation (Steyn *et al*., 2007). Water scarcity in the beginning of the growth period causes far less yield reductions than water-stresses in the middle and late growing period (Table 3; Figure 6) (FAO, 2008a). This is partially due to the fact that the mother tuber stores sufficient water for germination and early juvenile phases (Figure 2; Figure 6) (Berger *et al*., 2006). Water limiting conditions around the phases of stolonisation, tuber initiation and tuber growth must be avoided (Berger *et al*., 2006; FAO, 2008a; FAO WATER, 2015), whereas the supply may be restricted at the initial vegetative stages as well as the ripening stage (FAO WATER, 2015).

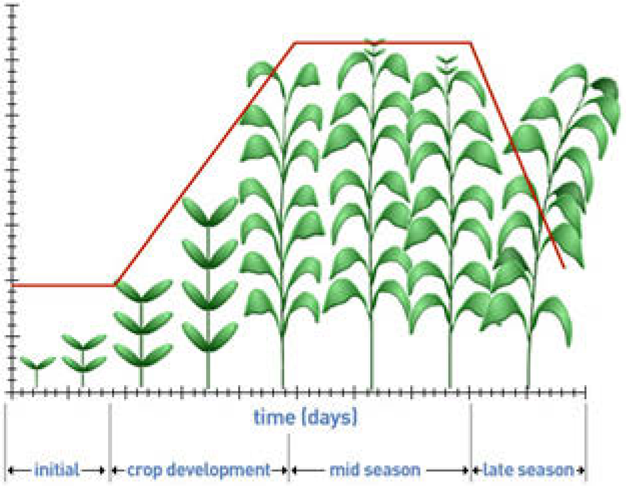

Figure 6: Schematic depiction of the growth stages of a potato plant. The red line indicates the critical water requirement of the respective stages (modified after FAO WATER, 2015).

Al-Mahmoud *et al*. (2014) cultivated multiple potato genotypes under field conditions, applying three different water-stress-levels. They found that tuber yields and grades were significantly affected by drought. Small sized and deformed tubers appeared to correlate with the severity of water stress. There were also significant differences in the relative water content of the crops, suggesting different coping strategies.

A recent study by Vasquez-Robinet *et al.* (2008) claims that *S. tuberosum* ssp. *tuberosum* (H.) is more susceptible to water-stress conditions than its progenitor *S. tuberosum* ssp. *andigena* (H.). *S. tuberosum* ssp. *tuberosum* is comparably sensitive to soil water deficits. The severity of the water-stress impact depends on the growth stage the plant is in (Figure 6). The soil water content must not be depleted by more than 30 - 50 % of its field capacity or else stress conditions set in. Water-stress in the middle to late growing season has a much greater impact on the yield than in the early growth stages. Nonetheless, potato cultivars vary in their sensitivity to water deficit (FAO WATER, 2015).

Haverkort *et al*. (1990) and Munns & Pearson (1974) showed that once stolons are initiated, they will try to produce tubers due to the fact that water deficit results in a preferential supply of assimilates to the tubers. Therefore, the dry matter production and its accumulation in the tubers are an important parameter for the assessment of adaptation to drought-stress conditions (Heuer & Nadler, 1995).

1.8 Global warming and climate change

Bohnert *et al.* (1995) as well as the Intergovernmental Panel on Climate Change (IPCC; 2014) agree that the biosphere is constantly being exposed to an array of stresses. It is commonly understood that stresses generally limit crop productivity and production (Araus *et al.*, 2002; Lisar *et al.*, 2012). Especially abiotic stresses have a great impact on the distribution of plant species across different types of environments and habitats (Tester & Bacic, 2005). Globally many countries face various problems related to paucity of water resources and other abiotic as well as biotic stresses (Humphreys *et al.*, 2008; IPCC, 2014). According to Bohnert *et al.* (1995) the most prevalent stresses commonly affect the water status of plants. In particular abiotic stresses such as extreme temperatures, chemical toxicity and drought as well as their concomitants have severe impacts on ecosystems (Chaves *et al.*, 2002; IPCC, 2014; Lisar *et al.*, 2012). Stresses increasingly cause disruptions in agriculture and may reduce the average yield of major crops by up to 50 % and, therefore, threaten food safety and security (Lisar *et al.*, 2012). Developing countries are frequently seen by IPCC (2014) as more sensitive to climate risks, such as drought, due to their reliance on climate-sensitive primary production activities. It is a common concern that extreme climate events will increase in frequency and intensity (Dai, 2011; IPCC, 2014; Lisar *et al.*, 2012).

Climate change is projected to increase threats from heat stress, extreme precipitation and flood events, atmospheric pollution and drought stress. Climate change impacts are strongest and most comprehensive on natural systems and developing countries. Both biotic and abiotic factors, especially anthropogenic activities, cause rapid changes in climatic patterns. Various studies conducted in recent years conclude that the negative impacts of climate change have been more common than positive impacts. Altered precipitation patterns may change the hydrological system, thus affecting the water resources in both quantity and quality. The annual greenhouse gas (GHG) emission has increased on average by 2.2 % CO_2-equivalent between 2000 and 2010 compared to 1.3 % CO_2-equivalent annually from 1970 to 2000. The IPCC has calculated temperature scenarios for the year 2100 in which they estimate the global average temperature to increase by 3.8 to 4.7 °C compared to pre-industrial times if no further mitigation measures are taken. The temperature increase is strongly linked to the increase in GHG's, which are primarily produced by economic and population growth. Furthermore, the global average land and water surface temperature shows a clear increase. One of the most severe concomitants of the rising sea temperatures can be seen as the volumetric gain, which causes a significant raise in the average sea level, and therefore the loss of arable land (IPCC, 2014).

The climate change may also influence the distribution and coverage of the dominating natural vegetation as well as crop varieties and management practices in given areas. Large, fast and intense climate change can translate to vegetation stress, plant loss and, in some cases, even desertification (Bachelet *et al.*, 2001).

Since the Green Revolution in the 1980's, modern agriculture has been intensified strongly by increasing the inputs such as water, fertilisers and pesticides. Water, however, is more often rendered to be the limiting factor in yield formation (Lisar *et al.*, 2012). The cultivation of water-intensive crops (*e.g.* C_3-crops) and the massive usage of fertilizers further increase the amount of required water (Lisar *et al.*, 2012; Liu *et al.*, 2015) without necessarily increasing the yield (Liu *et al.*, 2015). Shaxson & Barber (2003) also argue that intensive agriculture may lead towards soil compaction and salinisation which further reduces the infiltration rate of water into the soil as well as the soil water holding capacity.

Political constraints, rising costs, and groundwater scarcities (in some cases even exhaustion) mean that less water is available for the agricultural sector. Conflicts of interests and competition for water supplies impose a worldwide problem (Shock & Feibert, 2002). Deficit irrigation is seen by Shock & Feibert (2002) as an approach to address these issues. It is commonly defined as a strategy which allows the crop to withstand a tolerable degree of water stress in order to reduce irrigation costs and potentially increase revenues (English & Raja, 1996; Shock & Feibert, 2002). A study by Ahmadi *et al.* (2016) revealed that deficit irrigation practices resulted in significantly higher water productivity compared to the other treatments.

Regulated deficit irrigation (RDI) and partial root-zone drying (PRD) are two irrigation methods which attempt to decrease the water demand of the agricultural sector. The PRD technique requires the adaptation of the irrigation system to allow alternate drying and wetting of parts of the root zone. RDI on the other hand, allows one half of the root zone to dry out while irrigating the other half. The treatment reverses cyclically (Loveys *et al*., 2000; Stikic *et al*., 2003). PRD uncouples the biochemical signals in response to water-deficit from the hydraulic signal and physical effects of limited water availability (Bacon,2003). PRD is based on the assumption that a minor narrowing of the stomatal apertures may reduce water loss significantly while having almost no effect on the CO_2-uptake (Jones, 1992). The mixed root signals can result in good yields with considerable water savings and a higher WUE (Loveys *et al*., 2001). PRD furthermore induces the growth of secondary roots, which reduces the crops vulnerability to drought (Kang *et al*., 1998; Zhang & Tardieu, 1996).

1.9 Rain-fed agriculture

There is mounting evidence that climate change will influence rain-fed agriculture adversely (IPCC, 2014). Rain-fed agriculture is commonly defined as a cropping system in which water is only supplied naturally by precipitation (Rosegrant *et al.*, 2002; Makurira, 2010). Therefore, rain-fed agriculture depends on the ability of the soil to store moisture, as well as on precipitation patterns (Rockström *et al.*, 2007; Rosegrant *et al.*, 2002). Such systems are implemented in almost all parts of the world and therefore in nearly all hydrological regimes (Humphreys *et al.*, 2008; Wani *et al.*, 2009). Rain-fed cropping systems, supplemented by livestock systems, will predominantly form the base of food and financial stability for poor, rural people globally (Rockström *et al.*, 2007).

Projections by the IPCC (2014) indicate that the variability of precipitation will intensify, but so will the frequency of extreme weather conditions, like drought spells and floods. Rain-fed agriculture can be seen as a risky practice due to the high temporal and spatial variability of precipitation (IPCC, 2014; Wani *et al.*, 2009). The variability of the climate is a major constraint to yield improvement as well as commercialization of rain-fed crops. Furthermore, it increases the difficulty to respond to economic opportunities such as trade, emerging markets and globalization (Wani *et al.*, 2009).

Rain-fed cropping systems cover circa 80% of the world's cropland and account for approx. 60% of the produced staple crops (FAO, 2016; FAOSTAT, 2013; FAOSTAT, 2015b). In the arid and semi-arid climate zones, rain-fed agriculture plays a major role concerning the nutrition and self-preservation of communities (Rockström *et al.*, 2007; Wani *et al.*, 2009). In these rather dry climates, the yields from rain-fed crops are strongly limited and may even be reduced by as much as 50% compared to fully irrigated crops, according to Rosegrant *et al.* (2002). Alongside the low productivity in dry sub-humid to arid regions, factors such as food-insecurity, impoverished livelihoods, as well as environmental degradation, arise (Rockström *et al.*, 2007; Wani *et al.*, 2009). Long term yield increases in predominantly dry regions are primarily due to increased production areas, as the average yields stagnate at a low level (Rockström & Falkenmark, 2000; Wani *et al.*, 2003; Wani *et al.*, 2009). The high risks, as well as comparably low potential yields, impose a threat to peasant communities and, especially, to smallholder farmers (Humphreys *et al.*, 2008).

Water is the most challenging production factor in the arid, semi-arid and dry sub-humid regions of the world. These regions cover roughly 40% of the global land area and host about 40 % of its global population (Rockström *et al.*, 2007).

In dry regions rain-fed agriculture predominantly produces the lowest yields per unit land area whereas in temperate regions, with highly productive soils and reliable rainfall patterns, the highest yields are possible (Rockström & Falkenmark, 2000; Wani *et al.*, 2003). In dry or arid regions roughly 5 to 10 % of the precipitation can be used physiologically by the plant compared to roughly 50 % in temperate, arid regions (Figure 1) (Rockström *et al.*, 2007). The available amount of water determines the potential yield; 1 to 2 t ha^{-1} and 4 to 5 t ha^{-1} in arid and temperate climates respectively (Rockström *et al.*, 2007, Rockström & Falkenmark, 2000). Lisar *et al.* (2012) proclaim that water is of highest importance because it provides the medium in which most of the cellular activities and functions take place. Therefore, it can be seen as the central molecule of all physiological processes (Lisar *et al.*, 2012) and water-stress-tolerant crops and cultivars are, according to Lisar *et al.* (2012), of the greatest economic importance.

Direct evaporation from the soil surface is typically the main source of water loss during the cultivation period (Figure 7). This unproductive loss cannot be eliminated, but rather minimised through vigorous genotypes and management practices (Cooper *et al.*, 1983; Leuning *et al.*, 1994). Direct evaporation from the soil surface is fastest when the soil is moist and uncovered by a canopy, as well as when evaporative demand is high. As a crop grows, the soil water-loss shifts from evaporation to transpiration. Therefore, a fast seedling development rate, or an early canopy establishment, benefit soil water conservation. The genotypic characteristics of leaf area development can strongly influence the water-use-efficiency of a crop. For the crop this imposes a trade-off between early vigour and available soil water in late-season generative yield forming stages. Excessive water use in early vegetative stages may render an insufficient amount of water for the actual yield formation (Passioura & Angus, 2010).

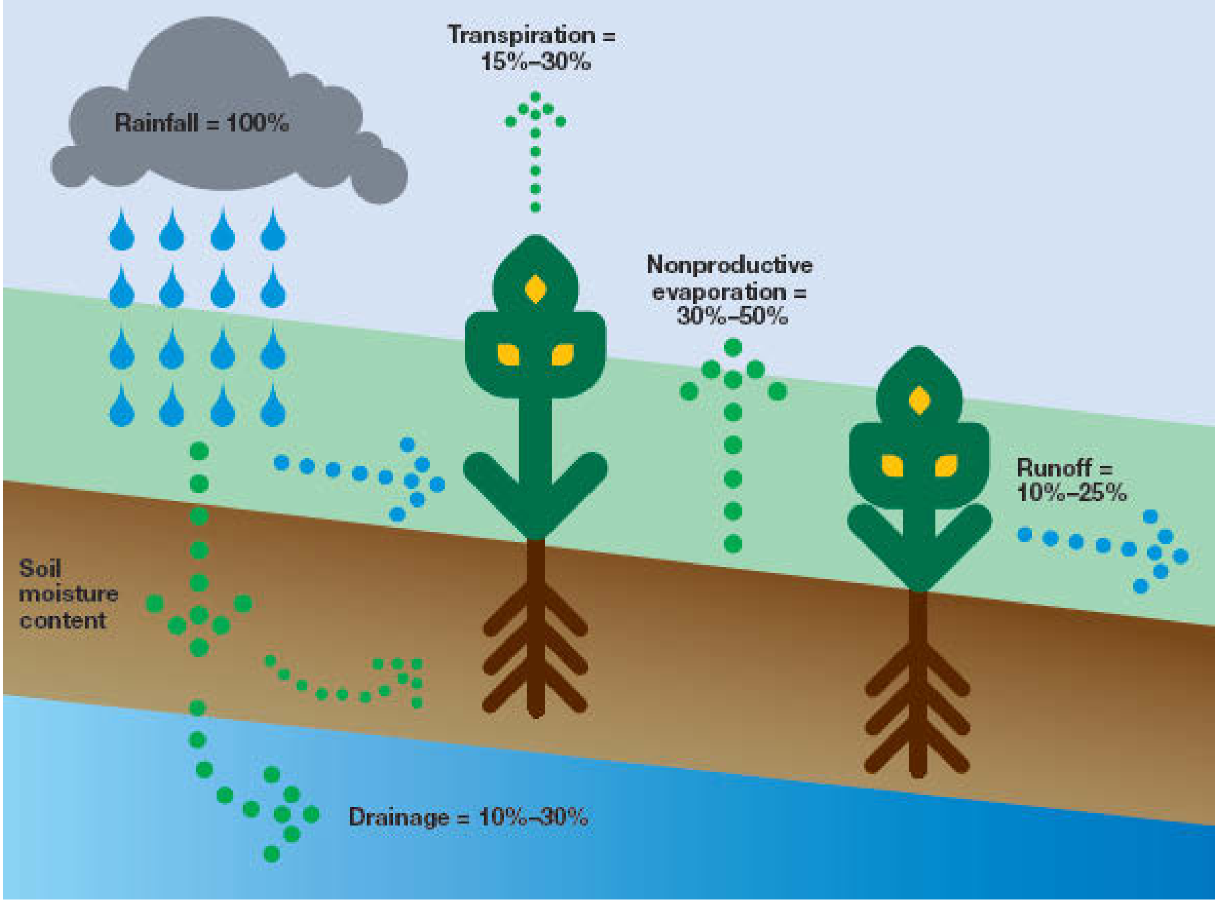

Figure 7: Common precipitation partitioning pattern. Water losses are indicated on a field level via non-productive evaporation, drainage and surface runoff (Rockström *et al*., 2007).

Residual water which accumulated during the previous fallow, or which is unused by the preceding crop or forage, can pose as an important water source in rain-fed cropping systems (Passioura & Angus, 2010). Fallowing is a common practice in semi-arid and some sub-humid environments (Sims, 1977). Retaining stubble from the previous crop is often seen as the most effective way to reduce soil evaporation and surface runoff, thereby increasing infiltration during precipitation events (Foley & Silburn, 2002; O'Leary & Connor, 1977). Soil water hardly evaporates from depths exceeding 30 to 60 cm during a dry summer (Suleiman & Ritchie, 2003) and the stored soil water can be used by the successive crop (Passioura & Angus, 2010). Deeply stored water is typically accessed only late in the growing season where it can be critical for yield forming stages (Berger *et al*., 2006; Saini & Westgate, 2000).

According to Humphreys *et al.* (2008), rain-fed cropping systems feature a great improvement potential which may further benefit the environment and enhance or restore ecosystem services. Various technical options aiming at a better crop use of prevailing precipitation are suggested by Humphreys *et al.* (2008). These prospects include the development of improved or adapted varieties, agronomic management, and in-field water harvesting, as well as supplementary irrigation (Humphreys *et al*., 2008; Wani *et al*., 2003). An integrated approach would achieve maximum benefit by combining adequate soil and site-specific water, nutrient as well as crop management. Furthermore, suitable policy-settings such as infrastructure and market access must be adapted (Humphreys *et al*., 2008).

Increasing the actual yield in water-stressed environments is far more complex than increasing the potential yield in unstressed environments. Understanding the resulting genotype by environment interactions is essential for the selection, design and the interpretation of the results (Hall & Richards, 2013). The greatest immediate possibility to improve water-limited yields is seen by Passioura & Angus (2010) to be a reduction of the yield gaps between potential yield and actual yield, rather than increasing the potential yield.

Richards *et al*. (2002) found out that historical increases in yields are mostly due to genetic improvements in water-limited potential yield, and are, furthermore, associated with the introduction of semi-dwarf varieties which have a greater H.I.'s. Passioura & Angus (2010) suggest that reducing the often large gap between potential and actual yield would be a greater immediate opportunity for improving water-limited yields, than improving the potential yield. The crop identity equation can be a useful diagnostic tool to analyse causes of, and find possibilities to reduce large yield gaps (Passioura & Angus, 2010).

1.10 Potato responses to water-stress and drought conditions

It is commonly understood that drought has the most adverse impact on agricultural production on a global scale (Akıncı & Lösel, 2012; Bohnert *et al.*, 1995; Pilon-Smits *et al.*, 1995; Selote & Khanna-Chopra, 2004). Although drought is a natural climatic phenomenon, no uniform global definition exists (Wilhite, 2000). Kramer & Boyer (1995) as well as Dai (2011) suggest that drought can be seen as a re-occurring extreme climatic event in which the precipitation is subnormal for a natural or agricultural system over land. In the field, drought can cause an array of plant stresses such as water, temperature, nutrient and light stress (Kramer & Boyer, 1995; Verslues *et al.*, 2006).

Water deficit stress in plants is commonly defined as a state in which the transpiration rate exceeds the water supply rate. More specifically the water supply via the root and vascular system cannot meet the physiological demand (Lisar *et al.*, 2012). Lisar *et al.* (2012) subdivide water stress into (i) physiological drought, under which the existing soil water is not plant available (due to *e.g.*: extreme temperatures, high soil salinity, unfavourable water potentials), and (ii) environmental drought in which the volume or the replenishment of soil water is unable to meet the plants' demand.

The manifold reactions towards water-stress stimuli commonly affect the growth, productivity and yield of the crop adversely (Lisar *et al.*, 2012; Pilon-Smits *et al.*, 1995). According to Lisar *et al.* (2012), stomatal closure is the first response to water stress in plants. Lisar *et al.* (2012) furthermore proclaim that the photosynthetic activity of all higher plants abates with a decline in the plant's relative water content. Therefore all physiological processes subsequent to photosynthesis can be adversely influenced. Water deficit stress can lower the water potential in the plant, as well as the turgor pressure to an extent which threatens normal physiological processes (Lahlou *et al.*, 2003; Lisar *et al.*, 2012; Vasquez-Robinet *et al.*, 2008). The concentration of solutes (in the cytosol and apoplast) increases, which causes a reduced cell enlargement and, furthermore, a retarded growth, as well as failure in reproduction (Lisar *et al.*, 2012). In addition, the mineral nutrient uptake and allocation within the plant are also restricted, as they rely on water as a medium of transport (Lisar *et al.*, 2012). Reactive oxygen species (ROS), as well as rising tissue temperatures, can further affect the plant's physiology and productivity negatively (Lisar *et al.*, 2012; Tambussi *et al.*, 2000).

The driving force for water uptake by a plant is a steep gradient in the water potential Ψ [MPa] (Table 6) (Verslues *et al.*, 2006). Mathematically, Ψ is defined as the chemical potential of water in relation to the partial molar volume (Kramer & Boyer, 1995). The direction of water movement is always along the gradient towards the lower potential. The water potential in the atmosphere Ψ_A depends on the relative humidity (rH), whereas the leaf (Ψ_L) and root (Ψ_R) water potential depend on the crop species and genetic characteristics. The soil water potential Ψ_S is determined by the soil type and the water content. The Ψ_S declines with increasing soil dryness. As the soil water potential of a drying soil progressively decreases, a range of responses are triggered that allow the plant to (i) avoid water loss, (ii) allow water uptake to continue at reduced Ψ_S or (iii) allow the plant to tolerate a reduced tissue water content. The threshold point of Ψ_S from which wilting plants cannot recover is commonly defined as the permanent wilting point (Verslues *et al.*, 2006). At this threshold point the acquired water is insufficient to rehydrate the tissues.

Table 6: Example values for the various water potentials at critical passage stages (Verslues *et al.*, 2006).

Critical stages of passage	Symbol	Example value [MPa]
Atmospheric water potential (at 50 % rH)	Ψ_A	-93.5
Leaf water potential	Ψ_L	-0.6 to -2.5
Root water potential	Ψ_R	-0.2 to -0.4
Soil water potential (moist soil)	Ψ_S	-0.1

The water potential of a plant cell Ψ_C depends on its osmotic potential Ψ_O and on its turgor pressure Ψ_T (Equation 1). Ψ_O inversely correlates with the concentration of osmolytes (osmotically active metabolites) in the cell. Ψ_O and Ψ_T can be seen as antagonistic processes as Ψ_T raises the Ψ_C and Ψ_O lowers the Ψ_C. When a plant cell loses water, its turgor potential declines, thus resulting in a stronger negative cell water potential (Verslues *et al.*, 2006).

$$\Psi_C = \Psi_O + \Psi_T \qquad (1)$$

Processes directly or indirectly dependent on the turgor pressure are very susceptible to a drop in Ψ_T. Cell elongation, especially leaf expansion, is directly dependent on the Ψ_T and therefore very sensitive to water deficit (Verslues *et al.*, 2006). Furthermore, the activity of many enzymes declines and therefore the whole plant metabolism is adversely affected (Liu *et al.*, 2006; Yordanov *et al.*, 2003). Pre-eminently, the nitrate-reductase activity is limited thus affecting all subsequent N-processes, such as reduction of NO_2^- to NH_4^+, the synthesis of amino acids and the assembly of proteins (Foyer *et al.*, 1998; Sepehr *et al.*, 2012).

The phytohormone abscisic acid (ABA) is commonly known to be a key regulator in controlling plant responses to many abiotic stresses, including low tissue water potential (Liu *et al.*, 2006; Verslues *et al.*, 2006). Among others, foliar ABA accumulation regulates stomatal conductance and root growth, accumulation of compatible solutes and synthesis of late embryogenesis abundant (LEA) proteins (Verslues *et al.*, 2006). A key aspect for understanding the whole response of low cell water potential is seen in a better understanding of upstream sensing and signalling controlling ABA accumulation and downstream signals modulating the responses to ABA.

Early studies on water relations revealed that plants are able to take up water from the soil until it reaches a suction of about -1.5 MPa (also known as the wilting point). This idea might apply for pot-grown plants but not for the heterogeneous soil water extraction profile of a crop maturing in dry conditions. The surface layers are dryer due to a higher root density and longer residence time (Christopher *et al.*, 2008; Dardanelli *et al.*, 2004).

1.11 Strategies for coping with water deficit

Water-limiting conditions have multidimensional effects on plants which generally reduce their overall productivity (Chaves *et al.*, 2002; Devi *et al.*, 2009; Lisar *et al.*, 2012; Vasquez-Robinet *et al.*, 2008). Within the *Plantae* different mechanisms have evolved with which they respond to water deficit stress (Vasquez-Robinet *et al.*, 2008). They may react either with avoidance or the development of various adaptation techniques which increase their tolerance (Chaves *et al.*, 2002; Devi *et al.*, 2009; Vasquez-Robinet *et al.*, 2008). The most striking differences between avoidance and tolerance strategies are summarized in table 7. The reactions are generally based on an altered phytochemical metabolism (Lisar *et al.*, 2012; Vasquez-Robinet *et al.*, 2008). As a result of the metabolic changes, the gene-expressions are transcripted in altered fashions which induce a cascade of internal signalling events, causing the biochemical and morphological adaptations (Ingram & Bartels, 1996; Lisar *et al.*, 2012; Vasquez-Robinet *et al.*, 2008).

Table 7: Differences between drought tolerance and avoidance strategies in plants (modified after Agriinfo, 2015; Lisar *et al.*, 2012; Luu & Maurel, 2005; Manschadi *et al.*, 2008; Sadok & Sinclair, 2010; Sadok & Sinclair, 2011; Vasquez-Robinet *et al.*, 2008).

Parameter	Avoidance	Tolerance
Tissue water content	favourable level maintained	unfavourable levels set in
Involved features	anatomic/morphologic	genetic/metabolic
Aim	- reduce water loss - acquire more water	- maintain normal physiology - shift metabolic partitioning towards seeds
Timing	vegetative phase	generative phase

Stress avoidance and tolerance do not occur in a linear temporal progression, after stress initiation or during progressively increasing severity of a stress. For example, LEA-proteins accumulate prior to significant dehydration but the accumulation of ABA (which then causes stomatal closure) is triggered by a certain degree of tissue-dehydration (Verslues *et al.*, 2006).

According to Verslues *et al.* (2006), a clear distinction between tolerance or avoidance strategies cannot be made as many molecular events initiated by low cell water potential do not fit strictly into one classification. Rather than attempting to classify the diverse stresses at a molecular or physiological level, the authors suggest that the consideration of tolerance or avoidance mechanisms is more useful in clarifying the appropriate types of experiments and interpreting the data of a particular event in the plants integrated response to low tissue water potential.

Even after the stomata have been closed the crops are still being exposed to solar irradiation. The incoming solar radiation is absorbed but cannot be metabolized due to an arrested CO_2-fixation (Lisar *et al*., 2012, Tambusi *et al*., 2000). Therefore, water-stressed plants very often also face radiation-stress which may cause damage through the formation of reactive oxygen species (ROS) (Lisar *et al*., 2012, Tambusi *et al*., 2000). ROS emerge from the transmission of electrons on oxygen (O_2) molecules (Tambusi *et al*., 2000). These oxygen-species are highly reactive and react in the chloroplasts predominantly with thylakoid-lipids as well as with pigments and proteins of the photosynthesis apparatus (Foyer & Noctor, 2003; Foyer & Noctor, 2005; Liu *et al*., 2006). Therefore, the ability to cope with ROS (e.g.: limiting damages, controlling the amount of ROS's) influences the performance of a crop under drought conditions.

Verslues *et al*. (2006) suggest that under short-termed or mild water-stress conditions an increased root growth or decreased stomatal conductance seem most promising to increase crop plant productivity. The trade-off in this case can be seen as the reduced photosynthesis caused by a low availability of CO_2 or a shift of the resources towards root-growth at the cost of reproductive and photosynthetic tissue. Long time or severe water-stress conditions can cause changes in the reproductive process including premature fruit abscission, reduced fruit setting as well as the formation of smaller seeds and an accelerated seed ripening (Verslues *et al*., 2006).

1.11.1 Drought avoidance strategies

Stomatal closure is an immediate and reversible response to water-stress conditions (Lisar *et al*., 2012). The sensitivity of stomatal closure under drought conditions is a key trait in avoiding water-stress. A higher sensitivity (towards VPD or progressive soil drying) would arrest the transpiration earlier and reduce the water use, leaving a larger portion of water to be used for yield formation.

Turner (2004) has found that cereal grain yields are closely related to water availability at anthesis. Recent studies by Kholová *et al.* (2010a) as well as Zaman-Allah *et al.* (2011a) confirm that genotypes with a conservative water use early in the growing season render soil water reserves to be metabolized later in the reproductive season. Therefore, reducing pre-anthesis transpiration results in a higher performance (Turner, 2004).

Genotypic variability in phenology is also seen as a vital trait to avoid terminal drought stress (Borrell *et al*., 2006). Early flowering genotypes can achieve higher performances by simply escaping water-stress conditions during the critical yield forming stage.

The root to shoot ratio describes the ratio of root biomass (water supply) to shoot biomass (demand water). Unfavourable conditions increase the root to shoot ratio while favourable conditions reduce it (Harris, 1992). Furthermore, the spatial configuration of the root system is a very important determinant of the water uptake capacity of a plant (Bacio *et al*., 2003). The three-dimensional root structures vary greatly within genotypes of various crops (Bouma *et al*, 2001; Manschadi *et al*., 2008). Root traits benefiting physiology during water stressed conditions include rooting depth and angle, spatial root length distribution and root length density (Manschadi *et al*., 2008).The root-to-shoot ratio is further increased by ABA, which not only closes the stomata but also increases root vigour while decreasing shoot growth (Verslues & Bray, 2006).

As mentioned before, the Ψ_S correlates directly with the soil water content and therefore the soil Ψ decreases further as it progressively loses water (Verslues *et al*., 2006). Water can only be acquired as long as the root cell Ψ is stronger negative than the soil Ψ (Ψ_C / Ψ_S> 1) (Kramer & Boyer, 1995). Some plant species have evolved techniques to lower their Ψ_O and therefore their Ψ_C without altering the Ψ_T. This can be achieved through so called osmotic adjustment (Zhang *et al.*, 1999). Considering equation 2, at a given cell water potential the Ψ_T can be raised by accumulating solutes inside the cell and thus lowering the osmotic potential. Additional solutes are actively accumulated as a response to low Ψ_C. It is of great importance that these accumulated solutes (so called compatible solutes, e.g.: proline, glycine betaine) themselves do not interfere with cellular functions (Zhang *et al.*, 1999). The trade-off of osmotic adjustment is that an increased accumulation of compatible solutes is resource and energy intensive for the plant and might not affect the water uptake under very severe conditions (Kramer & Boyer, 1995).

1.11.2 Drought tolerance strategies

The enhanced production of biosynthates aims at the maintenance of normal physiological processes as well as the protection of cellular structures (Close, 1997; Verslues *et al.*, 2006). This is partially achieved by altering the resistance of water flow (Vasquez-Robinet *et al.*, 2008). Special water channel proteins (aquaporins) are involved in adjusting the water status according to prevailing environmental conditions (Luu & Maurel, 2005). The activity-level and concentration of aquaporins can affect the plant's hydraulic conductivity and influence the transpiration (Luu & Maurel, 2005; Sadok & Sinclair, 2010; Sadok & Sinclair, 2011; Yang *et al.*, 2012).

In many cereals so-called stay green-lines have been identified (Vadez *et al.*, 2011). They are able to retain more green leaves under terminal drought and produce more grain yield and biomass compared to lines and hybrids without the stay-green trait (Borrell *et al.*, 2000; Rosenow *et al.*, 1983). In these stay-green lines more nitrogen is allocated to the leaves from early growth stages, thus increasing the specific leaf nitrogen concentrations (Borrell & Hammer, 2000). The leaf senescence is delayed, thus enhancing radiation use efficiency as well as transpiration efficiency and therefore increasing the yield (Borrell *et al.*, 2001).

1.12 Water productivity

Passioura (1977) defines a crop identity, which describes the water-limited potential yield of a certain genotype under a certain environment (Equation 2):

$$Y = T * TE * HI \qquad (2)$$

Y: yield; T: amount of transpired water; TE: transpiration efficiency for produced biomass (i.e. ratio of produced biomass and transpired water); HI: harvest index (i.e. weight of a harvested product as a percentage of the biomass weight of a crop)

Sinclair *et al.* (1984) describe five possible points which could influence a crop's water use efficiency (WUE):

(i) Biochemical alterations: either improve photosynthetic efficiencies or modify the biochemical composition of plant products. This approach might decrease current levels of proteins, lipids or carbohydrates and render the plant products unfit to be marketed.

(ii) Alterations of the cropping environment: this approach is to be understood as a geographical solution, thus focusing crop production in regions with a more humid climate and therefore a lower VPD. Alternately the cropping season can be shifted towards periods of lower VPD.

(iii) Stomatal physiology: stomatal sensitivity towards prevention of excessive transpiration rates could be important to improve crop WUE, particularly arresting transpiration during times of high VPD. This approach could prolong the growing season in order to compensate for the lack of assimilated CO_2, which would further increase the potential for major crop losses due to pathogens, pests and environmental stress.

(iv) Improving HI: improvements of the HI directly culminate in improvements of a crop's WUE. The HI is already high for most crops, except under water-limiting conditions which can lead to greatly reduced HI's. Dwarfing and early maturing varieties were developed to improve the HI.

(v) Increase the proportion of transpired water: methods increasing the amount of soil water which is plant available would improve overall WUE's. Such management practices comprise of minimizing surface runoff, deep percolation and soil evaporation. Greater rooting depths would allow more soil water to be exploited but also may lower the H.I. and increase the risk of a rapid exhaustion of soil water prior to yield formation.

Transpiration is defined by Condon *et al.* (2002) as the emission of water vapour (H_2O) through the stomatal apertures located on the foliage. During this crucial step atmospheric carbon (CO_2) is assimilated and metabolized (Condon *et al.*, 2002; Lisar *et al.*, 2012). The vapour efflux ratio depends on the stomatal conductance as well as the concentration gradient of both CO_2 and H_2O inside and outside the leaves (Condon *et al.*, 2002). The transpiration rate is highly complex as it depends on both genotype and environment (G x E-interaction) (Shamim *et al.*, 2014; Sinclair, 2012; Vadez *et al.*, 2014; Wani *et al.*, 2009). The expression of (water-stressed) genes depends on the prevailing environment and is displayed in the gene-environment-interaction (G x E-interaction) of a genotype (Schafleitner *et al.*, 2007). Many recent studies such as Schafleitner *et al.* (2007) and Vasquez-Robinet *et al. (2008)* discovered several genes to be affected by water limiting conditions. Among others several genes controlling mitochondrial activity were affected negatively (Vasquez-Robinet *et al.*, 2008). Furthermore, Vasquez-Robinet *et al.* (2008) found out that antioxidant genes, transporter genes and chaperone genes were altered.

The amount of produced yield per unit water used is generally defined as water productivity of a crop (Condon *et al.*, 2002; Turner, 1997; Vadez *et al.*, 2014). Condon *et al.* (2002) specifies three levels of water productivity: (i) at plot level the water use efficiency (WUE) is defined as total biomass per evapo-transpiration, (ii) at plant level the transpiration efficiency (TE) is defined as total biomass per water transpired, and (iii) at leaf level the intrinsic water-use efficiency (WUE_i) is stated as the ratio of instantaneous assimilated CO_2 to emitted H_2O. This thesis will focus on the plant level of water productivity.

$$WUE\ [g\ l^{-1}] = \frac{total\ DM_{Biomass}}{Evaporation + Transpiration} \tag{3}$$

$$TE\ [g\ l^{-1}] = \frac{total\ DM_{Biomass}}{Transpiration} \tag{4}$$

$$WUE_i = \frac{CO_2\,Assimilation}{H_2O\,Transpiration} \tag{5}$$

$$WUE_i = \frac{g_c(c_a - c_i)}{g_w(w_i - w_a)} \tag{6}$$

$$WUE_i \approx 0.6\,c_a * \frac{(1-\frac{c_i}{c_a})}{w_i - w_a} \tag{7}$$

WUE: water use efficiency; $DM_{Biomass}$: dry mass of plant tissues; TE: transpiration efficiency; g_c: stomatal conductance to CO_2; g_w: stomatal conductance to H_2O-vapor; w_i - w_a…..H_2O-vapor concentration gradient between the foliage and the atmosphere; c_a - c_i: CO_2 concentration gradient between the foliage and the atmosphere.

Equation 3 sets the dry weight of the plant tissues in relation to the water required to produce them. The WUE includes the amount of unproductive evaporation which did not contribute to yield formation or metabolism. Although evaporation must be accounted for it might bias the evaluation of genetic sensitivities.

The TE (Equation 4) does not include non-productive-evaporation and therefore gives a much better insight in genotypic differences in transpiration. Furthermore, equation 2 gives an insight in the whole plant performance.

Equations 5 to 7 describe the relationship between the concentration of carbon (CO_2) and water vapour in the stomatal chamber and the atmosphere, respectively (Condon *et al.*, 2002). These formulas (Equation 5, Equation 6, Equation 7) describe the intrinsic water-use-efficiency as described by Condon *et al.* (2002). In order to achieve a high WUE_i the assimilation to transpiration-ratio must be kept low. This can be achieved by altering the c_i value, as the atmospheric carbon concentration can be seen as relatively stable in a short term perspective (IPCC, 2014). The c_i can be reduced by a low stomatal conductance and high photosynthetic efficiency (Condon *et al.*, 2002). Improving TE at leaf level increases the TE of crop biomass (Passioura& Angus, 2010). In water-stressed environments any increase in TE should increase crop yield, provided the H.I. does not decline (Richards, 2006).

In contrast to the strong atmospheric effects on TE, there is no evidence that crop management has an impact on TE. The increased effectiveness of water-use from fertiliser management is due to reduced soil evaporation and not increased TE (Passioura& Angus, 2010).

Many past evaluations of crop TE have had to rely on measurements of surrogate traits due to the complexity of measuring only the transpiration in the field. The indirect surrogate approaches consist of carbon isotope discrimination (CID) (Araus *et al.*, 2003), specific leaf area (SLA) (Lahlou *et al.*, 2003; Liu & Stützel, 2003; De Souza *et al.*, 2014), chlorophyll fluorescence (Nageswara Rao *et al.*, 2001; Zrůst *et al.*, 1994), and lysimetric and gravimetric (Ratnakumar *et al.*, 2009; Sinclair & Ludlow, 1986; Vadez *et al.*, 2008; Vadez *et al.*, 2014) measurements. Lysimetric or gravimetric systems can be considered as direct TE measurement methods if the pot can be sealed and, therefore, no evaporation takes place. According to Ratnakumar *et al.* (2009), Vadez *et al.* (2008) as well as Vadez *et al.* (2011) gravimetric or lysimetric approaches would permit the whole plant water use to be monitored throughout its life cycle while supplying robust data. Furthermore, the TE, TR as well as the WUE can be measured from the same individual crop.

According to climate scenarios of the IPCC (2014) the CO_2 concentration is expected to increase in the foreseeable future, thus increasing the TE of C3 crops (Wall *et al.*, 2006). According to Long *et al.* (2006) C4-crops shows a neglible growth response to elevated CO_2 levels, although the TE of C4 crops is greater compared to C3. This reflects the lower CO_2 concentration in the stomatal chambers of C4 plants (Rawson, 1977).

The study carried out by Monneveux *et al.* (2013) concluded that large portions of the research achievements on drought tolerance in cereals could be transferred to improve performances in potatoes.

The soil water extraction by crops is determined by the (i) soil water content, (ii) evaporative demand, (iii) soil physical properties and the (iv) physiological status of the crop. Crop root systems which are affected by pathogens or chemical toxicities will extract less soil water than crops not suffering from such limitations (Passioura& Angus, 2010). On the other hand, a higher crop nitrogen status may increase water extraction by the crop according to Angus & Van Herwaarden (2001).

Transpiration depends on the soil type, the prevailing climate as well as the genetic resource potential and the water status (Dai *et al.*, 2011). Therefore, the transpiration rate of a given genotype is determined by two major factors: (i) the H_2O vapour pressure deficit (VPD) of the stomatal chamber in contrast to the atmosphere, as well as (ii) the plant available soil water content (Shamim *et al.*, 2014; Vadez *et al.*, 2014).

1.12.1 Transpiration response to vapour pressure deficit

As long as the soil water content remains at a sufficient level, a plants transpiration rate depends primarily on its metabolic pathway as well as the prevailing atmospheric VPD (Bueckert, 2013; Condon *et al.*, 2002; Guralnick *et al.*, 2008; Vadez *et al.*, 2014). The VPD is defined as the deficit between the amount of moisture currently in the air and the potential holding capacity at full saturation (Monteith & Unsworth, 1990). The VPD differences between plant leaf and atmosphere cause a potential gradient which drives the vapour efflux. In comparison to the stomatal chamber, the atmospheric gaseous mixture consists of a relatively high CO_2-concentration and mostly a relatively low H_2O-concentration (Condon *et al.*, 2002). The vapour pressure gradients adapt as long as the stomata are open causing CO_2 to be acquired and H_2O to be emitted by the stomatal chambers (Condon *et al.*, 2002; Vadez *et al.*, 2014). The VPD is directly influenced by air temperature (T) and relative air humidity (rH) (Wikidot Inc., 2015), a VPD increase would therefore directly correlate with an increase in T and TR as well as a decrease in rH and TE. Next to the VPD and irradiation, the TE at leaf level also depends on the CO_2 concentration within the stomatal chambers (Condon *et al.*, 2002). Condon *et al.* (2002) state that the TE correlates inversely with the stomatal CO_2 concentration.

Recent studies indicate inter- and intra-specific variation of sensitivity regarding the stomatal response to altering VPDs. These variations have been found in various crop species such as sorghum (Choudhary *et al.*, 2013), peanut (Devi *et al.*, 2010), chickpea (Zaman-Allah *et al.*, 2011b), cowpea (Belko *et al.*, 2012), maize (Yang *et al.*, 2012) and pearl millet (Kholová *et al.*, 2010b). Reduced TR at high VPD may result from limiting hydraulic conductance within the plant as water flow from the roots to the transpiration sites is constricted (Lisar *et al.*, 2012; Sadok & Sinclair, 2010; Sinclair *et al.*, 2008).

Various recent studies have proven that TR varies greatly with the VPD and that certain stages within a plant's life cycle, e.g.: grain filling or tuberisation stage, critically require water (Manshadi *et al.*, 2006; Vadez *et al.*, 2013a; Vadez *et al.*, 2014; Zahman-Allah *et al.*, 2011b). Araus *et al.* (2003) postulate that especially the reproductive stages are susceptible to water deficit and that a sufficient amount of water is critical prior and post anthesis. Recent studies on peanut (Ratnakumar *et al.*, 2009), durum wheat (Araus *et al.*, 2003), chickpea (Zahman-Allah *et al.*, 2011b) and pearl millet (Vadez *et al.*, 2013a) suggest that low water use in the vegetative stage results beneficially towards the yield.

The TE of a genotype can be seen as constant in a given environment. The TE increases with increasing humidity as well as decreasing VPD (Tanner & Sinclair, 1983). The strong correlation of TE and VPD leads to a possibility of increasing crop growth when VPD is lowest (Richards, 1991), however, this might cause insufficient water availability in yield forming stages (Turner, 2004). Optimal behaviour will vary according to the location and the prevailing climate (Condon *et al.*, 2004).

Kholová *et al.* (2010b) and Vadez *et al.* (2014) argue that traits restricting high TR under high VPD act beneficial in conserving soil water. Yang *et al.* (2012) proclaim that the TR can be regulated by the activity and concentration of aquaporins in a plant.

1.12.2 Transpiration response to progressive soil drying

As mentioned before, the Ψ_C equilibrates with that of the water source during water-stress conditions (Verslues *et al.*, 2006). A crops response to a drying soil can be seen as reducing Ψ_C, in order to allow further uptake of water. This can be achieved either by tissue dehydration or by plant-induced adjustments which result in low tissue Ψ while avoiding water loss.

Suleiman & Ritchie (2003) describe soil drying as a two stage process. At first, a fully saturated soil drains freely due to gravitational force until the soil-specific field capacity is reached (Akıncı & Lösel, 2012). Then the soil surface progressively loses water via evaporation, drainage and plant uptake. When the top layers are dry, soil water is still lost by the soil's ability to conduct water to the surface (Suleiman & Ritchie, 2003).The evapo-transpiration (evaporation and water-acquisition by plant roots) diminishes the soil moisture content further, until the wilting point at which plants suffer from severe water-deficit stress and die (Akıncı & Lösel, 2012). Therefore, a plants relative TR can be used as a surrogate measure for the soil water content (Devi & Sinclair, 2011; Kholová *et al.*, 2010a).

Transpiration in response to progressive soil drying follows a common pattern over an array of species (figure 8) (Devi *et al.*, 2009; Sinclair, 2012; Vadez *et al.*, 2013a,b; Vadez *et al.*, 2014). The response pattern can be separated into two phases: phase one is the initial phase in which the water supply is still sufficient to meet the plants demand. In phase two the soil water supply is unable to satisfy plant transpiration and therefore stomatal closure is initiated in order to avoid excessive water and turgor pressure loss. The second phase is permeated by a steady decline in transpiration (De Souza *et al.*, 2014).

The literature commonly uses the framework of the fraction of transpirable soil water (FTSW) for decline in transpiration to quantify the genotypic variances in stomatal sensitivity of crops towards progressive soil drying (e.g.: Choudhary *et al*., 2013; De Souza *et al*., 2014; Devi *et al*., 2009; Gholipoor *et al*., 2012). Hereby the daily normalised transpiration ratios (NTR) are plotted against the fraction of transpirable soil water (FTSW) and fitted with a two-segment linear regression curve, the intersection of which indicates the soil moisture threshold value (FTSW-threshold) for decline in transpiration (see figure 8). The literature suggests that the available soil water during yield forming stages increases with the FTSW-threshold because an early response towards soil drying arrests transpiration early and therefore reduces the amount of water used in the relatively unsusceptible vegetative growth (Choudhary *et al*., 2013; De Souza *et al*., 2014; Devi *et al*., 2009; Gholipoor *et al*., 2012; Passioura & Angus, 2010; Vadez *et al*., 2014).

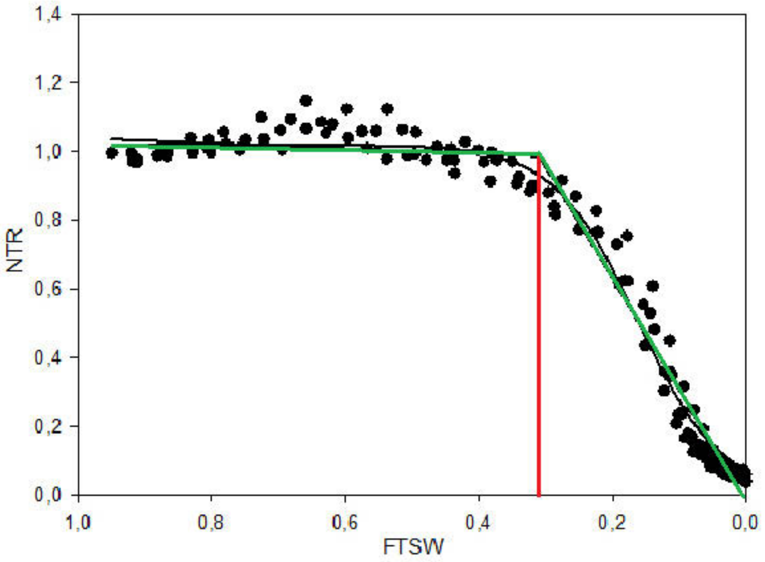

Figure 8: The daily normalised transpiration ratios (NTR) are plotted against the fraction of transpirable soil water (FTSW) and fitted with a two-segment linear regression curve, the intersection of which indicates the soil moisture threshold value for a decline in transpiration. A high FTSW-threshold indicates a higher sensitivity towards soil dryness and therefore the potential to conserve more soil water during vegetative growth.

De Souza *et al.* (2014) and Devi *et al.* (2009) proclaim that the point during the soil drying cycle at which stomata conductance starts declining (in response to soil water-deficit), is specific to the genotype. This key trait could explain genotypic differences in TE. Lisar *et al.* (2012) further suggest that the increased stomatal resistance under stress conditions indicates the efficiency of a species to conserve water. An early stomatal response to progressive soil drying (e.g.: a high FTSW-threshold) limits the water use in early vegetative cropping stages, thus potentially conserving soil moisture. The withheld soil moisture can be further used in the generative yield forming phases which critically require water (Passioura & Angus, 2010; Vadez *et al*., 2014).

The FTSW-threshold is seen as an efficient method to separate cultivars with regard to their response to water-limiting conditions. The FTSW-threshold for decline in transpiration was evaluated for an array of crops such as maize (Muchow & Sinclair, 1991; Ray & Sinclair, 1997; Ray *et al*., 2002), sorghum (Choudhary *et al*., 2013; Gholipoor *et al*., 2012), potato (De Souza *et al*., 2014; Liu *et al*., 2006) and peanut (Devi *et al*., 2009), to name a few. The

FTSW-thresholds ranged from 0.3 to 0.4 for maize, 0.3 to 0.5 for sorghum, 0.2 to 0.6 for peanut and 0.2 to 0.4 for potato respectively.

Sinclair & Ludlow (1986) have established a protocol for the experimental setup of a greenhouse pot experiment to measure a crop's sensitivity to a progressively drying soil (i.e.: it's FTSW-threshold). The protocol has been implemented by many studies on a wide variety of crops (De Souza *et al.*, 2014; Devi *et al.*, 2009; Gholipoor *et al.*, 2012; Muchow & Sinclair, 1991; Ray & Sinclair, 1997).

1.13 Research hypothesis

The objective of this research was to investigate and determine genotypic differences in transpiration response to a progressively drying soil within a set of potato cultivars. According to the underlying hypothesis, there are genotypic differences in the stomatal sensitivity towards progressive soil drying. These varying sensitivities strongly influence the available soil water at yield forming stages and therefore the ability to produce economic, marketable yields.

It is postulated that an early restriction of transpiration at higher soil water content conserves soil water which is available later at yield-forming stages. According to the underlying framework, high FTSW-threshold cultivars should therefore feature a higher transpiration efficiency to the detriment of biomass production. Hereby, the theoretical framework underlying the FTSW-concept, which was described in the previous sections, shall be applied.

The following research questions will be addressed:

- Are there genotypic variations for transpiration in response to progressive soil drying within a set of potato genotypes?
- At which fraction of transpirable soil water (threshold) does transpiration start to decline?
- Is the FTSW-threshold linked to higher transpiration efficiency?

2 Material and methods

Explains the used matierals, experimental setup and approach towards the investigation of the research-questions.

2.1 Glasshouse setup

The transpiration experiment is conducted in a greenhouse at the 'Universitäts- und Forschungszentrum Tulln' (UFT) which was located in Tulln an der Donau, Lower Austria (48°32'025''N, 16°06'954''E). The town is situated about 160 m above sea level. The modern glasshouse was self-regulated in regards of prevailing environmental factors.

The temperature was set within the boundaries of 15 to 25 °C. The cabin-climate was regulated automatically by a heating element and by ventilation through windows. The adjustable windows were secured with mosquito nettings to prevent infiltration of pests into the cabin. Furthermore, a shading canvas could be unreeled at a height of approx. 425cm above the ground. The prevailing VPD in the greenhouse cabin was calculated by subtracting the average actual vapour pressure (VP) from the average saturated vapour pressure (SVP) as seen in Equation 8, Equation 9 and Equation 10. The VPD-calculations can be weighted towards periods of higher environmental water demand by altering the θ-parameter from 0.5 to 0.75 (Tanner & Sinclair, 1983), thus giving more weight to phases of high temperature (T) and low relative humidity (rH).

$$average\ SVP = \theta * \left(0.611 * \exp\left(\frac{17.27 * T_{max}}{T_{max} + 237.3}\right)\right) + (1 - \theta) * 0.611 * \exp\left(\frac{17.27 * T_{min}}{T_{min} + 237.3}\right) \tag{8}$$

$$average\ actual\ VP = \frac{\frac{SVP_{max} * rH_{min}}{100} + \frac{SVP_{min} * rH_{max}}{100}}{2} \tag{9}$$

$$VPD = average\ SVP - average\ actual\ VP \tag{10}$$

The compartment was equipped with four portable metal plant tables (168 x 120 x 60 cm). Hereby a rough grid served as table top. Furthermore, the greenhouse cabin was fitted with eight 400 Watt high pressure sodium vapour lamps with clear outer bulb (Master Agro 400W E40 1SL, PHILLIPS, Amsterdam, Netherlands). The lighting hung from the ceiling at a height of 2.25 m and thus 1.32 m above the top edge of the pots. The lamps individually emitted a nominal luminous flux of 57 000 lm at full emission. The lights were turned on at 07:00 a.m. and run until 08:00 p.m. This resulted in approximately 12 hours of light emission at full bulb potential (qualitative and quantitative) due to a warm-up phase.

The photosynthetic active radiation (PAR) was measured with a photon-flux-meter (Fieldscout Light Sensor Reader and Fieldscout Quantum Light Sensor, Spectrum Technologies, Inc., Illinois, U.S.A.).The PAR-measurements were taken twice, one at cloudy (March 26th) and once at sunny, cloudless (April 15th) conditions at 12:30 p.m. respectively. In order to measure the maximum potential of irradiation, the plants were cleared from the trays to prevent potential shading. The PAR assessments were then executed at a height of approx. 28 cm (the height of the pots) above the grids.

2.2 Substrate and pot preparation

The planting substrate consisted of a homogeneous mixture of four ingredients: three different substrates and a chemical compound fertiliser.

- The first substrate, silica sand, was purchased as commercial filter sand (Filtersand, Scherf GmbH & Co. KG, Hartberg, Austria). The grain diameter ranged from 0.4 to 0.8 mm. Furthermore the silica (SiO_2) content was greater than 96 %. The sand had been washed and fire dried by the manufacturer. It is stated to be lime-free, pH-neutral as well as aseptic. The final planting substrate consisted mostly (50.7 % $w\ w^{-1}$) of this silica-rich sand. This component was absolutely dry.
- The second substrate was a clay-rich farm soil which was collected from one of the farmers fields right next to the glasshouse in Tulln an der Donau. It was sampled in the third week of December 2014. Subsequently it was left to dry for seven weeks in

an unoccupied cabin in the glasshouse at ambient room temperature. After the soil was dry, it was milled with a self-loading roll to crumble the stable aggregates into finer particles. In order to ensure a homogeneous distribution among and within the pots the ground soil was sieved with an analytic sieve (Test Sieve, 200 mm diameter x 50 mm height, 2.00 mm mesh size, Retsch GmbH, Haan, Germany). The nutrient analysis of this clay-rich farm soil was conducted at the Institute of Soil Research (IBF; Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences Vienna) by Amtsdir.Ing. Brauner and can be found in the appendix.

- The third substrate compound was a compost soil (KKS Kompostkultursubstrate, Klasmann-Deilmann GmbH, Geeste, Germany) which made up 4.98 % (w w^{-1}) of the growth medium. The compost was of horticultural standards. It stated to have the following parameters: 250 mg N l^{-1}, 300 mg P l^{-1}, 500 mg K l^{-1} as well as a total porosity of 85 % (v/v) and a dry bulk density of 150 kg/m^3. The compost is essential for the texture and nutrient supply of the growth medium.

A chemical fertiliser (ImmergrünBlaukorn, Raiffeisen Ware Austria AG, Wien, Austria) was added to ensure optimum nutrient supply during the experiment. It stated to consist of 15 % N, 6% P, 12 % K and 2 % Mg. The blue granules had to be milled into a fine powder (≤ 2 mm grain size)to ensure an even and homogenous distribution throughout the whole substrate. Hereby the pulverised fertiliser was mixed with some farm soil for several minutes in a cement mixer (AltradLescha). To be precise, 347.4 g of pulverised fertiliser was mixed with 14,652.6 g of the milled farm soil. The resulting mixture of exactly 15 kg was mixed with an additional 15 kg of pure clay-rich soil in a cement mixer (AltradLescha, Burgau, Germany) for three minutes. The final product (30 kg of soil and fertiliser) from this procedure is further referred to as 'fertiliser mixture'.

The exact amounts of the single components were calculated according to the soil volume in the pots and the estimated nutrient requirement of the crop (see table 5). The proportions of the various substrates were calculated for the nutrient requirement of approx. 90 kg ha^{-1} N, 40 kg ha^{-1} P and 160 kg ha^{-1} K. The substrate was mixed to reach an expected content of 526.7 mg kg^{-1} (N), 91.1 mg kg^{-1} (P_2O_5) and 86.9 mg kg^{-1} (K_2O).

The substrates were grinded, weighed (with CP 16001 S, Sartorius AG, Göttingen, Germany; IFS 60K0.5D, Kern & Sohn GmbH, Balingen-Frommern, Germany) and mixed. The four compounds (sand, clay soil, compost, fertiliser mixture) were mixed with each other in batches. The components of one batch (illustrated in Table 8) were loaded gradually into a cement mixer. Each batch was mixed for three minutes. Each pot was filled with six kilogram of substrate. Therefore 840 kg were required to fill all 140 pots with the homogenous growth medium.

Table 8: Composition of planting substrate.

Component	Weight [kg]	Percentage [%] (w w^{-1})
Sand	15,211.1	50.70
Farm soil	12,296.4	40.99
Compost	1,492.5	4.98
'Fertiliser Mix'	1,000.0	3.33
Total	**30,000.0**	**100.00**

Round, black polypropylene pots (HR 28 Y, seven litre volume, 205 mm diameter x 280 mm height, slightly tapered, CEP AGRICULTURE, Thiers, France) were modified to suit the purposes. Hereby the bottom of the outer layer of the pots was wrapped with three layers of adhesive tape. This measure was meant to prevent the rim of the bottom of the pot from penetrating the sealing equipment. After that, each pot received a felt disc (average 16 cm diameter) which covers the bottom of the inside layer. The felt prevented substrates from leaking out through the drainage holes while it allowed gases to efflux. The felt circles were then covered with 125 g (measured with CP 16001 S) of coarse silica sand (0.5 – 2.0 mm grain size) respectively. The sand (Quarzsand Casafino, 0.5 – 2.0 mm grain size, Quarzwerke Österreich GmbH, Melk, Austria) was distributed evenly over the felt circles and permitted an adequate drainage and aeration.

The pots were then filled with precisely six kilogram (measured with CP 16001 S) of the homogenous substrate mixture. During this filling phase the pots received labels with their respective serial number for identification. The weight of each filled pot was then recorded with a precision scale (CP 16001 S).

2.3 Planting material

The experiment was conducted with potato seed tubers. Hereby seven cultivars from two different seed companies were organised. The genotypes varied in origin, adaptation and intended use (as seen in Table 9). The varieties were estimated by their respective breeding companies to be the most drought tolerant of their assortment.

Table 9: Overview of the planted varieties and their genotypic characteristics (ECPD, 2016a; 2016b; 2016c; 2016d; 2016e; 2016f; HZPC, 2016).

Producer	Variety	Origin	Release Date	Time to maturity	Purposes
BRAC	Cardinal	U.K.	1910	early	table, processing
BRAC	Diamant	Netherlands	1968	early	table, processing
HZPC	Caesar	Netherlands	1991	early	table
HZPC	Desiree	Netherlands	1962	medium	table
HZPC	Farida	Netherlands	----	late	table
HZPC	Mondial	Germany	1987	late	table
HZPC	Spunta	Netherlands	1967	medium	multiple purposes

The Bangladesh Rural Advancement Committee (BRAC, Dhaka, Bangladesh) supplied the cultivars Diamant as well as Cardinal. The seed tubers were shipped to the UFT in September 2014. They were delivered on a bed of fennel seeds (*Foeniculum vulgare* L.). According to BRAC, the fennel should prevent premature sprouting of the tubers. Immediately upon arrival the seed tubers were stored in a cold room (4 to 6 °C) in total darkness.

The five cultivars Caesar, Desiree, Farida, Mondial and Spunta were provided by the Dutch company HZPC Holland B.V. (XG Joure, Netherlands) and were shipped to the UFT on December 13th 2014. Upon their arrival they were also stored in the dark cold room.

On January 30th, roughly two weeks prior to planting, all of the delivered seed tubers were moved out of the cold rooms to ambient room temperature and natural light conditions. The tubers remained under these conditions until they were planted mid-February 2015. These

favourable conditions stimulate sprouting processes. Therefore, the seed tubers were planted when they had reached the BBCH stage 03.
The 20 most uniform and homogenous tubers of each genotype were selected to enter the experiment. They were chosen according to their shape, size, number of active eyes and physical health (*e.g.:* free of scabs, not pitted).

On February 13th 2015 the selected tubers were planted. Prior to planting the fresh weight and the number of active eyes of each tuber were recorded. The tubers were then planted centric three to four centimetres deep into the dry substrate. These initial tubers were in BBCH stage 03 (according to Hack *et al.*, 1993) at the time of planting. Then the pots were placed on cachepots (Sottovaso Rotondo, Iniezione 22 Terracotta, Teraplast S.p.a., Castelgomberto, Italy) which were distributed evenly on the four tables. Hereby five by six (in total 35) pots were set up on each grid respectively. Due to the high workload the planted tubers were not watered until the next day, February 14th 2015.

2.4 Custom sealing gear

In order to measure the true individual transpiration (and related parameters), the evaporation had to be arrested. This was accomplished by the application of custom made sealing equipment to each pot. The sealing gear for each pot consisted of following items:

- one bamboo stick (290 mm long, 7mm diameter)
- two plastic binders (Universalbinder, Windhager Handels GesmbH, Thalgau, Austria)
- two adhesive tape strips (14 mm width, Isolierband, Kopp Austria GmbH, Aigen, Austria)
- two transparent plastic bags (PE-LD, 400 x 600 mm)
- one plastic pipe (approx. 500 mm length, 4.5 mm diameter, Baumband ligature souplevit cep, Botanique Editions, Brouilly, France)
- one stopper
- one basal stick
- one foam strip (custom made, enveloped in cling film)

The sealing package for each pot was modified to a standard weight of 53.0 g by adding surplus slices of the plastic pipe to each bag. The sealing equipment was not mounted until the young plants had reached an average height of roughly 40 cm (BBCH 17 to 21) (Lago *et al.*, 2012; Sinclair & Ludlow, 1986). In order to ensure a tight seal around the stem without damaging the tissue, restricting the physiology or the metabolism a custom approach was required. Hereby spongy foam strips coated with cling film met the needs. Therefore 70 foam strips (approx. 150 x 30 x 10 mm) were cut out of a large sheet. They were gently but firmly wrapped in three to four layers of clear plastic cling film to prevent vapour efflux. Finally the excess tips were cut off to ensure a homogenous strip. As depicted in Figure 9 they will have firmly enveloped the stem, watering pipe and bamboo stick.

Figure 9: Close up photo of the coated foam strip wrapped around the stem, bamboo stick as well as the watering pipe and fixed with a strip of tape.

2.5 Experimental setup and treatments during the growth period

The experiment can generally be separated into two phases. The first phase is defined as the 'pre-experimental phase'. It started with the initial watering of the planted mother tubers on February 14th. To begin, each of the 140 pots received 1700 ml of water. Subsequently more water (200 to 300 ml) was added individually to reach the respective field capacity (FC). FC was estimated to be reached as soon as water started to flow out of the bottom of the pot. During this first period the plants were left to emerge and grow under optimum environmental conditions. Roughly ten days after planting the sandy loam showed first signs of cracking due to evapo-transpiration. Therefore on February 25th the pots additionally received 300 ml of water respectively to maintain well-watered conditions. In this initial phase the pots were arranged in groups according to their variety. On March 3rd the pots were rotated once by 180° around their own vertical axis to allow an even light distribution among the abundance of shoots.

Starting from February 19th the BBCH stages were recorded every alternate day throughout both experiment phases. During the pre-experimental phase, the BBCH recordings were assessed at 08:15 a.m. and during the experimental phase at 02:00 p.m. Solely on March 9th the BBCH stages were not assessed.

Furthermore, the chlorophyll concentration of selected leaves was measured with the chlorophyll-meter SPAD-502Plus (Konika Minolta Inc., Tokyo, Japan). Hereby the two youngest unfolded leaves which were most exposed to the irradiation were measured.

Due to the unsterilized nature of the field soil various weeds emerged within days of the initial watering. They were pulled out by hand every alternate day until the pots were sealed. The uprooted weeds were deposited on the soil surface of the pots they emerged from in order to maintain the nutrient concentration in each pot respectively.

At the end of the pre-experimental phase (March 8th) the pots were watered to their respective field saturations. Hereby they were allowed to leach out or take up excess water caught in the cachepots overnight (Sinclair & Ludlow, 1986).

The second phase is referred to as the 'experimental phase' which started on March 9th. At first the plants were sorted according to their uniformity within their genotype. Hereby 42 pots (six of each genotype) were terminated from the experiment due to physiological deformations, intragenotypical heterogeneity or, as in one case, a phytopathogenic infection. The remaining 98 pots were then further subdivided into two groups.

Group one consisted of 28 pots (four of each variety). They were harvested in order to determine the biomass accumulation during the pre-experimental phase. Hereby at first all shoots of each pot were cut at soil level with a knife (Cuttermesser 18 mm, Fiskars Germany GmbH, Herford, Germany). The bases of the shoots were exempted from foreign particles prior to being bagged in paper pouches (Flachsackweiß, 2 kg, Pacovis Österreich GmbH & Co KG, Vienna, Austria). Then the initial tubers were unearthed, rinsed with warm water and dried briefly with paper towels. The touch dry tubers were cut into three to five millimetre thick slices in order to aid the following drying process. Then the sliced tubers were placed in paper bags. The harvested plant tissues of each pot were bagged individually. The next step was to record the fresh weights of the biomasses with precision scales (CP 16001 S and PC 4400, Mettler Toledo, Greifensee, Switzerland). After the fresh weights were taken the paper bags containing the samples were placed in a drying oven for 48 hours at 60 °C. The plant tissues were weighed again in order to determine their dry masses.

The second group comprised of the ten most homogenous and uniform phenotypes of each genotype (in total 70 pots). Due to an abundance of shoots per pot (≤ 14 shoots per pot) each pot was reduced to its main shoot by cutting the excess shoots at the soil surface level, as in compliance with the protocol from Sinclair & Ludlow (1986). These single shoots were selected to be most representative and homogeneous within their respective varieties. The next step was to apply the sealing gear on each pot. In this regard the first step was to insert the bamboo and basal stick vertically into the substrate at close proximity to the single shoot. Then the watering pipe was connected to the basal stick. The stopper was applied on the other end of the pipe. The fully assembled watering hose was fixed with a strip of adhesive tape alongside the bamboo stick. As seen in Figure 9 the foam strip firmly enveloped the watering pipe, the bamboo stick as well as the stem. It was then fixed with a strip of adhesive tape roughly three centimetres above the soil surface. The stem area directly under the foam strips had to be free of foliage in order to ensure a tight seal. The next step was to deposit the excess pipe slices on the soil surface. Then the pots were individually placed in the two interleaved plastic bags which were then sealed around the foam strip with a binder. The second binder was mounted around the stem and the bamboo stick and therefore supported the statics and stability of the plant. It constantly had to be moved upward as the shoot elongated as it should be located in the top third of the shoot. Figure 10 depicts the fully applied sealing equipment. Immediately after sealing all pots were weighed to get an initial weight record. These individual initial weights will further be referred to as ‘initial weight’ of a specific pot.

Figure 10: Pot with a young potato plant and fully applied sealing gear.

After sealing the pots were evenly divided among two different treatments. They were cultivated either under well-watered (WW) or under water-stressed (WS) conditions. Therefore five plants of each genotype were grown under each watering regime. Hereby the sealed pots were divided into five blocks. Each block withheld two pots of each genotype, one WW and one WS pot respectively. Within each block the 14 pots were arranged in a fully randomised fashion.

The weight difference within 24 hours reflects the plants transpiration rate within this period. Therefore, all pots were weighed daily starting at 07:30 a.m. The daily transpiration rate (TR) was assessed gravimetrically with CP 16001 S. Furthermore, the pots were always measured in the same sequence in order to maintain temporal accuracy.

The sealed pots lost water solely through transpiration. Due to the fact that the different genotypes use water in different quantities, the transpired water had to be replenished to a certain degree in order for all pots to undergo similar kinetics of soil drying. Therefore, a watering threshold was set for both treatments. If the daily transpiration rate exceeded the respective benchmark the difference was replenished. This was accomplished by supplying the appropriate amount of water through the irrigation pipe. Hereby the stopper was removed from the loose end of the pipe. Then the individual amount of water which had to be replaced was carefully weighed in beakers (Jena^{er}Glas 400 ml, G20, Schott AG, Main, Germany; Griffin Beaker, PP, 600 ml, VITLAB GmbH, Grossostheim, Germany) on a precision scale (CP 16001 S). The individual volume of irrigation water was furthermore injected with syringes (Omnifix 50 ml, B. Braun Melsungen AG, Melsungen, Germany; BD Discardit 5 ml, 10 ml, 20 ml, Becton Dickinson SA – Ctra. Mequinenza, Fraga (Huesca), Spain) directly into the pipes. The syringes were modified with customised pipette tips (1000 µl Blue, graduated tip, TipOne, Star Lab GmbH, Hamburg, Germany) which fitted nicely into the mouth of the pipe. The modified syringes as well as the beakers were flushed with the irrigation water prior to their use. This was done to moisten the surfaces and therefore minimise the biases in the watering process. After the full amount of required water had been supplied to a pot the irrigation pipe had to be flushed from residual water. Hereby any water remaining in the irrigation pipe was blown towards the soil surface by injecting a syringe full of air into the pipe.

- WW treatment

The plants which were exposed to the WW treatment received sufficient water throughout the whole experimental phase. Their threshold was set at 240 g under their initial weight. Each pot was re-watered daily to return the pot weight to the benchmark value. The threshold was set at approx. 85 % of the soil holding capacity and therefore provided optimum water conditions without causing anoxic conditions in the root zone.

- WS treatment

The WS pots, however, were only partially re-watered. If their daily transpiration exceeded a certain threshold level, in this case 80 ml, the excess water had to be replenished. Hereby the pots were managed to progressively lose water in a controlled manner. Therefore, gradual soil drying was simulated and all WS entries were subjected to similar kinetics of water stress. This allowed a progressive development of water-deficit stress over a few weeks.

For each plant, the daily relative TR was calculated as the ratio of the daily water loss from the WS-plant to the mean daily transpiration of WW-plants of the same genotype (Equation 11). This normalisation buffered large daily environmental changes in the measurements (e.g.: weather fluctuations).

$$TR_n = \frac{TR_{WS}}{\emptyset\, TR_{WW}} \tag{11}$$

The normalised transpiration rate (NTR) sets the current TR of any given day in relation to the average TR of the first four days (Equation 12). This second normalisation accounts mainly for potential variations in plant size. This approach is based on the assumption that the water content of the pots is still at sufficient levels during the first few days. Therefore, the average initial TR may serve as a reference value of the individual TR at well-watered conditions. The ratio declines with decreasing TR as the soil gradually dries out. The experiment ran until every WS-pot had reached a NTR ≤ 0.1. In other words: until the TR had declined by ≥ 90 %.

$$NTR_n = \frac{TR_n}{\frac{TR_1+TR_2+TR_3+TR_4}{4}} \tag{12}$$

The fraction of transpirable soil water (FTSW) was calculated as the fraction of the total transpirable soil water remaining in the soil at any time. As equation 13 suggests, it is calculated by relating the current soil water content to the soil water content at termination. The soil water content of any pot may be calculated by subtracting the pot weight at termination from the pot weight at any given time.

$$FTSW_n = \frac{pot\ weight_n - pot\ weight_{Termination}}{pot\ weight_{Initial} - pot\ weight_{Termination}} \tag{13}$$

In order to assess accurate transpiration measurements and related parameters it was of greatest importance that all plants remained completely unharmed (*e.g.:* no damages). Especially the main transpiring organs (unfolded leaves) had to remain completely intact in order to measure the whole genotypic potential.

2.6 Harvest

The plants were harvested on April 10th and 11th after the final measurements had been taken (biomass weight determination, SPAD-reading, BBCH assessment). At this stage of the experiment all WS-pots displayed physiological signs of water stress. Furthermore the NTR of all pots had reached a value ≤ 0.1, thus the potential TR was reduced by 90 %. At termination the plants had on average reached the BBCH stage 60.

Hereby the tissues of each plant were divided into five categories: (1) leaves, (2) stems and flowers/buds, (3) roots, (4) initial tuber and (5) new tubers. The segregation of the tissue samples permitted an accurate allocation of photosynthates and water throughout the plants organs.

Each pot was harvested individually and in the same specific sequence. Hereby at first the senescent tissues (dead leaves and buds) were collected from the plastic bag covering the space between the stem and the wall of the pot. Then all unfolded leaves (≥4 cm length) were cut with a pair of scissors from the plant. The third step was to remove the sealing gear as well as the plant label from the pot. Then the trimmed stem and shoots were cut with a pair of scissors into pieces of approx. five centimetre length to facilitate the drying process. The stem was cut at its base at soil level. The fifth step was to spill the content of the pot (substrate and sub-surface biomass) into a plastic sorting tray (Stapelkasten 25 l, PE-HD, Paul Craemer GmbH, Herzebrock-Clarholz, Germany). The felt circle was removed and the conglomerated lump of substrate was broken apart by applying physical pressure with bare hands. Then the majority of the root system as well as the tubers and stolones were carefully lifted out of the loosened soil. The residual substrate in the tray was sampled (described below) and then discarded after each pot. In the seventh step these subsoil biomasses were washed thoroughly with warm water in order to remove adhesive soil particles. Then the cleaned tissues were separately laid out on paper towels for circa ten minutes to drain and dry prematurely. Hereby the tubers(initial and new) were cut in approx. two millimetre thick slices with a knife (Cuttermesser 18 mm). This crucial step will have allowed the tubers to dry faster in the oven and, therefore, inhibit decay. After the brief drying process the underground tissues were bagged separately and weighed individually (with CP 16001 S) to record their fresh weights.

In addition to the plant tissue harvest, soil samples were taken from the WS-pots only. Hereby the residual substrate of the individual pots from the plastic container was mixed thoroughly by hand. Persistent lumps of substrate were crumbled by hand to ensure a homogenous mixture of the whole remaining substrate. Then, in total roughly 50 g of substrate were carefully sieved through the fingers into three paper bags (Flachsack weiß, 5 dag, Pacovis Österreich GmbH & Co KG, Vienna, Austria). The fresh weight of the bagged soil samples was recorded with CP 16001 S.

Finally, the paper bags containing the biomasses and soil samples were placed in preheated drying ovens (Memmert Universalschrank UFE 600, Linder Labortechnik, Overath, Germany). The tissue samples were dried at 65 °C in three ovens simultaneously whereas the soil samples were fitted in one oven at 105 °C. Depending on the biomass category (1 to 5), the samples required varying drying periods to become absolutely dry. The leaf (1) and shoot (2) samples required 48 hours, the roots (3) 72 hours and the tubers (4, 5) 120 hours to be absolutely dry, whereas the soil dried within 24 hours. All of the dried samples were weighed between April 13th and April 17th with a high precision scale (2001 MP2, Sartorius AG, Göttingen, Germany). Hereby the samples were moved from the ovens to ambient room temperature roughly 15 minutes prior to the weighing process. During this acclimatisation period the samples cooled down and therefore minimised biases during the dry weight assessment. Furthermore the samples were moved out of the drying ovens in small batches. Each batch consisted of averagely 50 paper bags standing on a tray.

Figure 11 gives an overview of the glasshouse cabin shortly after the sealing gear was applied.

Figure 11: Overview of the glasshouse cabin and the different potato cultivars with applied customised sealing gear.

2.7 Statistical analyses

The raw data was recorded and prepared in Microsoft Excel 2010 (Version 14.0.7155.500, Microsoft Corporation, Redmond, USA). The compiled data sets were then analysed with the software Statistical Analyses Systems (SAS Version 9.4, SAS Institute Inc., Cary, USA). A two-way analysis of variance (ANOVA) and two one-way ANOVA's (one for each treatment) were run with the compiled data sets. The ANOVA's were followed by Student-Newman-Keuls (SNK) tests. The SNK approach is more powerful and less conservative than Tukey's range test.
Graphs were produced through SigmaPlot (Version 12.5, Systat Software Inc., San Jose, USA). Hereby a piecewise two-segment linear regression was fit to the NTR as a function of FTSW using the Global Curve Fit Wizard-function from the software.

3 Results

The results of the glasshouse experiment are generally separated into environmental conditions and crop-responses towards progressive soil drying.

3.1 Environmental conditions in the glasshouse

Generally speaking, the climatic conditions in the glasshouse cabin were at optimum conditions for potato crops, thus, allowing precise measurements of responses towards progressive soil drying.

3.1.1 Temperature

The automated glasshouse cabin maintained the average minimum and maximum air temperature at 12 °C and 22 °C, respectively. During the first half of the dry down experiment the temperature remained relatively stable, while the second half indicated a higher fluctuation and peak-spikes which occurred due to the outside temperature conditions. At the end of the experiment, the temperature peaked at 29 °C for two days (Figure 12).

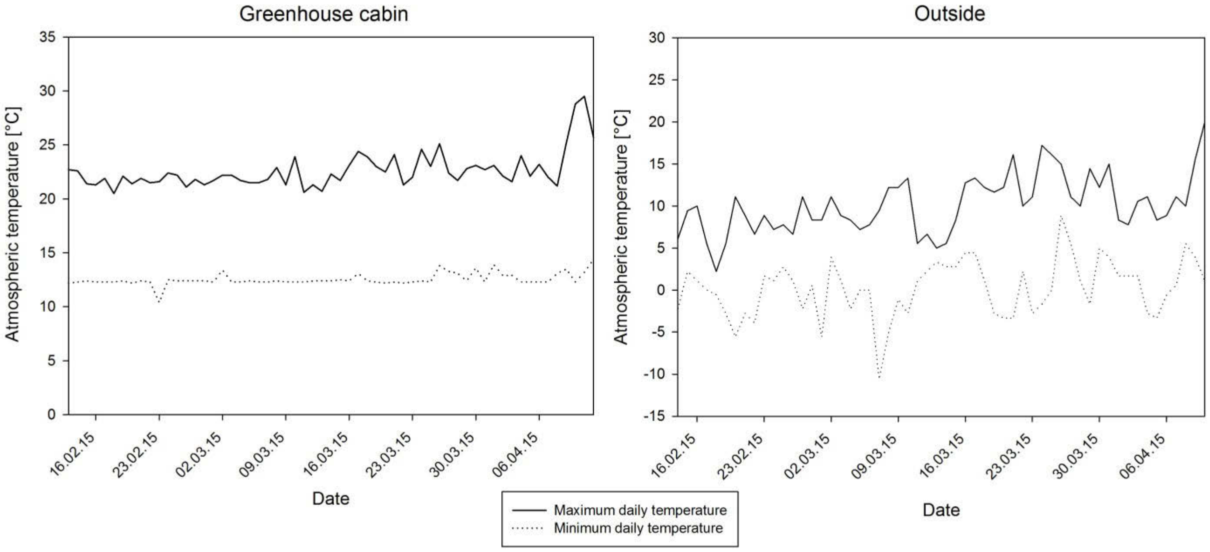

Figure 12: Minimum and maximum air temperature [°C] inside the glasshouse cabin (left) and outside the glasshouse (right) during the experimental period.

3.1.2 Relative humidity

The cabin hygrometer recorded the humidity and maintained the cabins' relative humidity averagely between 28 to 58 % (Figure 13). The relative humidity inside the glasshouse cabin was influenced by the air-moisture-content outside the glasshouse, as is apparent in Figure 13.

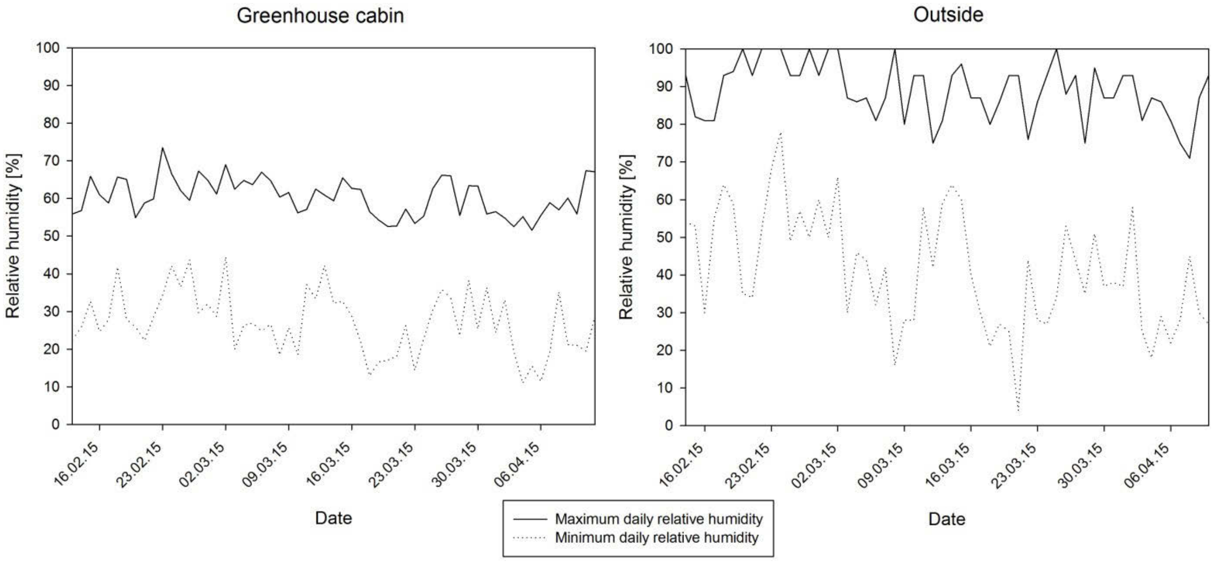

Figure 13: Minimum and maximum relative humidity [%] inside the glasshouse cabin (left) and outside the glasshouse (right) during the experimental period.

3.1.3 Vapour pressure deficit

The average regular VPD (θ = 0.5) prevailing in the glasshouse cabin ranged from 1.0 to 1.5 kPa (Figure 14). The calculated VPD exceeded the 2 kPa threshold only on single episodes. The daily atmospheric VPD was weighted (θ = 0.75) towards periods of higher transpirational demand, e.g. lower relative humidity and higher temperature. The average weighted VPD is slightly higher than the regular VPD (Sinclair *et al.*, 1984; Sinclair, 2012) as it averaged around 1.5 to 2 kPa.

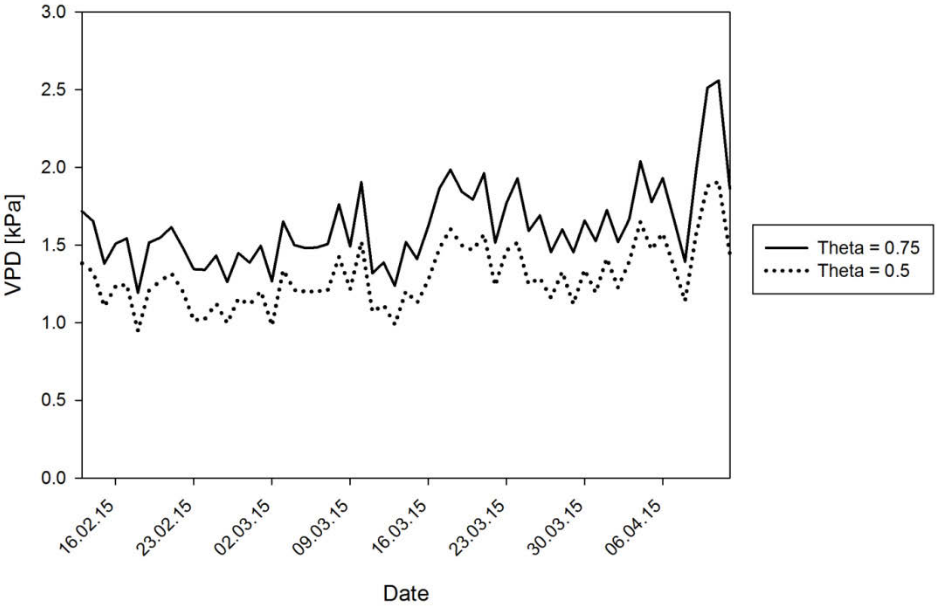

Figure 14: Weighted (dotted line) and regular (solid line) vapour pressure deficit (VPD) [%] inside the glasshouse cabin during the experimental period. The weighted VPD's were calculated with a higher theta-value (0.75), thus laying more focus on periods of high temperature or low relative humidity.

3.1.4 Photosynthetically active radiation

The PAR-readings measured an average photon flux density of 323 µmol m^{-2} s^{-1} at cloudy and 1,185 µmol m^{-2} s^{-1} at sunny conditions at pot level in the glasshouse cabin.

3.2 Responses of potato cultivars to progressive soil drying

The genotypic responses of potato crops towards progressive soil drying were documented by several means of parameters.

3.2.1 Fraction of transpirable soil water-threshold

The individual daily NTR-data are plotted against the retroactively calculated FTSW-values and fitted with a two-segment linear regression curve. The intersection of the fitted linear regressions indicate the FTSW-threshold point at which transpiration starts to decline as a response to progressive soil dryness (Figure 15). The FTSW-threshold values range from approx. 0.24 to 0.32 in this set of cultivars under these specific environmental conditions (Table 10). The highest threshold values were measured with Spunta (0.320) and Farida (0.295). The lowest were found among Mondial (0.244) and Diamant (0.249). The coefficients of determination were found to be mostly between 90 and 95 % for all of the fitted two-segment regressions (Table 10).

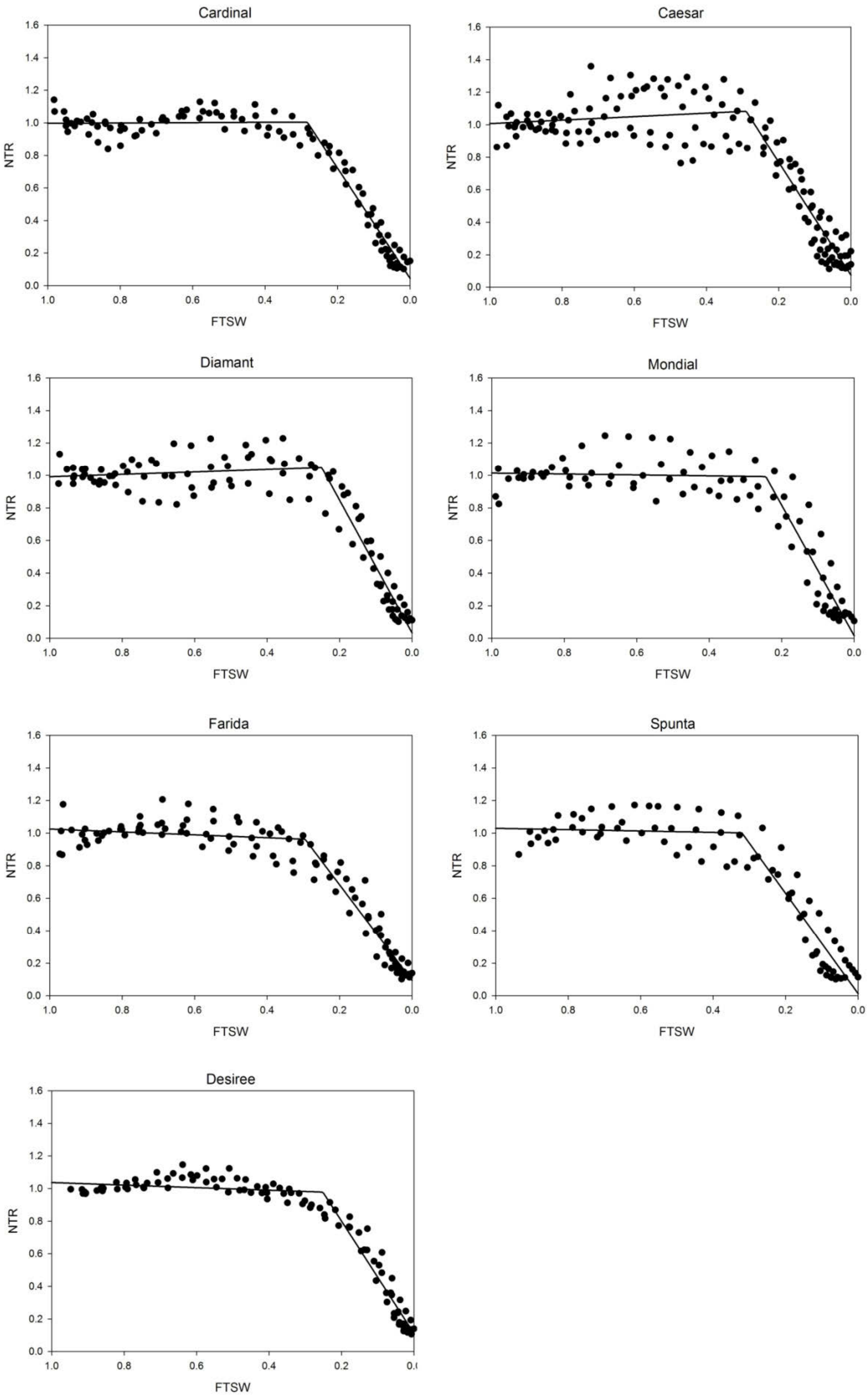

Figure 15: Normalised transpiration ratio (NTR) as a function of fraction of transpirable soil water (FTSW) for seven potato cultivars (Caesar, Cardinal, Desiree, Diamant, Farida, Mondial, Spunta) from a glasshouse pot experiment. The solid line in each graph is the regression fit using the piecewise two-segment linear regression; the intersection of which indicates the FTSW-threshold for decline in transpiration.

Table 10: Summary of results of the dry-down experiment for seven potato cultivars: fraction of transpirable soil water (FTSW) threshold for decline in transpiration, coefficient of determination (R^2) and slope (k) of the linear regression after the FTSW-threshold point has been reached.

Cultivar	FTSW-threshold	R^2	k
Cardinal	0.2837	0.9620	-3.38
Caesar	0.2718	0.8955	-3.71
Diamant	0.2491	0.9256	-4.07
Mondial	0.2437	0.8897	-4.01
Farida	0.2950	0.9430	-2.95
Spunta	0.3204	0.9147	-3.08
Desiree	0.2515	0.9660	-3.45

3.2.2 Total transpiration

The total transpiration [ml] is defined as the amount of water each individual plant used during the dry down phase of the experiment. It was calculated for each plant as the sum of water volume transpired each day (Equation 14).

$$Total\ Transpiration\ [ml] = \sum_{k=1}^{n} Daily\ Transpiration_n\ [ml] \qquad (14)$$

The variety ($p \leq 0.0001$), treatment ($p \leq 0.0001$) and interaction of these factors ($p = 0.002$) all had significant influences on the total amount of water used by plants during the experiment.

In general, the WS-treated plants used roughly 51 % less water, compared to the control plants which used on average 3262.1 ml. Within the control plants the variety had a significant influence on the total amount of water transpired ($p \leq 0.0001$). Caesar transpired the smallest amount of water, it used significantly less compared to all other cultivars, except Cardinal. Furthermore, Spunta and Desiree transpired significantly higher amounts of water than Cardinal and Caesar (Figure 16). The highest water consumption was observed in Spunta, it used 3995.3 ml and therefore transpired roughly 22.5 % more than the WW-average.

Within the water-stressed plants there were significant differences ($p = 0.01$) in the amount of water transpired. Under WS-treatment Cardinal transpired significantly less compared to Diamant and Desiree (Figure 17). Cardinal used the smallest and Diamant the highest amount of water.

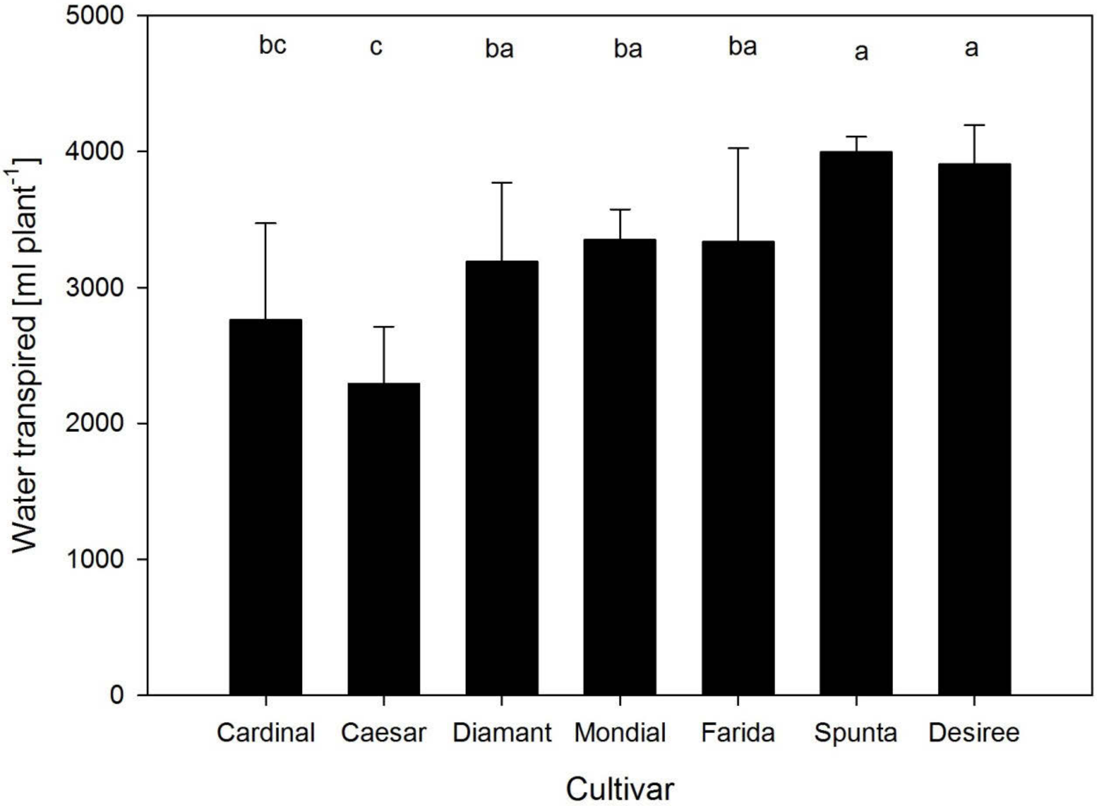

Figure 16: Transpiration [ml plant^{-1}] of potato cultivars under well-watered (WW) conditions; means with the same letter are not significantly different.

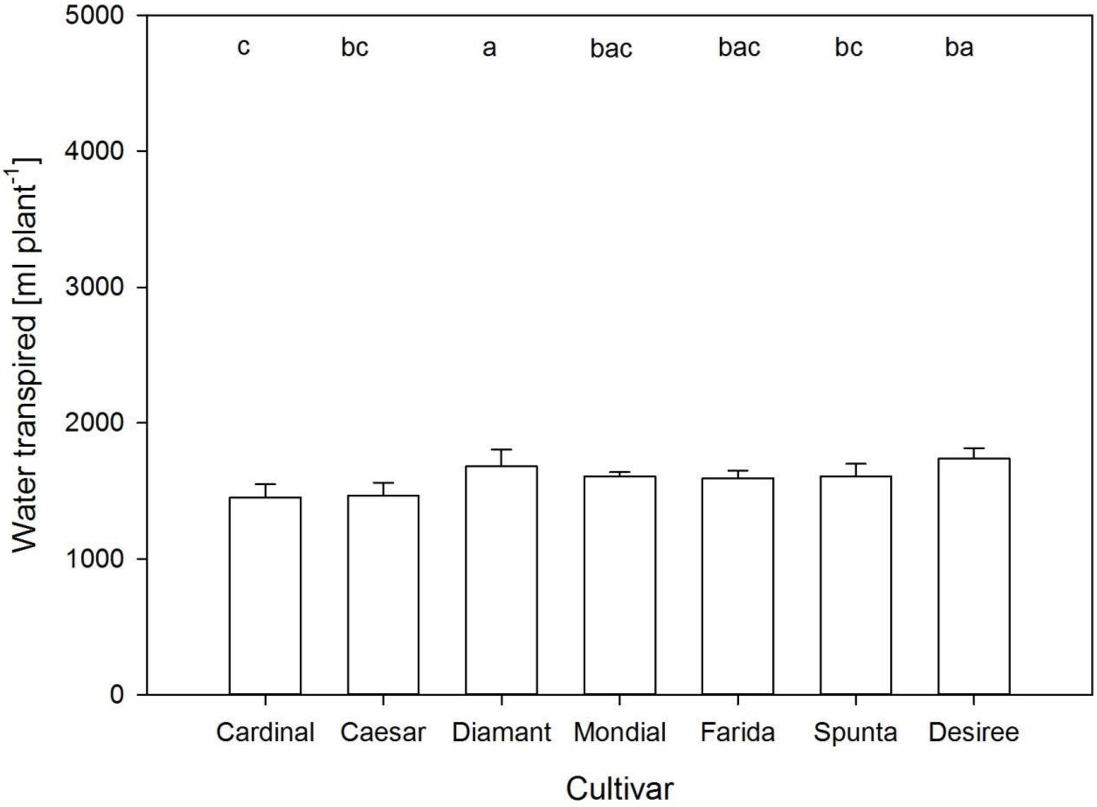

Figure 17: Transpiration [ml plant^{-1}] of potato cultivars under water stressed (WS) conditions; means with the same letter are not significantly different.

3.2.3 Initial shoot dry mass

The initial shoot mass represents the biomass build-up of the main shoot at the end of the pre-experiment phase. Their dry masses were obtained through destructive sampling of five pots of each cultivar. The average initial shoot DM production for all varieties was approx. 1.6 g plant^{-1}. Spunta had the highest amount of initial shoot dry mass ($p = 0.001$) (Figure 18). Cardinal featured the lowest initial shoot development, it produced roughly 30 % less than the average. Caesar's performance was close to average.

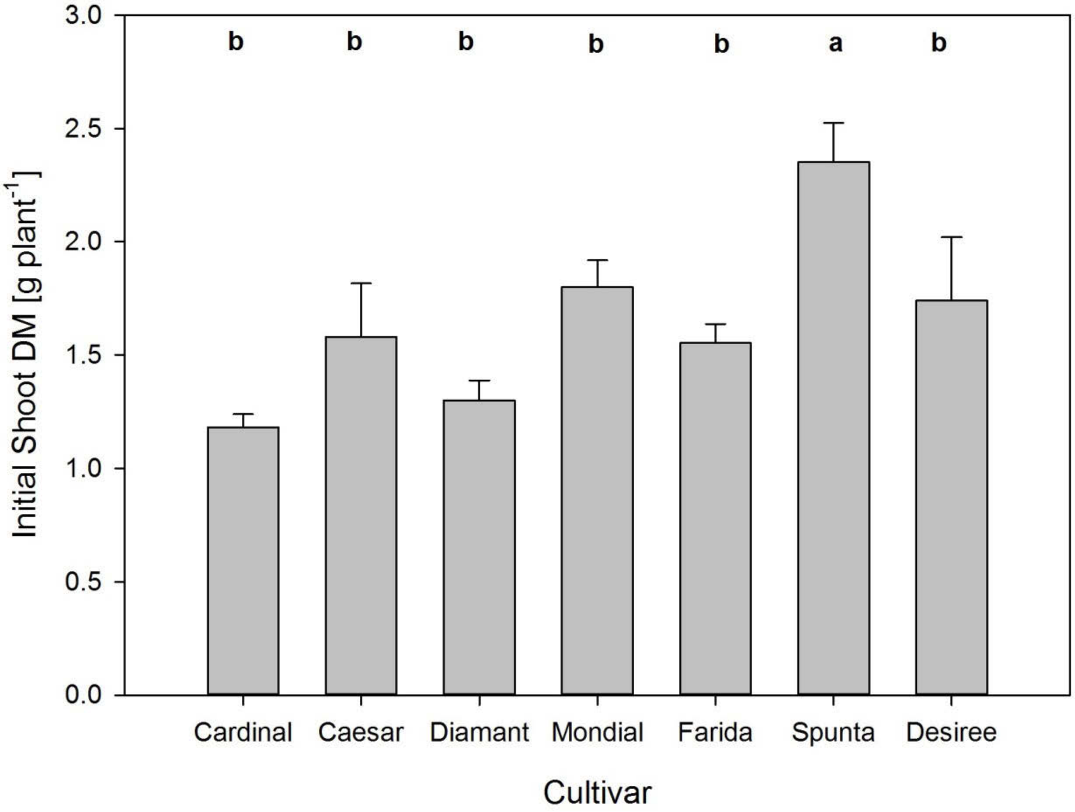

Figure 18: Initial shoot dry mass (sum of stem and leaves) of potato cultivars grown under optimum water conditions in a glasshouse pot experiment; means with the same letter are not significantly different.

3.2.4 Accumulated total dry mass

Total plant dry matter (TDM) was calculated by summing up the dry masses of the separately harvested tissue parts at the end of the experiment. The TDM was calculated as the sum of tuber DM, stem DM and leaf DM (Equation 15). The combined dry masses from stems and leaves form the shoot dry mass. The Tuber dry matter considers only the dried tuber biomass, without stolons.

$$TDM\ [g] = Tuber\ DM[g] + Stem\ DM\ [g] + Leaf\ DM\ [g] \tag{15}$$

The accumulated TDM (AccumTDM) refers to the dry biomass produced only during the period the water treatment was applied. It was calculated by summing up the dry masses from tubers, leaves and stems at termination and deducting the initial dry mass (Equation 16):

$$AccumTDM\,[g] = TDM\,[g] - Initial\,Shoot\,DM\,[g] \quad (16)$$

The AccumTDM production was significantly influenced by the water treatment ($p \leq 0.0001$) as well as by the varieties ($p = 0.023$). The interaction between the two factors was not significant at a 5 %-level ($p = 0.052$). As the interaction is non significant, the values illustrated in Figures 19 and 20 consist of pooled data.

The average biomass production from WS-plants was reduced significantly by approx. 40 % compared to the WW-plants (Figure 19). Considering both water treatments, Cardinal featured the lowest gain in TDM formation. It produced significantly less TDM during the dry-down cycle compared to Desiree. The largest mean TDM accumulation was found in Spunta, which produced 22 g plant^{-1} and thus roughly 15 % more than the average of all cultivars. Caesar and Farida featured roughly the same biomass build-up, they both performed average.

The AccumTDM depicts a very similar pattern as the total transpiration of the control plants, hence cultivars which produced more biomass also used more water. Caesar was the exception as it produced roughly the same amount of biomass as Spunta while it consumed significantly less water (Figure 20).

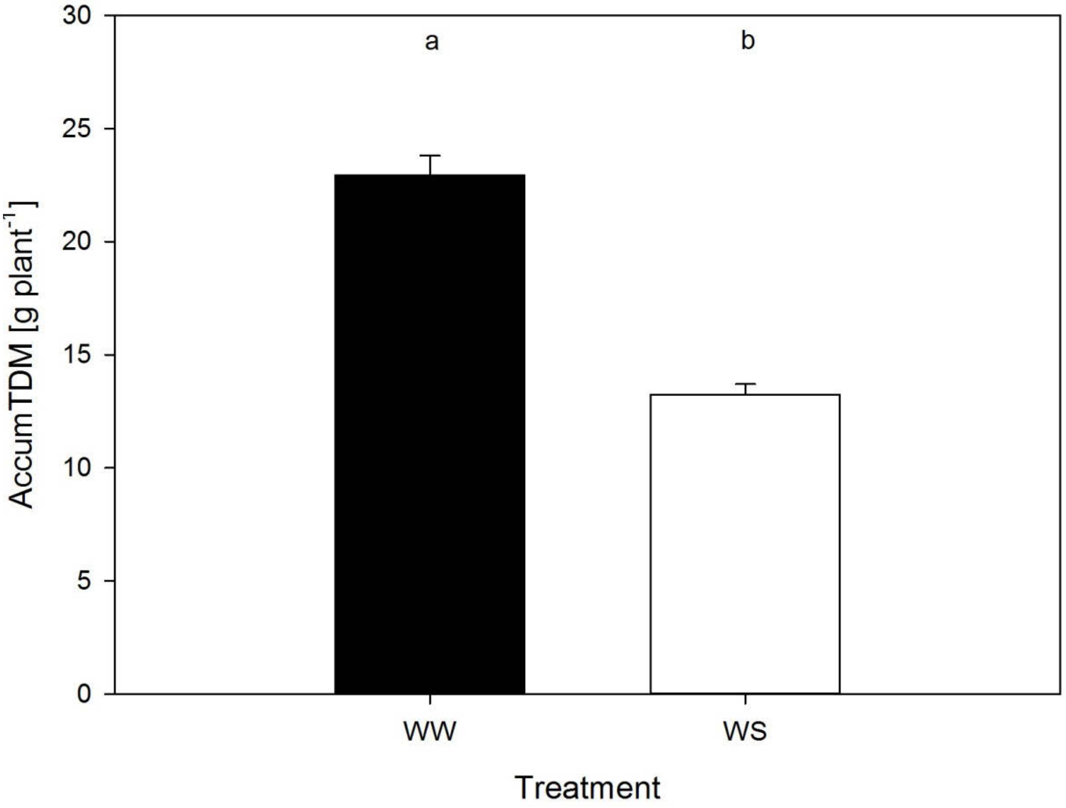

Figure 19: Total plant biomass (AccumTDM; summed tuber and shoot masses) produced under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

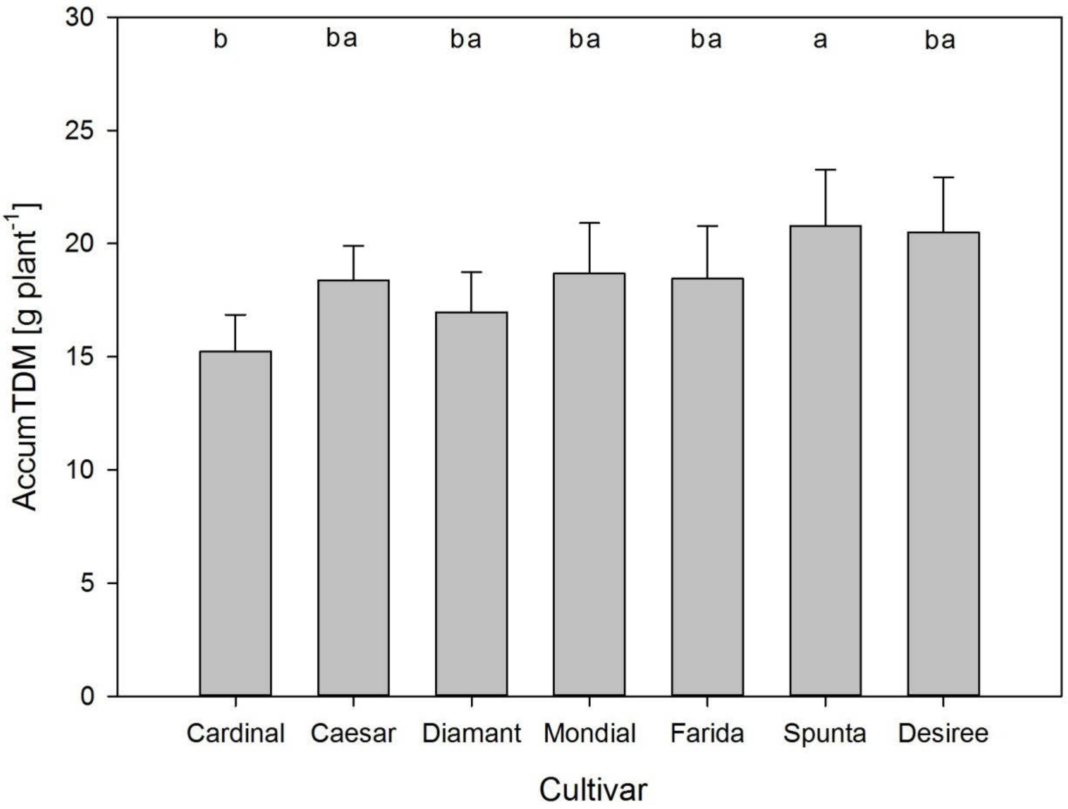

Figure 20: Average total biomass (AccumTDM; summed tuber and shoot masses) of potato cultivars grown under both well-watered and water-limited conditions; means with the same letter are not significantly different.

3.2.5 Transpiration efficiency for accumulated total dry mass

The TE for AccumTDM only considers the biomass build-up during the dry-down cycle and sets it in relation to the water used in that same period (Equation 17). The TE for AccumTDM of a plant is measured in gram biomass per litre water transpired.

$$TE\ AccumTDM\ [g\ l^{-1} plant^{-1}] = \frac{AccumTDM\ [g]}{Total\ Transpiration\ [l]} \tag{17}$$

The ANOVA results inform that both the water treatment ($p \leq 0.0001$) and the variety ($p \leq 0.0001$) had significant effects on the TE for AccumTDM. The interaction of these factors was non significant.

Generally speaking, the WS-plants displayed a significantly higher TE compared to the control plants. The WW-plants displayed an average TE of 7.1 g l^{-1} plant^{-1}. In comparison, the TE of WS-plants was roughly 20 % more than that of WW-plants (Figure 21).

All tested cultivars displayed very similar TE-performances, except Caesar. Without Caesar the average TE over both treatments was calculated to be 7.35 g l^{-1} plant^{-1} for each cultivar respectively (Figure 22). These six cultivars (Cardinal, Diamant, Mondial, Farida, Spunta and Desiree) displayed TE-performances in very close proximity to one another. Averaged over both water treatments, Caesar performed significantly better. It featured the highest TE for TDM as it was roughly 32 % more efficient compared to the other six cultivars. The lowest TE was found in Diamant which could only produce approx. 6.8 g l^{-1} $plant^{-1}$. The second lowest TE-performance was observed in Spunta.

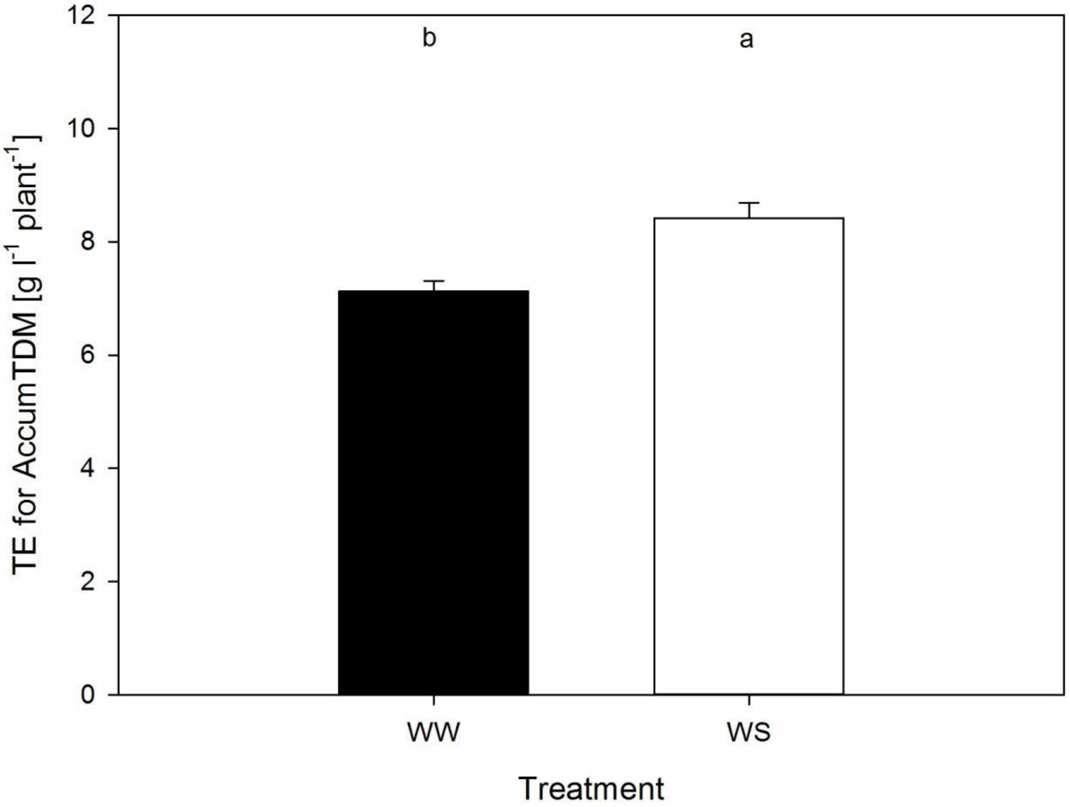

Figure 21: Average transpiration efficiency for total plant dry mass (TE for AccumTDM) of potato cultivars grown under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

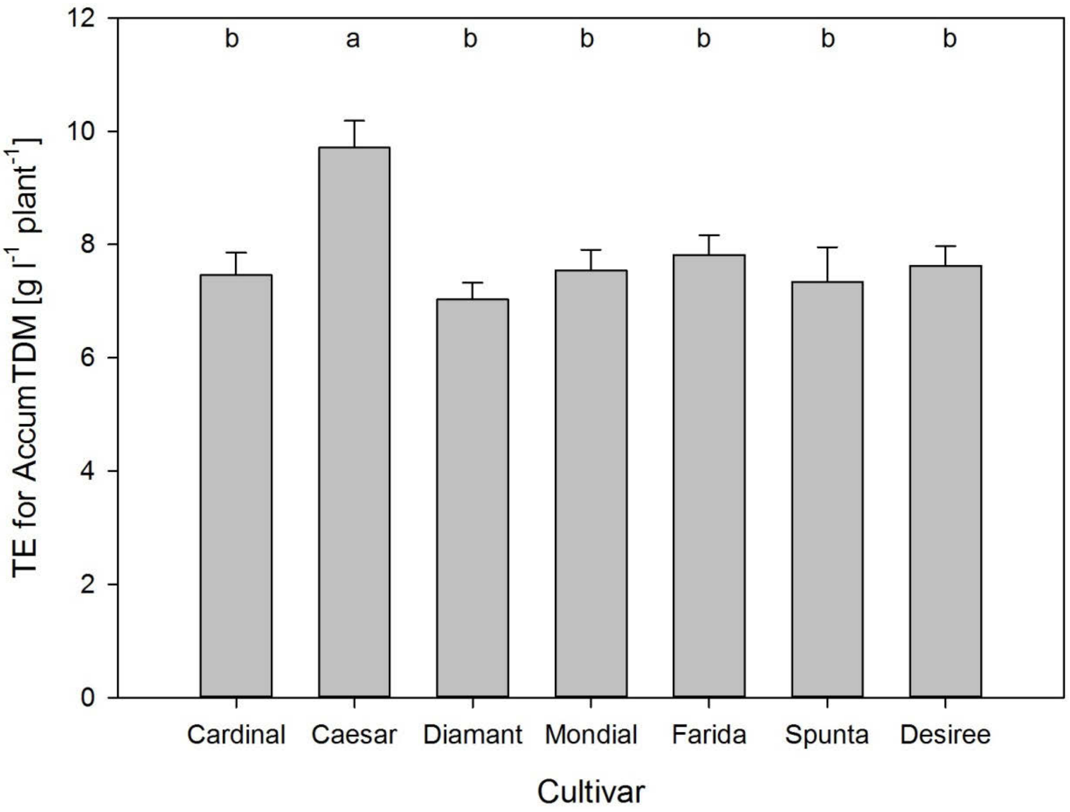

Figure 22: Transpiration efficiency for total plant dry mass (TE for AccumTDM) of potato cultivars across well-watered and water-stressed treatments; means with the same letter are not significantly different.

3.2.6 Coefficient of transpiration

Similar to TE, the coefficient of transpiration (CT) offers a framework to quantify the water use to biomass build-up ratio. The CT of a plant informs how many litres of water must be transpired in order to produce one kilogram of biomass (Equation 18).

$$CT\ TDM\ [l\ kg^{-1} plant^{-1}] = \frac{Total\ Transpiration\ [l]}{AccumTDM\ [kg]} \tag{18}$$

Results of the statistical analysis showed that both the water treatment ($p = 0.003$) and the variety ($p \leq 0.0001$) had a significant effect on the CT-performance of the tested cultivars. The interaction of these two factors was not significant.

The average CT-performance of WW-plants was measured at 143.7 l kg^{-1} plant^{-1}. Under water-stress it was reduced significantly by approx. 16 % (Figure 23).

According to the CT-performances, Caesar was the most efficient in converting water into biomass. Its mean CT was measured at 104.9 l kg^{-1} plant^{-1}which is significantly less compared to all other cultivars. Furthermore, Caesars CT was approx. 25 % less compared to the average of the other six cultivars combined. The six less efficient cultivars displayed very similar CT-performances (Figure 24) which circle around 139.5 l kg^{-1} plant^{-1}. Farida and Spunta exhibited the second and third lowest CT for TDM. The highest value was found with Diamant (147 l kg^{-1} plant^{-1}).

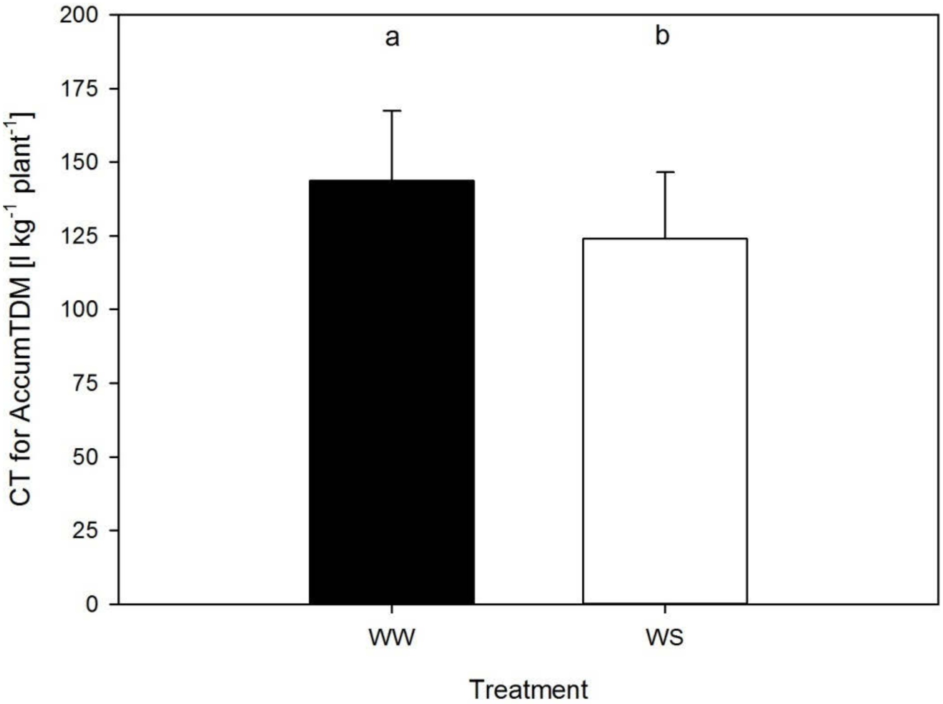

Figure 23: Average coefficient of transpiration for total plant dry mass (CT for AccumTDM) of potato cultivars. Graph displays pooled values from seven potato cultivars grown under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

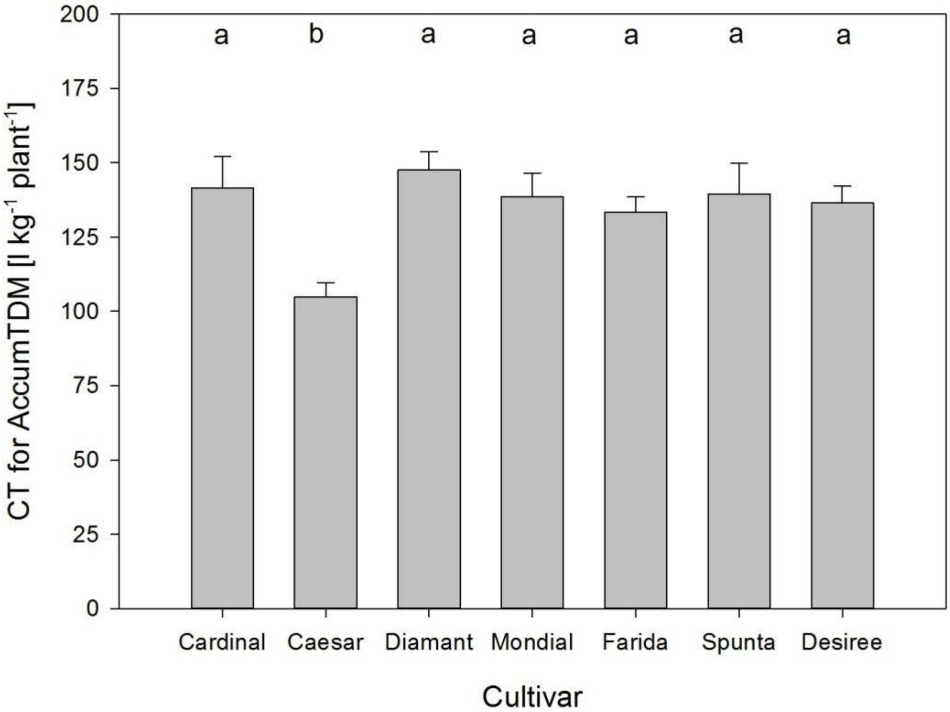

Figure 24: Coefficient of transpiration for total plant dry mass (CT for AccumTDM) of individual potato cultivars across well-watered and water-stressed treatments; means with the same letter are not significantly different.

3.2.7 Accumulated shoot dry mass

Similarly to the AccumTDM, the accumulated shoot dry mass refers to the shoot tissue build-up during the dry-down phase of the experiment. The initial shoot mass is subtracted from the final shoot mass, thus resulting in the accumulated shoot dry mass (Equation 19).

$$Accumulated\ Shoot\ DM\ [g] = Final\ Shoot\ DM\ [g] - Initial\ Shoot\ DM\ [g] \tag{19}$$

The ANOVA concluded that the treatment (p = 0.0002) as well as the variety (p ≤ 0.0001) had significant effects on the amount of shoot biomass produced during the dry-down experiment. The interaction of these factors was found to be non-significant.

The set of control plants were able to produce significantly more shoot biomass compared to the water-stress treated pots. The mean gained shoot biomass from stressed pots was reduced by approx. 30 % compared to the control plants (Figure 25).

Under consideration of both treatments it becomes evident that Mondial exhibited the highest shoot biomass production during the water-stress application. It produced significantly more shoot biomass compared to all other cultivars except Desiree (Figure 26). Caesar and Spunta produced roughly the same amount of shoot biomass during treatment application.

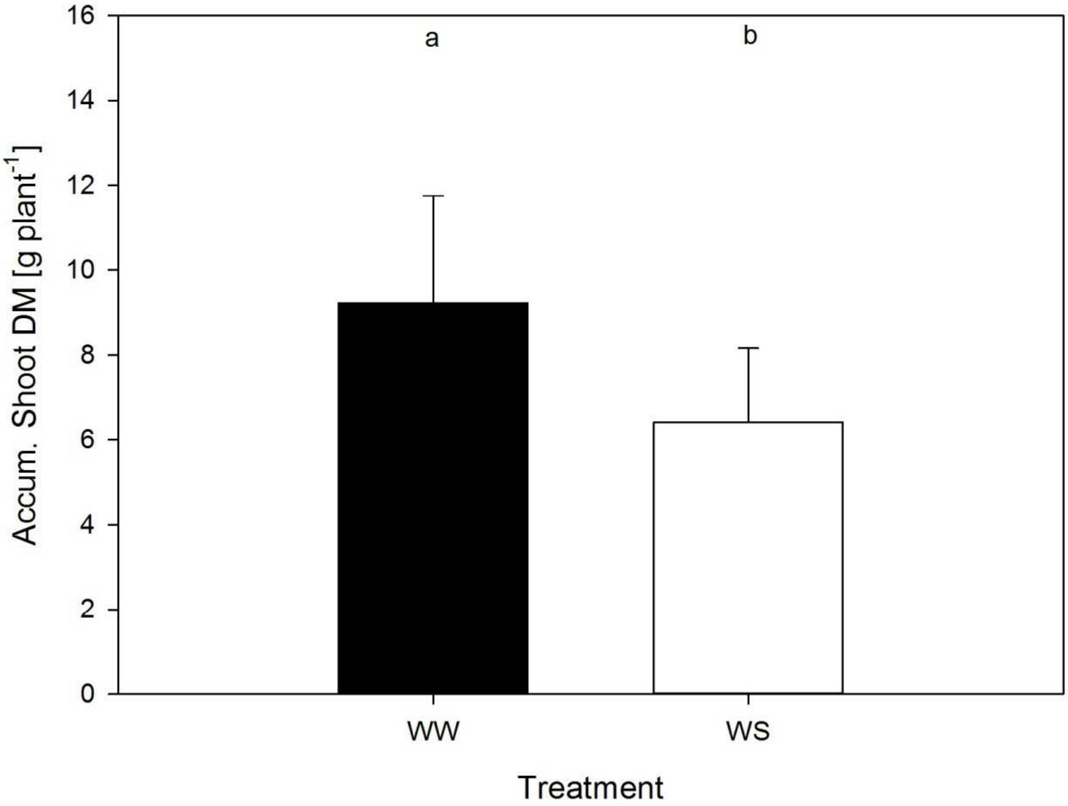

Figure 25: Average shoot dry mass (accumulated shoot DM, summed leaf and stem masses) of potato cultivars grown under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

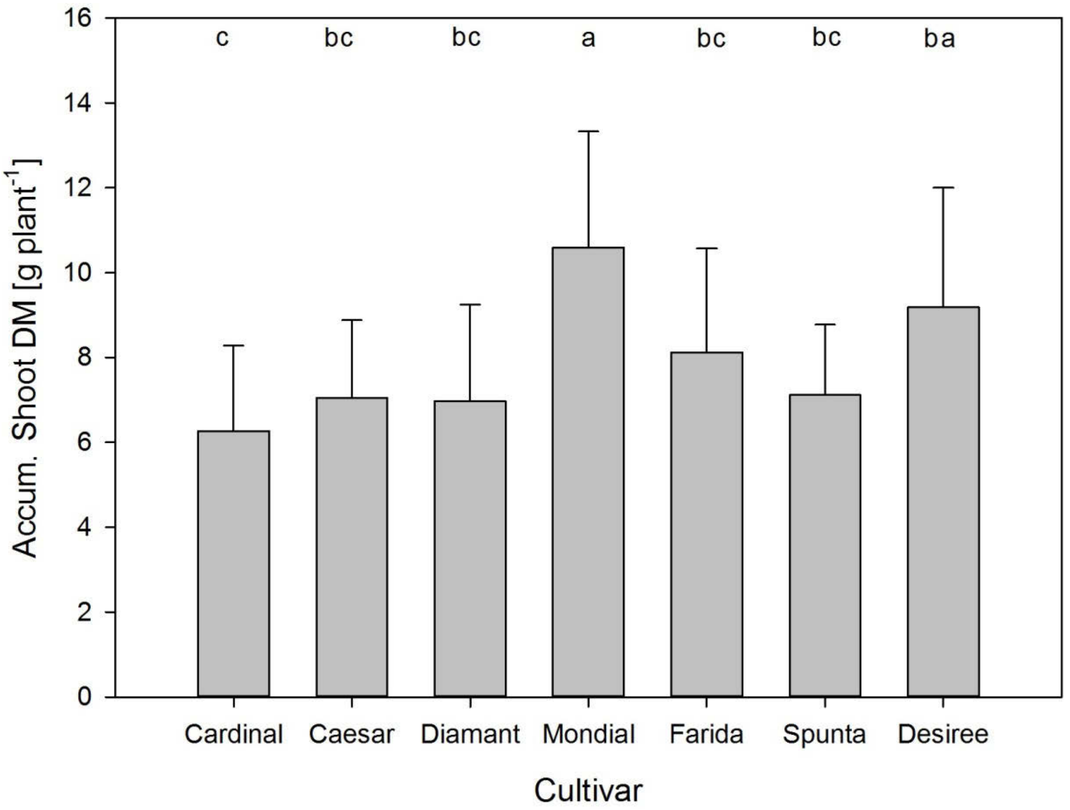

Figure 26: Average shoot dry mass (accumulated shoot DM, summed leaf and stem masses) of individual potato cultivars across well-watered and water-stressed treatments; means with the same letter are not significantly different.

3.2.8 Tuber dry mass

The variety ($p = 0.018$) and the treatment ($p \leq 0.0001$) both had a significant impact on the tuber DM formation. The interaction of these factors was found to be non-significant with an $\alpha = 0.05$.

Similarly to other tissues, the tuber mass was reduced significantly by water-stress treatment (Figure 27) as well. The mean performance across all cultivars from WW-treated plants was found to be 13.7 g plant^{-1}. Under WS-conditions it was reduced significantly by approx. 49 %.

Considering both treatments, Spunta was found to feature the highest tuber dry mass production, 14.8 g plant^{-1}. It produced significantly more tuber biomass than Farida, Cardinal and Mondial. Mondial produced the smallest amount of tuber DM. Caesar's tuber yield was insignificantly less than Spunta's (Figure 28).

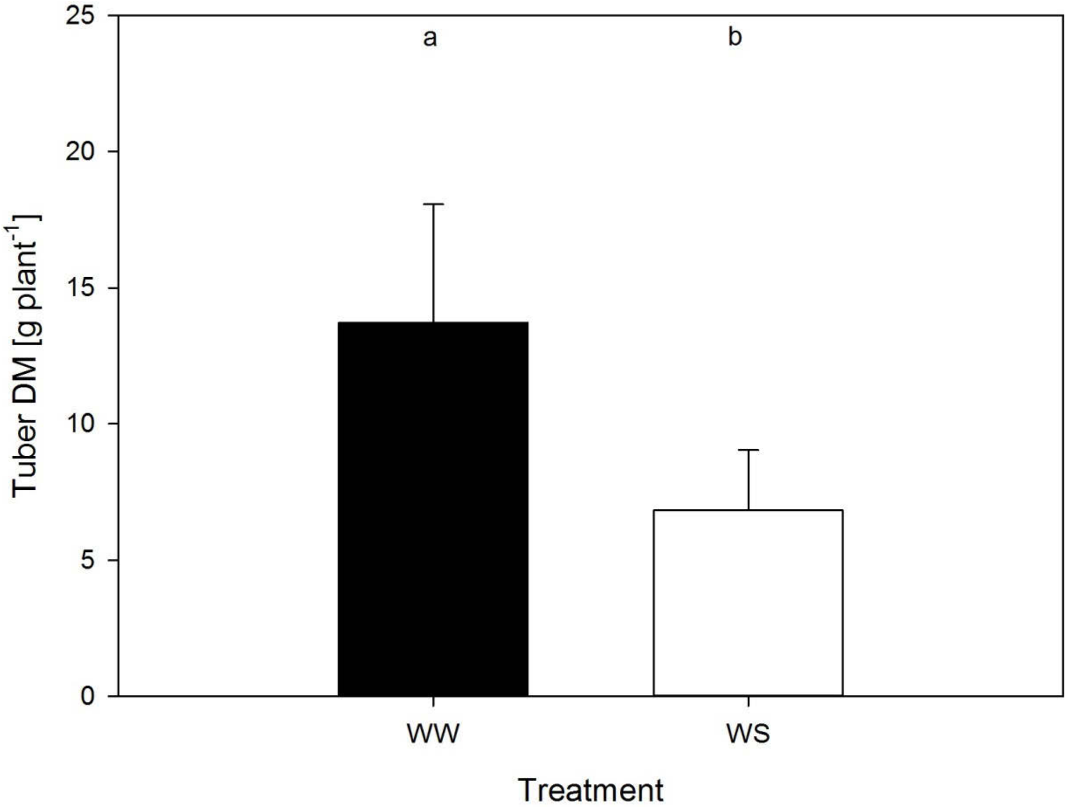

Figure 27: Tuber dry mass (Tuber DM) of potato cultivars grown under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

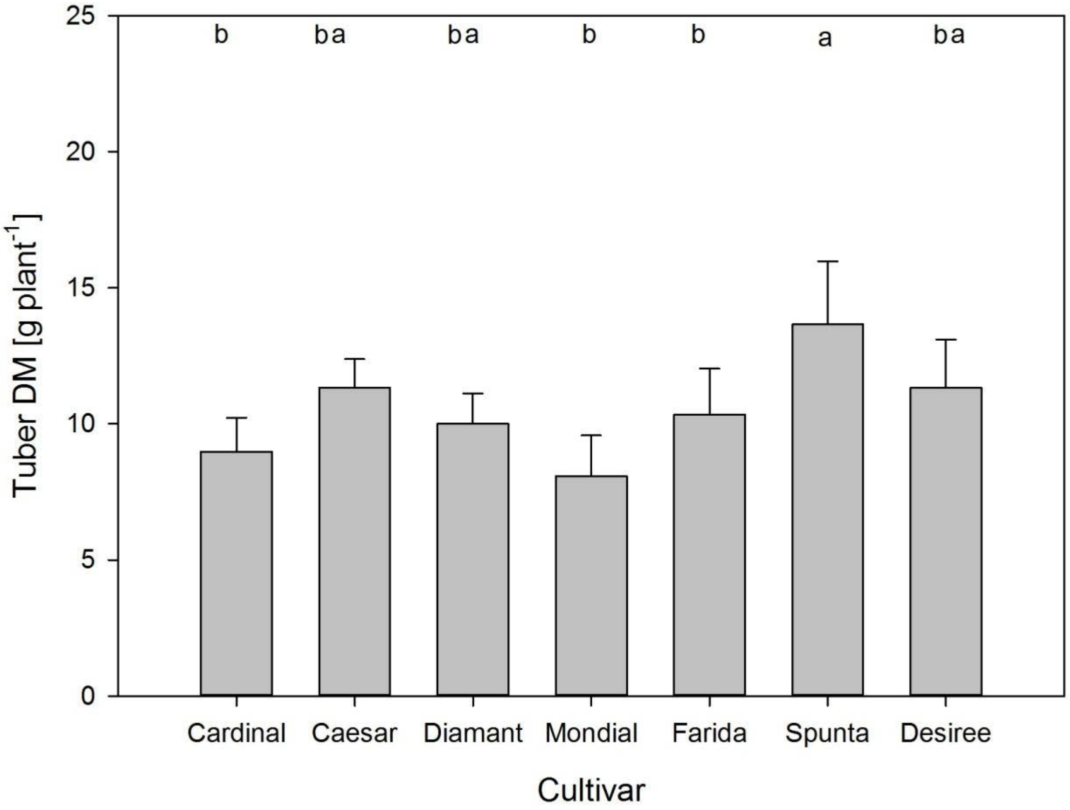

Figure 28: Average tuber dry mass (tuber DM) of individual potato cultivars across well-watered and water-stressed treatments; means with the same letter are not significantly different.

The pooled tuber DM values feature relatively large high standard errors (Figure 27 and 28). The high error bars in figure 27 are due to genotypic differences in tuber onset and maturity stage. Furthermore, especially the high-biomass-cultivars such as Spunta, Desiree and Farida seem to exhibit comparably large intragenotypical variances in tuber production (Figure 28).

3.2.9 Harvest index

The harvest index (HI) of each plant was calculated as the ratio of tuber DM to TDM (Equation 20).

$$HI = \frac{Tuber\ DM\ [g]}{TDM\ [g]} \qquad (20)$$

The results of the ANOVA suggest that the treatment ($p \leq 0.0001$) as well as the variety ($p = 0.0003$) both have significant effects on the HI. The interaction of these two factors is rendered non-significant.

The harvest index of the WS-treated plants was significantly lower compared to the control plants. The WW-treated plants achieved an approx. 20 % higher HI than the WS-treated pots (Figure 29). The mean HI of all WW-treated plants was found to be 0.55.

Across both treatments, Spunta featured the highest and Mondial the lowest mean HI. Mondial performed significantly worse compared to the other six cultivars. They performed in close proximity to one another, their mean harvest index was calculated to be 0.54. The HI of Mondial was found to be roughly 30 % less compared to the mean of the six other cultivars. Caesar's performance was insignificantly lower than Spunta's (Figure 30).

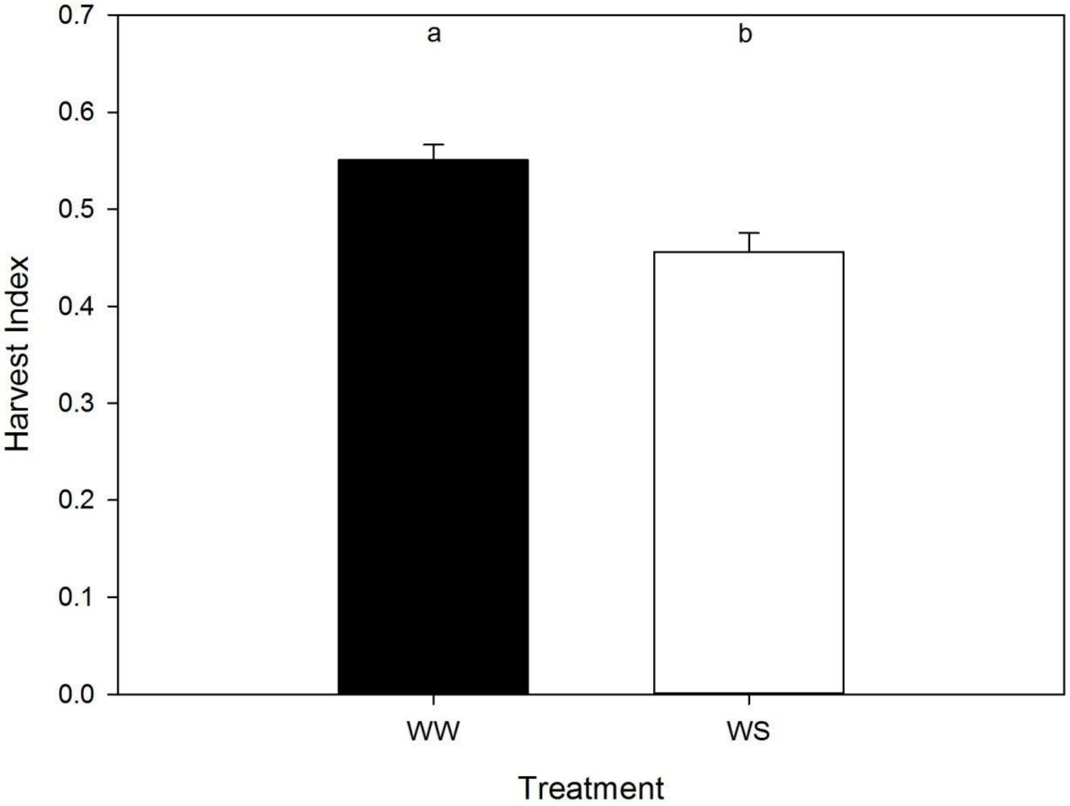

Figure 29: Harvest indices of potato cultivars grown under well-watered (WW) and water-stressed (WS) conditions; means with the same letter are not significantly different.

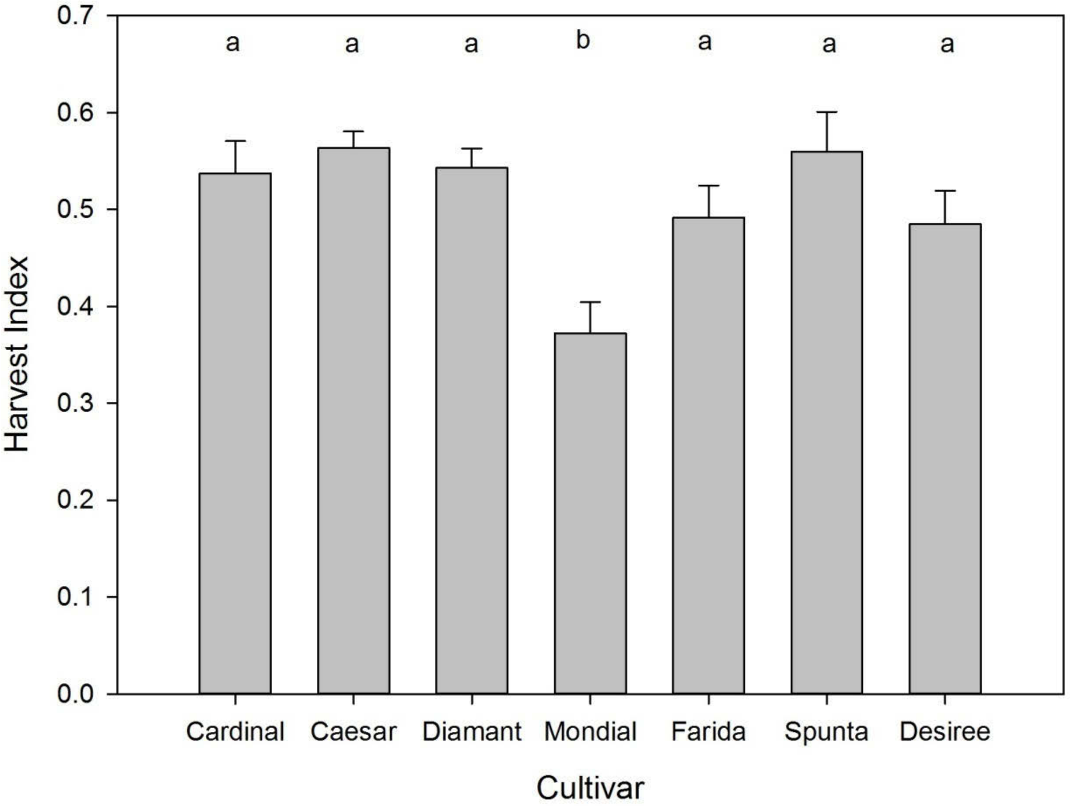

Figure 30: Average harvest index of indivual potato cultivars across well-watered and water-stressed treatments; means with the same letter are not significantly different.

3.2.10 Relative changes in biomass production due to decreaced water supply

For each potato cultivar, the relative difference in dry biomass of plant organs (DM of leaves, stem and tuber) under WW and WS conditions was calculated as seen in equation 21.

$$\text{Relative Change } [\%] = \frac{DM_{WS}*100}{DM_{WW}} - 100 \qquad (21)$$

The DM of all plant organs were reduced under the water-stress treatment, except for the leaf DM in Caesar (Figure 31). Caesar was the only cultivar, which was able to maintain its leaf DM under water-stress. Excluding Caesar, the average reduction in leaf DM was calculated to be 29 %. Diamant featured the greatest reduction in leaf DM (approx. 33 %).

Under WS conditions the stem DM was also reduced by 29 %. Caesar featured the smallest reduction and Diamant the largest.

The relative reductions in tuber DM appeared to be most striking of all measured output parameters. Cultivars Spunta, Mondial, Farida and Desiree displayed decreases of up to roughly 60 % compared to WW-treated control plants. Caesar exhibited with a reduction of 27 % the smallest relative loss in tuber DM production.

- **Tolerance towards a decrease in water supply**

The tolerance towards a decrease in water supply (TDWS) is a common parameter used to quantify the drought tolerance as an index (Deblonde *et al.*, 1999; Lahlou *et al.*, 2012). The TDWS sets the tuber DM of WS-treated plants in relation to the tuber DM in well-irrigated pots (Equation 22).

$$TDWS\ [\%] = \frac{av.tuber\ DM_{WS}[g]*100}{av.tuber\ DM_{WW}\ [g]} \qquad (22)$$

The average drought tolerance index, expressed as TDWS, varies greatly with the cultivar. The lowest indices (roughly 40 %) were found in the rather vigorous cultivars such as Spunta or Farida. Cardinal and Diamant performed roughly the same, approx. 61 % respectively. Caesar featured the highest index, it achieved 73 %.

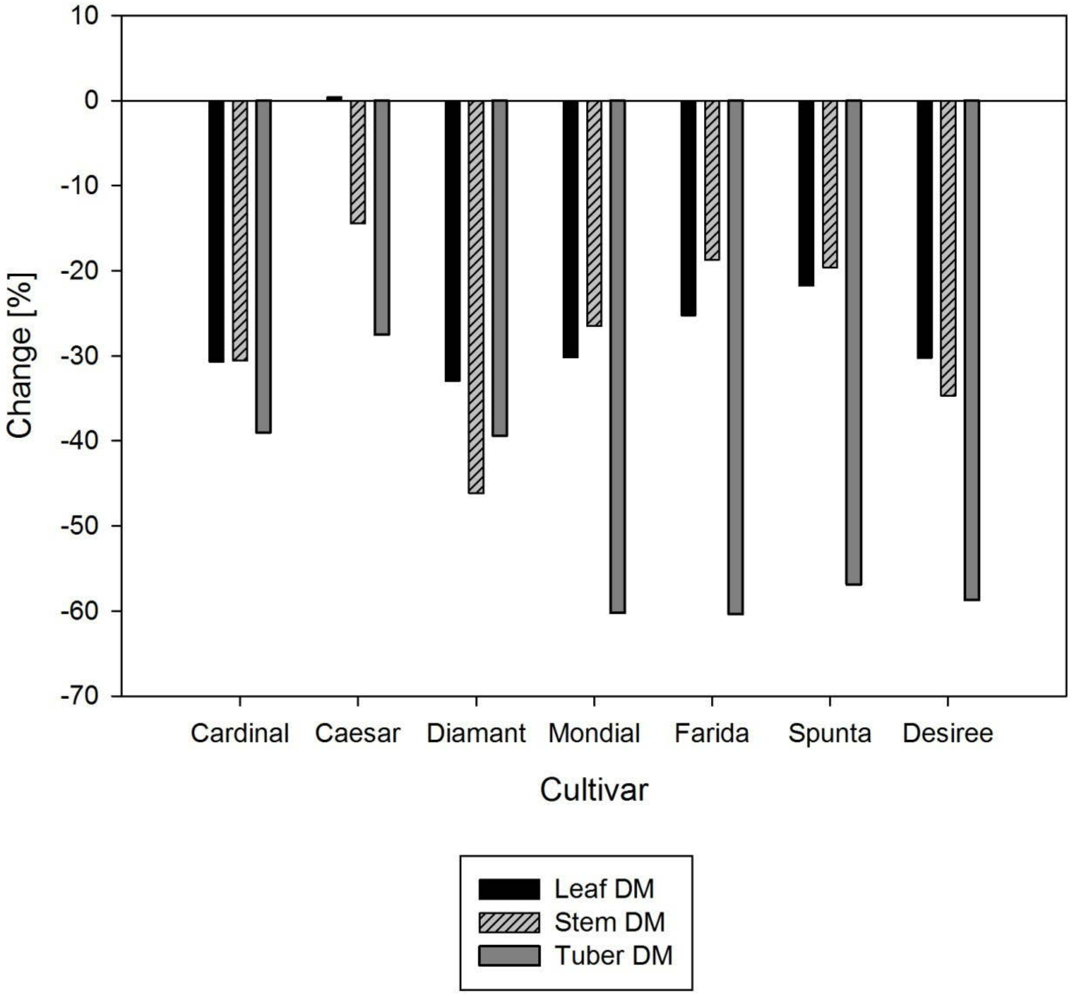

Figure 31: Relative changes in dry mass (DM) of leaves, stems and tubers of potato cultivars grown under water-stress conditions compared to respective well-watered plants.

3.2.12 Dry-down phases

The period in which the water stress treatment was applied is referred to as the dry-down cycle of the experiment. The dry-down cycle can be split into two phases: (i) phase I is defined as the period of the dry-down cycle in which a plant can maintain a transpiration level similar to that of WW-plants(NTR ≈ 1.0); (ii) phase II reflects the period in which the transpiration gradually decreases as a response to soil drying (Figure 32). The FTSW-threshold is postulated to be cultivar-specific.

Phase I reached from the application of the water treatment until the transpiration started to decline as a response to soil water deficit, e.g. the FTSW-threshold was reached. This region is characterised by a steady TR circling around a NTR of 1.0 (Figure 32) as there is sufficient soil water to sustain normal plant physiology. In this section the linear regression features a steady slope of approx. 0 (0.01 to 0.11).

Phase II stretched out from the FTSW-threshold to a NTR-threshold of ≤ 0.1, presumed that the plant is dead when it features such a low transpiration value. This phase is marked by a steady decline in daily transpiration, thus the slope of the linear regression in this phase must be negative. The slope of the linear regression ranged between -3 and -4.1 (Table 10).

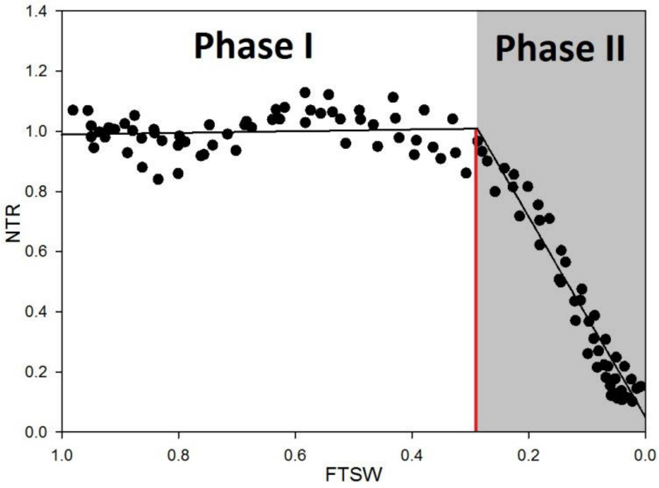

Figure 32: Exemplary illustration of the fraction of transpirable soil water (FTSW) plotted against the normalised transpiration ratio (NTR). The solid black line is the regression fit using the piecewise two-segment linear regression. The turning point of the fitted regression indicates the FTSW-threshold for decline in transpiration, thus separating the dry-down cycle in phase I (NTR ≈ 1.0) and phase II (NTR ≥ 0.1).

3.2.12.1 Duration of dry-down phases

The duration of each of the two phases of the dry-down cycle was retroactively calculated as a genotypic average (Figure 33). The durations differed between the cultivars greatly.
Phase I ranged between 12 (Spunta) and 18 (Diamant) days. Caesar and Diamant both remained the longest time in phase I, they required 17 and 18 days respectively before they exhibited a transpirational response to the progressive drying soil. Spunta and Farida displayed a higher transpirational sensitivity to the soil moisture content as they reduced their transpiration after 12 and 14 days respectively and therefore, at a higher soil moisture level.
The length of phase II also varied with the cultivars. Caesar featured the longest duration of phase II (15 days), followed by Spunta and Cardinal (12 days respectively). Mondial and Desiree passed through phase II fastest, they only required 8 days until their NTRs dropped below 0.1.
Caesar required the longest time (32 days) on average to go through both phases of the down cycle. Desiree, Mondial and Farida all reached their NTR-threshold fastest, nine days earlier than Caesar (Figure 33).

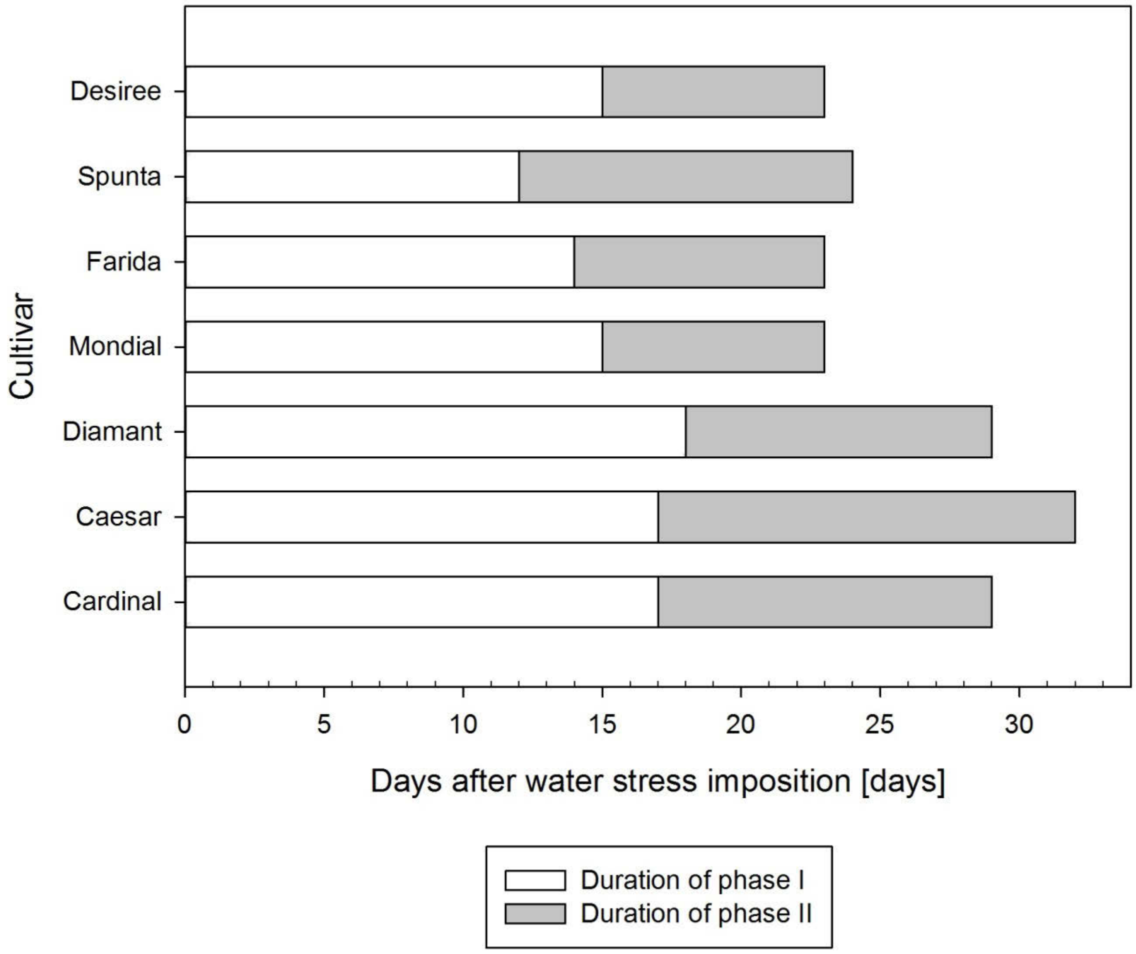

Figure 33: Duration of the phases I and II during the water-stress treatment (see Figure 32 for details) for individual potato cultivars.

3.2.12.2 Average daily transpiration in the dry-down cycle

The average daily transpiration varied greatly between the two phases as well as among the cultivars.

(i) Phase I

Phase I displayed large variation between the cultivars, they averaged at roughly 65 - 94 ml day^{-1} plant^{-1} (Figure 34). Caesar exhibited the lowest water requirement, it averagely consumed 64 ml day^{-1} plant^{-1}. Furthermore, it featured, together with Cardinal and Diamant, rather moderate water uses. In contrast, Spunta and Desiree featured the highest transpiration rates, averaging at roughly 93 ml day^{-1} plant^{-1}.

(ii) Phase II

In phase II however, the differences decreased as the cultivars‘ transpiration values ranged in closer proximity to one another, roughly 25 – 34 ml day^{-1} plant^{-1} (Figure 35). The lowest average daily transpiration value was found in Caesar. On average Caesar transpired very similar daily water amounts compared with Cardinal, Diamant and Mondial. Spunta required the highest daily amounts, averagely 35 ml day^{-1} plant^{-1}.

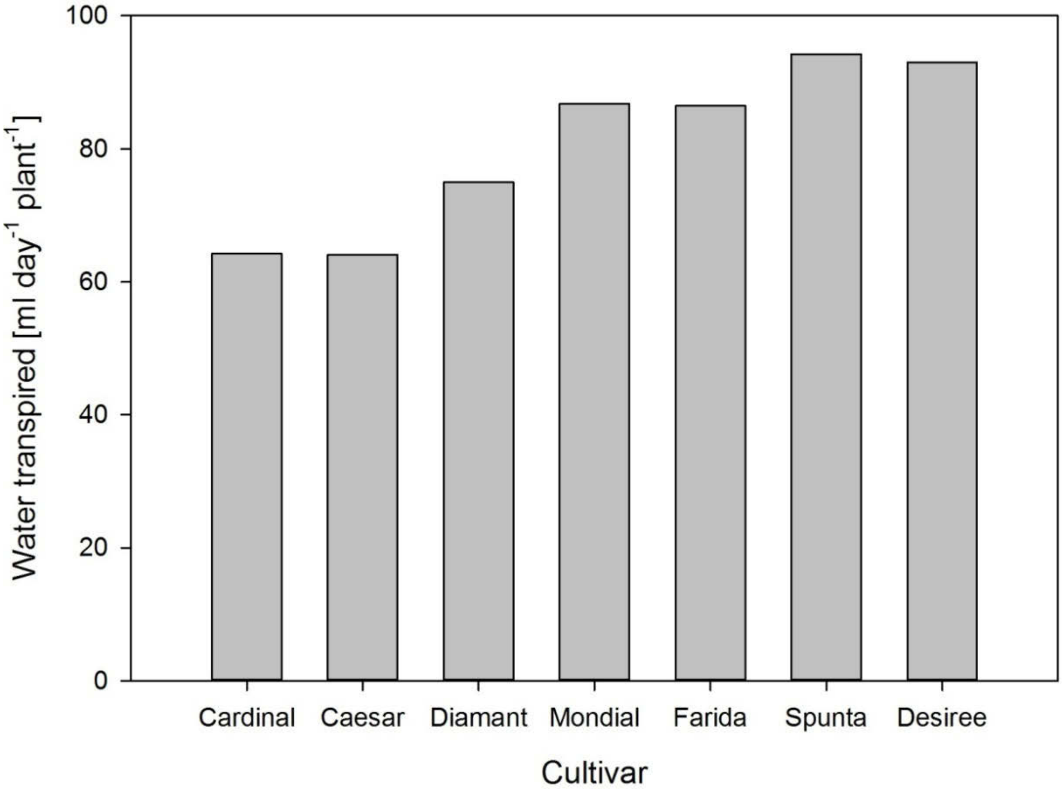

Figure 34: Daily transpiration rate (TR) of seven potato cultivars subjected to water-deficit stress; TRs were measured during phase I of the dry-down cycle (see Figure 32 for details), where soil moisture was at a sufficient level.

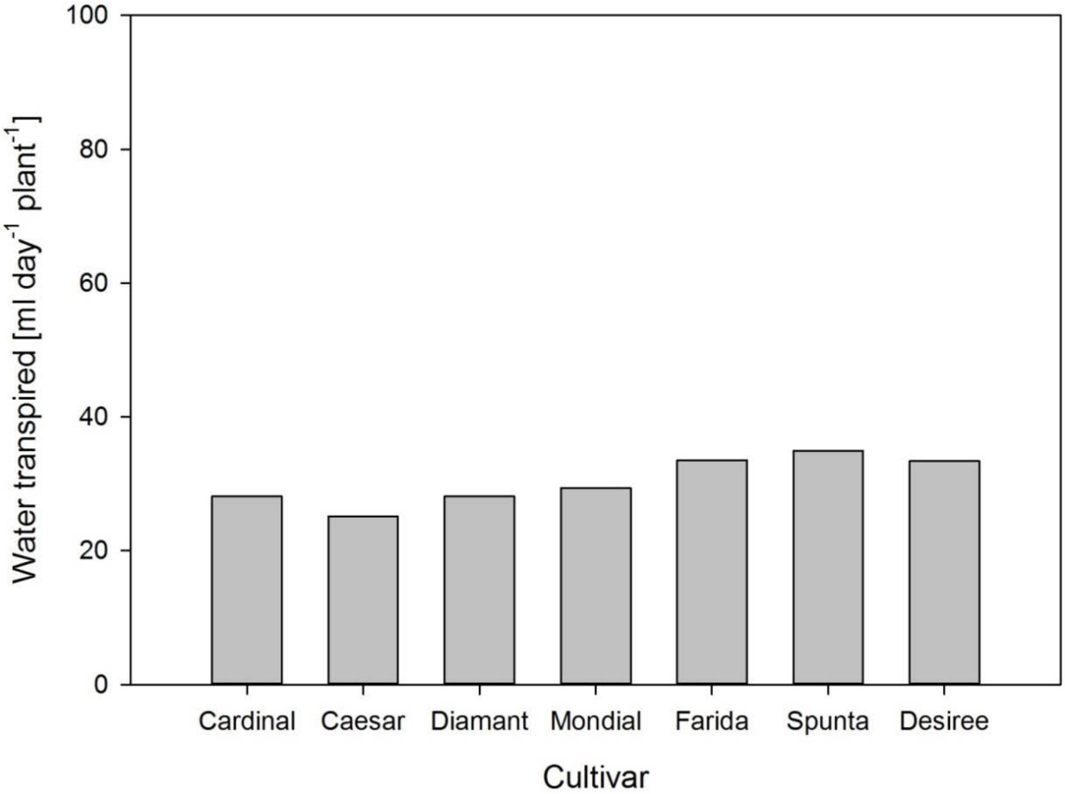

Figure 35: Daily transpiration rate (TR) of seven potato cultivars subjected to water-deficit stress; TRs were measured during phase II of the dry-down cycle (see Figure 32 for details), where soil moisture was at an insufficient level.

The sequence of the average daily transpiration rates, e.g. TR-pattern, of phase I can be found in phase II as well. Cultivars which transpired higher daily volumes in phase I also transpired higher daily amounts in phase II. Caesar was found to exhibit the smallest daily TRs in both phases while Spunta used the highest daily amounts of water in both phases.

It becomes obvious that the four cultivars Desiree, Farida, Spunta and Mondial, which reached their NTR-threshold fastest also transpired more water on a daily basis (Figure 34). The relative reduction in average daily transpiration between the two phases was found to be most severe in variety Mondial (-66 %). The smallest decreases were found in varieties Caesar (60 %) and Cardinal (56 %).

4 Discussion

The objective of this research was to determine genotypic differences in transpiration response to a progressive drying soil within a set of potato cultivars. The underlying hypothesis states that there are genotypic differences in the stomatal sensitivity towards progressive soil drying which strongly influence the available soil water at yield forming stages.

Hereby, plants from seven potato cultivars were exposed to controlled water-stress conditions in a glasshouse pot experiment. Their daily transpiration rates were assessed gravimetrically and their biomass was harvested at termination of the experiment.
It is postulated that an early restriction of transpiration at higher soil water content conserves soil water which is available later at yield-forming stages. According to the underlying framework, high FTSW-threshold cultivars should therefore feature a higher transpiration efficiency.

All physiological and agronomical parameters of potato plants examined in this study were sensitive to water deficit stress. The interaction of the two factors (treatment and variety) was not significant for most traits of observation.

4.1 Environmental conditions

The transpiration experiment was carried out in pots in a glasshouse. The environmental conditions were well adjusted for the potato crop cultivation. The atmospheric temperature range in the glasshouse cabin (12 to 22 °C) (Figure 12) was within the optimum boundaries for potato cultivation, as commonly suggested by Berger *et al.* (2006) and the FAO WATER (2015).

The prevailing humidity in the cabin resulted in a low calculated VPD (1 to 1.5 kPa; Figure 13). According to Choudhary *et al.* (2013), Vadez *et al.* (2013) and Yang *et al.* (2012), the VPDs which are smaller than 2 to 2.5 kPa do not affect plants transpiration too strongly. Therefore, the prevailing VPD in the cabin had little to no influence on the plants. Further, the VPD can be ruled out as an additional source of water-stress in this experiment and the full transpirational response to a drying soil could be observed.

The weighted average VPD (1.5 to 1.8 kPa) (Sinclair, 2012) is slightly higher, compared to the ‚regular‘ ambient average VPD (Figure 14). Correct assessment of the prevailing VPD, especially during physiologically relevant phases of the day, is a necessity when measuring transpirational habits towards a decrease in water supply. Only with the correct VPD assessment can its effects be accounted for.

The customised sealing equipment (Figure 9 and Figure 10) worked very well; as proof of the sealing qualities condensation was only found on the plant-faced side of the inner plastic bag. Further, the plants displayed no visible unexpected shortage or disturbance related to restricted sap flow.

4.2 Fraction of transpirable soil water-thresholds

Genotypic variations in the FTSW-threshold were discovered, though the threshold values were found to be in very close range to one another (0.24 - 0.32; Table 10). The obtained FTSW-thresholds are comparable to previous research in potato conducted by De Souza *et al.* (2014). The observed narrow range of FTSW-values for potato is in sharp contrast to those reported for sorghum (Gholipoor *et al.*, 2012; Choudhary *et al.*, 2013), maize (Ray *et al.*, 2002) and peanut (Devi *et al.*, 2009). The narrow range of FTSW-threshold values may be attributed to the narrow genetic background of the tested potato cultivars and, therefore, future studies should include more exotic germplasm.

Furthermore, this approach is influenced by the fact that potatoes simultaneously grow vegetatively and generatively in an indeterminate habit.

Potato crops would produce many shoots under normal circumstances, though in this experiment only the main stem was maintained. Therefore, cultivars producing contrasting numbers and masses of shoots are not assessed appropriately. Furthermore, this approach causes physical damage to the plant at soil level, leaving open wounds which can be colonised by pathogens more easily.

Results from FTSW-experiments, which were conducted in pots in a glasshouse, cannot directly be projected as actual behaviour in the field. Breeding for desirable FTSW-thresholds is very complex due to the nature of the FTSW-approach; it depends on a large set of external and intrinsic parameters which vary strongly under field conditions and between growth-sites.

The values obtained in the research conducted by De Souza *et al.* (2014) in Brazil are in general very similar to those observed in this study, though a bit higher in comparison. The slightly higher FTSW-values may be explained by the different environmental conditions of the Brazilian experiments. The VPD, for instance, was periodically elevated to a point (> 3 kPa) at which it influences the transpirational performance and therefore biases the measurements. Furthermore, De Souza *et al.* (2014) failed to prevent evaporation from the pots; instead they estimated the evaporative demand with additional pots in their setup and therefore worked with estimated values for evaporation.

According to the underlying hypothesis of this research, it would be expected that potato cultivars with higher FTSW-thresholds (e.g.: Spunta, Farida) would exhibit higher TE-performances compared to varieties which featured low FTSW-thresholds (e.g.: Diamant, Mondial) (see Table 10). The FTSW-thresholds were found in close proximity to one another and the TE-performances also displayed small differences between the cultivars, except for Caesar, which stood out significantly with its high TE. Therefore, no relation was found between the FTSW-threshold of a cultivar and it's TE-performance.

The plotted FTSW-data displays relatively high quality; visible in low scattering of the data points (Figure 15). Along the plateau region the data points display higher variability compared to the decrease in transpiration slope, as in compliance with topical research (De Souza *et al.*, 2014; Devi *et al.*, 2009; Sinclair & Ludlow, 1986).

4.3 Initial shoot dry mass

The water treatment was applied when all plants had grown to a certain phenological stage (BBCH 19 or greater). The water consumption of plants in this pre-experimental growth period was not recorded, and, therefore, no statements can be made towards the water usage in this period. Nonetheless, the shoot biomass build-up during this period displayed large variations (1.2 to 2.4 g plant^{-1}).

The differences in initial shoot DM within a cultivar were found to be quite low, as indicated by the low standard error bars in figure 18. The significant shoot DM differences between the cultivars, however, leave room to conclude that the juvenile plants were in different phenological stages or produced contrasting numbers and masses of shoots at the time of sealing and initial shoot harvest. Furthermore, the number of single shoots was not recorded. Therefore, only limited conclusions concerning the early vigour of the tested potato cultivars can be made. According to the obtained data, it seemed that Spunta featured the most vigorous juvenile growth habits as it produced significantly more shoot DM than other tested cultivars.

The timing of sealing was decided upon the phenological growth stage (BBCH-stage) the potato plants were in. The sealing gear was not applied until also the slowest growing cultivar had uniformly reached a BBCH-stage of 19 or greater. During this 23 day pre-experimental growth period no cultivar had surpassed the BBCH-stage 19.

The water-stress treatment had a severe impact on the biomass production and amounts of water transpired by all cultivars.

4.4 Total transpiration

The total transpiration refers to the accumulated amount of water transpired by each plant during the 32 day dry-down cycle of the experiment. The unique sealing technique prevented soil evaporation, therefore, the total transpiration values obtained in this study are a direct gravimetric assessment of the single (main)stem transpiration.

The water treatment and the cultivar both had a significant effect on the volumes transpired (Figure 16; Figure 17). Furthermore, this parameter was the only one with a significant interaction between the two factors. Contrasting varietal consumption habits exhibited under WW-conditions disappeared under the WS-treatment; the WS-treated pots required uniformly roughly 1.6 l plant^{-1}, approx. 50 % less compared to WW-treatment.

In the given environment, Spunta and Desiree both seemed to require comparably large amounts of water. Caesar displayed very moderate consumption behaviour as it consumed by far less water than the other tested cultivars within the same time period (Figure 16; Figure 17).

The average total transpiration of each plant was found to match the range described by De Souza *et al.* (2014). De Souza *et al.* (2014) measured over two experiments that the total amount of water used by each plant on average was approx. 3.1 l plant^{-1} for WW-treated replicates and 1.8 l plant^{-1} for WS-treated plants.

4.5 Accumulated total dry mass

The accumulated total dry mass (AccumTDM) refers to the biomass produced only during the dry-down cycle of the experiment. It was calculated by summing up the dry masses from tubers, leaves and stems at termination and deducting the initial dry mass obtained at treatment application.

The mean transpiration volumes were closely associated with the AccumTDMs. Generally, cultivars which featured a high transpiration also produced more biomass. Caesar was an exception, as it did not follow this pattern (Figure 20; Figure 16). Though Caesar transpired the smallest amount of water, it was able to produce roughly the same amount of biomass as higher transpiring cultivars under both treatments. Under WW-conditions Caesar produced just slightly more biomass compared to its WS-treated replicates (Figure 31). Therefore, Caesar was able to produce more biomass with less water, compared to the other tested cultivars. Furthermore, this ability of Caesar becomes more obvious when the TE-performances are examined.

4.6 Transpiration efficiency for accumulated total dry mass

The transpiration efficiency for accumulated total dry mass was calculated by relating the total weight of dried biomass produced during the dry-down cycle of the experiment to the amount of water transpired in that period.

The TE was influenced significantly by the water treatment and cultivar. Under WS-treatment the TE was higher compared to the WW-treatment (Figure 21), indicating a higher water-use-efficiency in plants when subjected to a drying soil, as in agreement with De Souza *et al.* (2014). The WW-treated plants, on the other hand, seemed to use water to some extent unproductively and therefore featured a lower TE.

In contrast to these findings, a study conducted by Devi *et al.* (2009) on peanut concluded that WW-treated plants (4.3 – 6.1 g l^{-1} plant^{-1}) experienced significantly higher TE-values compared to the WS-treated plants (0.6 – 2.5 g l^{-1} plant^{-1}). However, Devi *et al.* (2009) only recorded the TE for accumulated shoot DM, not for whole plant biomass.
Belko *et al.* (2012) found, in agreement with Devi *et al.* (2009), that the TE of cowpea cultivars among the WW-treated plants (1.8 – 3.7 g l^{-1} plant^{-1}) was higher than that of the WS-treated pots (1.2 – 3.3 g l^{-1} plant^{-1}). Belko *et al.* (2012) had assessed the TE for the whole plant biomass.

Two studies (Jones, 2014; Vos & Groenwold, 1989) indicate tendency of water use efficiency [kg l^{-1} $plant^{-1}$] to increase with closing stomata.

The obtained TE-values are in agreement with a study by Kaminski *et al.* (2014), who found the TE-values of potato crops to average around 6 g l^{-1} $plant^{-1}$ at ambient CO_2-concentrations. Though, Kaminski *et al.* (2014) did not reduce the number of shoots to one main shoot.

The mean TE-performances hardly differed between the cultivars, except for Caesar which stood out significantly with its comparably high TE for AccumTDM. The high TE of Caesar can be attributed to the comparably low water use (within both treatments) and a relatively high total biomass production under WS-conditions. It produced roughly the same amount of biomass as Farida or Mondial but required far less water. Therefore, Caesar is seen to be more water-use-efficient compared to the tested set of cultivars.

The by far highest TE was found in cultivar Caesar (Figure 22). According to the underlying hypothesis the highest TE should be found with the cultivar featuring the highest FTSW-threshold. Therefore, the hypothesis must be rejected because the highest TE-performance was found with a comparably low FTSW-threshold cultivar, Caesar. Furthermore, no relation was found between the FTSW-thresholds and TE-performances of the tested cultivars.

4.7 Coefficient of transpiration

In general, the CT was reduced under WS-conditions (Figure 23). As mentioned in the preceding paragraphs, this can be explained by a more productive water usage and no luxury consumption. As expected from the TE-performances, Caesar featured by far the lowest and most favourable CT-values, indicating it again to be the most water-use-efficient cultivar of the tested set.
The mean CTs from the study carried out by De Souza *et al.* (2014) are comparable to the measured CTs in this experiment. For the WW-treated plants, De Souza *et al.* (2014) measured a mean CT of 195 l kg^{-1} $plant^{-1}$ and 170 l kg^{-1} $plant^{-1}$ for WS-treated plants.

4.9 Harvest index

The WW-treated plants in this experiment obtained HIs of 55 %, whereas the WS-treated replicates averaged at 45 % (Figure 29). These indices are comparable to a study by Lahlou *et al.* (2003) on potato crops, who obtained mean HIs of 57 % and 52 % for WW and WS-treated pots, respectively, in two glasshouse experiments.

Spunta and Caesar exhibited very similarly high HIs (0.52 to 0.55). Cultivar Mondial exhibited the by far lowest HI compared to all other tested cultivars (Figure 30). This is due to its undesirable biomass allocation; although it produced an average AccumTDM, it produced the highest stem and lowest tuber DM. Caesar featured the highest mean HI among the tested set of cultivars.

4.10 Relative change in biomass

The relative change in biomass sets the biomass production of potato plants in the two treatments in relation to one another. The change is expressed in relative terms (%) and was calculated for three main plant tissues (leaves, stem, tubers).

As expected, the WS-treatment generally reduced all recorded organ DMs among all cultivars (Figure 31). The degrees of reduction differed between the tissues and the cultivars. Caesar has proven to feature the smallest reductions in tissue mass under WS-conditions compared to all other tested cultivars. Therefore, it experienced the water stress latest or could handle it best by adapting its physiology.

Tuber production was most severely reduced among the high-biomass cultivars such as Mondial, Farida, Spunta and Desiree (Figure 31). These vigorous cultivars used available resources early in the experiment and displayed widespread senescence among the mature leaves and inflorescences. Caesars mean tuber DM production is comparable to that of high-biomass cultivars, though it transpired less water to form the tubers. Caesar experienced the smallest reduction in tuber DM in comparison to the other cultivars. This is due to the fact that tuber DM accumulation is linked to higher light interception (Deblonde *et al.*, 1999; Jefferies, 1993). Caesar achieved this by maintaining its leaf canopy for a longer period.
The high standard error bars in figure 28 are due to the illustration of pooled data from both treatments and the large differences between the yields of the treatments.

All cultivars, except Caesar, reduced their leaf DM and, under the precondition that leaf DM and area are directly linked, their leaf area. A lack of water reduces cell expansion and therefore causes smaller leaves (Berger *et al.*, 2006). Further, in all cultivars except Caesar pre-existing mature leaves were continuously senesced, most probably as a long-term adaptation mechanism for decrease in water supply. Caesar was the only cultivar which was able to maintain its canopy, indicated by its leaf DM under WS-conditions (Figure 31).

The stem-tissue fraction produced by Mondial was by far the highest of all tested cultivars (Figure 26). High fractions of stem tissues are rather undesirable as they do not contribute to higher light interception, biomass production and consequently tubers, as seen in Mondials low HI.

Cardinal and Caesar both produced comparably little biomasses under WW-conditions. Under WS-treatment, Caesar was able to maintain its biomasses at a higher level, while Cardinal featured greater reductions.

The timing and masses of the stolons and roots were not assessed. According to Lahlou and Ledent (2005) (water)stress causes roots to grow significantly deeper. Therefore, a deeper root system with higher root DM indicates a better water-acquisition or soil exploitation and therefore higher ability to cope with a drying soil. Lahlou and Ledent (2005) proclaimed that drought resistance in potato cultivars is partly associated to their ability to extract water from a soil.

Tolerance towards a decrease in water supply

The tolerance towards a decrease in water supply (TDWS) relates the potential tuber yield achievable under optimum conditions to that obtained under WS-conditions. It gives an estimate on how much yield can be achieved under certain WS-conditions compared to optimum conditions.

Caesar peaked outstandingly at a 73 % average, compared to the other six tested cultivars the highest value obtained. Therefore, Caesar is indicated to be more drought-tolerant compared to the other six cultivars, which on average reached 40 to 55 % of potential tuber dry weight. In comparison, Lahlou *et al.* (2003) measured TDWS-levels of approx. 55 to 60 % in their pot experiments.
Caesars comparably high tuber DM production under WS-conditions and its comparably low-average tuber DM production under WW-regime cause this favourable ratio.

4.11 Duration of phases and daily transpiration rates

The dry-down cycle of the experiment can generally be separated into two phases (referred to as phase I and phase II). The two phases featured distinctive patterns of normalised daily transpiration ratios (Figure 32). In phase I, plants can maintain their normal transpiration because there is sufficient accessible soil water available. When the transpiration starts to decline, as a response to progressive soil drying (e.g.: FTSW-threshold is reached), phase I ends and phase II begins. The second phase of the dry-down cycle is characterised by a steady decrease in daily transpiration rates, until NTR ≤ 0.1 (e.g.: NTR-threshold) is reached; where the plant is assumed dead.

It becomes obvious that cultivars with vigorous growth habits and high biomass build-up (e.g.: Spunta, Mondial, Desiree and Farida) reached their respective FTSW and NTR-thresholds sooner compared to varieties with less strong growth habits (e.g.: Cardinal, Caesar) (Figure 33). The more vigorous plants reached their respective thresholds earlier than the rest due to the fact that they exhibited higher daily rates of transpiration. Cultivars transpiring high volumes in phase I also transpired high volumes in phase II of the dry down cycle of the experiment (Figure 34; Figure 35).

Caesar, Cardinal and Diamant all required the longest time to reach their respective FTSW-threshold and finally their NTR-threshold, second of which Caesar required more time to reach. As Caesar was the last to reach its NTR-threshold, it can be assumed that it coped best with low water conditions under these circumstances (Figure 33).

4.12 Intrinsic transpiration mechanisms

As mentioned previously, it is commonly known that stomatal apertures are sensitive to the evaporative demand. Some genotypes possess the ability to control their stomatal apertures and therefore, the ability to cap transpiration when the VPD crosses a certain threshold (Belko *et al.*, 2012; Kholová *et al.*, 2010b; Lisar *et al.*, 2012; Turner *et al.*, 1984; Verslues *et al.*, 2006; Vadez *et al.*, 2013b). This ability is said to be water-conserving, beneficial for crop yield and it increases the TE (Jones 2014; Sinclair *et al.*, 2005; Vos & Groenwold, 1989; Vadez *et al.*, 2013b).

It is well known that the plant transpiration rate is closely linked to atmospheric VPD. Vadez *et al.* (2013) summarised transpiration response to VPD (Figure 36) and identified four different patterns of transpiration response to increasing VPD (A, B, C, D) due to intrinsic properties of plants (e.g.: aquaporin content and activity, ability to regulate stomatal apertures, etc.). As seen in Figure 36, model plant B uses less water after the VPD-breakpoint compared to model plant A, therefore it may conserve the available soil water for later usage. Model plant C uses less water than A and B, whereas D uses the smallest amount of water under all VPD conditions compared to the other three model plants (Vadez *et al.*, 2013b).

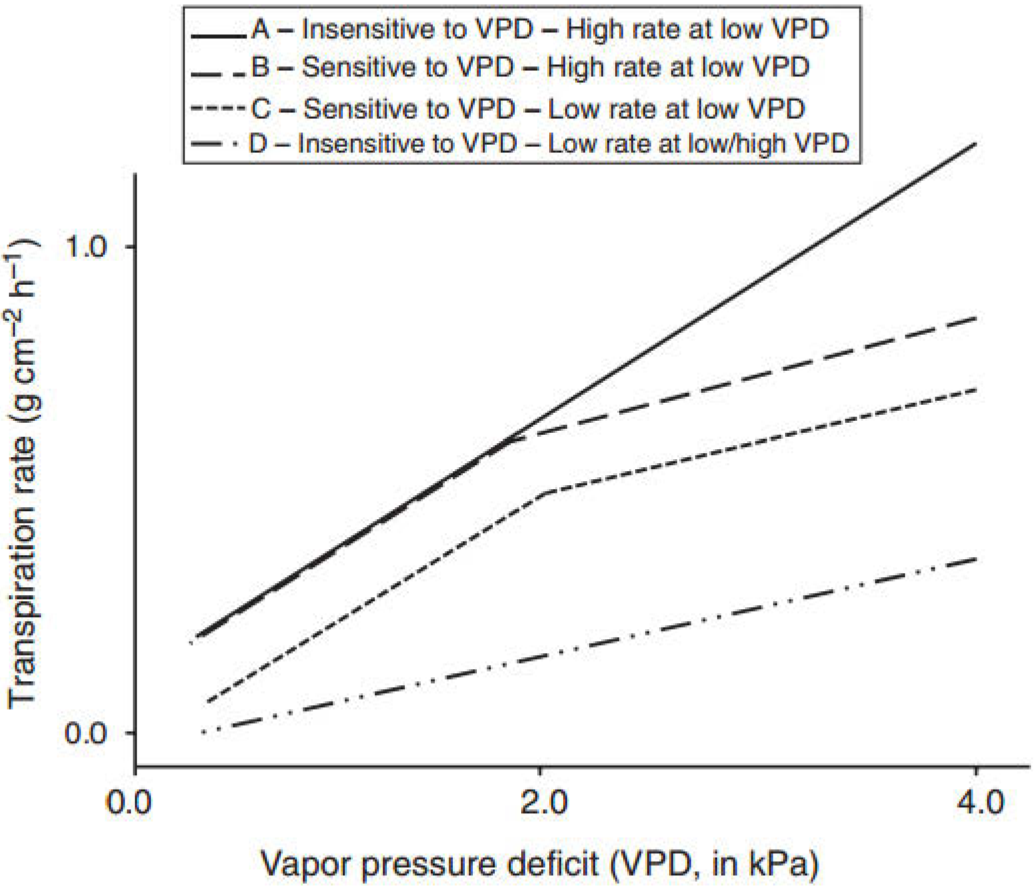

Figure 36: Relationship between transpiration rate (TR) [g cm^{-2} h^{-1}] and vapour pressure deficit (VPD) [kPa] of four model plants (A, B, C, D) (Vadez *et al.*, 2013b).

Applying this framework, model plant A would correspond to the high transpiring cultivars such as Spunta and Desiree; Farida, Mondial and Diamant would be equivalent to model plant B; Cardinal fits the response pattern of model plant C; the low TR from Caesar would correspond to model plant D. Therefore, Cardinal and Caesar can be considered 'water-saving' cultivars in comparison to the other tested varieties under water deficit conditions.

However, restricting the maximum transpiration also restricts the maximum potential yield. The water-use-efficiency would increase with closing stomatal apertures in a water-stressed environment or under high VPD conditions. Under moderate or no water-deficit as well as under low VPD conditions these traits are likely disadvantageous unless the genotypes exhibit certain flexibility in opening and closing their stomatal apparatus dependent upon water-stress (Obidiegwu *et al.*, 2015; Vadez *et al.*, 2013b).

5 Conclusions

The objective of this research was to investigate genotypic variation in transpiration efficiency (TE) among a set of potato cultivars. Seven cultivars were grown under well-watered (WW) and water-stressed (WS) conditions in a glasshouse pot experiment and their daily rates of transpiration and final dry biomass production were recorded. The imposed WS-treatment simulated a progressive soil drying condition.
The underlying hypothesis was that cultivars exhibiting an earlier reduction in transpiration rate in response to the fraction of transpirable soil water (FTSW) would conserve water and use it more efficiently later at yield-forming stages. Thus reducing the rate of transpiration at higher levels of FTSW would result in higher TE.

In line with this hypothesis, all potato cultivars responded to water stress by restricting their transpiration rate. The observed thresholds for decline in the rate of transpiration in response to FTSW ranged from 0.24 to 0.32. The range of FTSW-thresholds is similar to a previous transpiration study in potato but much narrower than those reported for other crop species. Therefore, a larger set of potato genotypes with wider genetic background need to be included in future studies.

Exposing plants to a progressive soil drying resulted in a reduction in transpiration. The average TE of well-watered (WW) plants was 7.13 g l^{-1} $plant^{-1}$, while under water-stress (WS) the average TE was increased to 8.56 g l^{-1} $plant^{-1}$. There were no significant differences between the potato cultivars in their TE (average 7.84 g l^{-1} $plant^{-1}$), except for Caesar, which had a TE that was roughly 25 % higher than the average value. Interestingly the FTSW-thresholds did not correlate with the TE of respective potato cultivars. The highest TE was found in the cultivar Caesar, which had an average FTSW-threshold, whereas the highest FTSW-thresholds were found in cultivars Spunta and Farida, with an average TE-performance. Hence, the underlying hypothesis that cultivars with higher FTSW-thresholds would exhibit lower TE was rejected.

Water stress reduced the dry mass of stems, leaves and tubers in all cultivars. However, the relative reduction in biomass production was lowest in Caesar, as this cultivar managed to maintain its leaf canopy development under WS-conditions. Caesar also exhibited the highest harvest index (HI) under water-stress conditions.

Previous research on transpiration in a range of crop species suggests that there is a genotypic variation in the rate of transpiration under non-stressed conditions, i.e. ample water supply and low atmospheric VPD, both between crop species and among genotypes of the same species. This is largely due to intrinsic differences in vigour, with more vigorous genotypes commonly having higher rates of transpiration. In agreement with previous research, the results of this study also revealed substantial genotypic variation in total transpiration and biomass produced under WW-conditions. The least vigorous cultivar (Cardinal) featured the lowest total transpiration, while the most vigorous cultivar used also the highest amount of water. Thus the potato cultivars did not differ in TE under WW-conditions. The results of this study indicate clearly that in investigating the response of crop genotypes to water-stress, the intrinsic rates of growth and transpiration should be considered, as less vigorous crops may show lower FTSW-values (i.e. delayed stomatal closure in response to soil-water-stress) despite having a higher TE. Plants featuring a high

TE might also exhibit low biomass production under optimum water conditions, as they display less vigorous behavior in comparison. Therefore, the relative yield loss must be considered in the TE-framework. As demonstrated for the potato cultivar Caesar in this study, such genotypes would have higher biomass production and yield under water-stress conditions (i.e. smaller yield gap between potential and achievable yield). Under WW conditions, however, they may not be as productive as those genotypes with higher vigour and transpiration rates (e.g. lower TE-values).

6 Zusammenfassung

Auf globaler Ebene ist Wasserknappheit eine der größten Limitierungen der modernen Landwirtschaft. Die Verbesserung der Transpirationseffizienz (TE; Verhältnis von erzeugter Biomasse zu verbrauchtem Wasser; g l^{-1}) wird allgemein als eine mögliche Strategie zur Verbesserung der Ertragsleistung von Pflanzen unter Trockenstress-Bedingungen gesehen. Pflanzen leiden unter Wasserstress, wenn die Transpirationsrate die Wasserzufuhrrate übersteigt. Die Reduktion der Transpirationsrate, als Reaktion auf ein steigendes atmosphärisches Dampfdruckdefizit (VPD), und eine höhere Empfindlichkeit gegenüber der Bodentrocknung durch eine verminderte stomatäre Leitfähigkeit bei höheren Bodenwassergehalten, gehören zu den vielversprechendsten Merkmalen zur Verbesserung der TE in Kulturpflanzen. Die zugrunde liegende Hypothese dieser Forschungsarbeit postuliert, dass Sorten, die eine frühere Reduktion der Transpirationsrate als Reaktion auf den Abfall des Anteils an transpirierbarem Bodenwasser (FTSW) aufweisen, Wasser sparen, welches später effizienter in der ertragsbildenden Phase verwenden werden kann. Somit würde die Verringerung der Transpirationsrate bei höheren FTSW-Werten zu einer höheren TE führen. Dabei ist die relative Veränderung der Ertragsbildung zu berücksichtigen, da eine höherer TE meist mit einer niedrigeren Biomasseproduktion einhergeht.

Ziel dieser Untersuchung war es, die genetischen Variationen der TE von ausgewählten Kartoffelsorten zu untersuchen. Hierbei wurden sieben Sorten unter optimalen Wasserbedingungen (WW) und unter Wasserstress (WS)- Bedingungen in einem Gewächshaus-Topf-Experiment kultiviert. Dabei wurden ihre täglichen Transpirationsraten und die produzierte Biomasse aufgezeichnet. Die WS-Behandlung simulierte eine fortschreitende Bodentrocknung.

Entsprechend der Forschungs-Hypothese, reagierten alle Kartoffelsorten auf eine fortschreitende Bodentrocknung mit einer reduzierten Transpirationsleistung (-51%). Die Grenzwerte für die Abnahme der Transpirationsrate in Abhängigkeit von der Bodenfeuchte reichten von 0,25 (Sorten Diamant und Mondial) bis 0,32 (Sorte Spunta). Die durchschnittliche TE der WW-behandelten Pflanzen betrug 7,13 g l^{-1} Pflanze^{-1}, während unter WS-Bedingungen die mittlere TE um 20% erhöht wurde. Es gab keine signifikanten Unterschiede zwischen den Kartoffelsorten in ihrer TE (durchschnittlich 7,84 g l^{-1} Pflanze^{-1}), mit Ausnahme von Caesar, die eine ungefähr 25 % höhere TE aufwies. Daher wurde die zugrunde liegende Hypothese, dass Sorten mit höheren FTSW-Schwellen niedrigere TE aufweisen, verworfen. Darüber hinaus reduzierten die WS-Bedingungen die Trockenmasse der Stängel (-27%), Blätter (-24%) und Knollen (-49%) in allen Sorten. Allerdings war die relative Reduktion der produzierten Biomasse am niedrigsten in Caesar, da es dieser Sorte gelungen war, ihre Blattmasse unter WS-Bedingungen zu erhalten. Caesar zeigte auch den höchsten Ernteindex (HI) unter WS-Bedingungen. Darüber hinaus überlebten die weniger wüchsigen Sorten (beispielsweise die Sorten Caesar, Diamant) länger unter WS-Bedingungen. Die Ergebnisse dieser Forschungsarbeit lassen darauf schließen, dass die intrinsische Wüchsigkeit eine wesentliche Rolle bei der Reaktion von Pflanzen auf ein Wasserdefizit spielt, da weniger wüchsige Sorten niedrigere FTSW-Grenzwerte aber eine höhere TE aufweisen. Die höhere TE geht oftmals Hand in Hand mit einer Reduktion der gesamten Biomasse, desshalb ist auch die relative Änderung der Biomasseproduktion unter Trockenstress-Bedingungen zu berücksichtigen

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8 List of Equations

9 List of Figures

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