University of Hohenheim
Faculty of Agricultural Science

Institute of Plant Production and Agroecology in the Tropics and Subtropics

Crop Waterstress Management in the Tropics and Subtropics (380c)

Genotypic responses to variable soil moisture availability in potato clones.

Thesis Prepared for the Degree
Master of Science

Leah Kuppinger

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Main supervisor: Prof. Dr. Folkard Asch

Co-supervisor: Prof. Dr. Georg Cadisch

In collaboration with the International Potato Center (CIP), Lima, Peru.

Abstract

Potato production worldwide is frequently affected by water scarcity, a situation that highly constrains crop yields, as potato is known for its susceptibility to drought stress. The ongoing climate change will entail increasing temperatures and further restrain seasonal water availability. Therefore it is important to examine drought resistance traits to sustain potato production. The aim of this study was to investigate the effects of drought during different development stages on plant growth and tuber production in 5 potato clones. In a field experiment, conducted in 2013 in the coastal arid region in southern Peru, five contrasting potato genotypes (varying for earliness) were subjected to 4 different irrigation treatments (i.e. fully watered throughout, until 54 days after planting (DAP), 67 DAP, and 80 DAP respectively) in a "split-split plot" design. Phenological observations and destructive samplings for above and below-ground biomass determination were conducted 6, 16 and 26 days after withholding irrigation in each treatment. Further, leaf area index, SPAD, chlorophyll fluorescence and leaf area expansion measurements were taken non-destructively and on a regular basis during the drying cycles. A stress severity index was developed relating the soil water deficit to the treatments and genotypes relative to fully watered conditions. The effect of drought stress on potato plants varied, depending on the development stage in which it occurred. Drought during tuberization stage inhibited tuber initiation, decreased tuber number and tuber size, reduced partitioning to tubers and sharply decreased tuber dry weight. Further, this early drought quickly reduced leaf area index in potato genotypes and thus limited C-capture and supply to sink organs but increased the amount of chlorophyll per unit leaf area due to a reduction in leaf expansion. Drought during the reproductive phase (flowering/berry formation) was shown to highly impact tuber dry weight, as photosynthates are driven away from tubers in favor of above-ground reproductive organs. Mild drought at a late development stage accelerated phenological development, promoted sink strength of tubers and increased tuber dry weight. Further, late drought induced premature senescence (reduction in chlorophyll content) in potato plants and highly reduced leaf area index due to shedding of senescenced leaves, by this promoting carbohydrate re-partitioning to tubers. Photosynthetic efficiency of PSII (Fv/m) in potato leaves was increased under drought conditions, especially at later

development stages, which was probably related to changes in SPAD and leaf area expansion. Root length of potato plants was reduced by drought, whereas early drought most affected average root length and late drought maximum root length. However, early senescencing/maturing potato genotypes often were less susceptible to water shortage in terms of tuber dry weight reduction than late senescencing/maturing genotypes, as they were often able to escape drought.

Keywords: *Biomass partitioning, Plant growth, Stress severity index, Phenological development stage,*

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List of Abbreviations

° = degree

µ = mi (µı)

µE= micro einstein

1^{st}= first

2^{nd}= second

3^{rd}= third

6^{th}…19^{th}= sixth…nineteenth

Al^{3+}= aluminium ion

App.= appendix

BBCH= Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie

BMZ= Bundesministerum für wirtschaftliche Zusammenarbeit und Entwicklung

C= celsius

Ca^{2+}= calcium ion

$CaCO_3$= calcium carbonate

CaO= calcium oxide

cc= volume unit (equate to 1 milliliter)

CEC= cation exchange capacity

CIP= Centro International de la Papa (International Potato Center)

cm^2= square centimeters

CO_2= carbon dioxide

Cu= copper

d= day

DAP= days after planting

DAWI= days after withholding irrigation

dS= decisemens

E= east

EC= electrical conductivity

et. al = and others

etc.= and so on

FeO_3= iron oxide

g= gram

Gen= genotype

GIZ= Deutsche Gesellschaft für Internationale Zusammenarbeit

h= hour

H= hydrogen

ha= hectare

i.e.= *id est* (that is)

K^+= potassium ion

K_2O= potassium oxide

kcal= kilocalorie

kg= kilogram

LPH= liter per hour

Lt= liter

LT-LB= Lowland Tropics Late Blight Resistance (heat tolerant)

LTVR= Lowland Tropics Leafroll Virus Resistance Population (heat tolerant)

m= meter

m^2= square meter

m^3= cubic meter

meq= milliequivalents

Mg^{2+}= magnesium ion

MgO= magnesium oxide

min= minute

mm= millimeter

Mn= manganese

MPa= mega pascal

MT = mega ton

N= nitrogen

Na^+= sodium ion

NH^{4+}= ammonium

No.= number

NO_{2-}= nitrogen dioxide

N_{total}= total nitrogen

P_2O_5= phosphorus pentoxide

PAR= photosynthetically active radiation

pH= negative logarithm of the hydrogen ion concentration

ppm= parts per million

rH= relative humidity

s= second

S= South

S= sulphur

SiO_2= silicon dioxide

ssp.= subspecies

t= ton

Vol %= volume percent

Zn= zinc

List of Symbols

α = Alpha
@= at
= number
%= percent
`` = arc second
`= arc minute
~ = about
± = plusminus
∑= sum
Ø = angular degree of wind direction, referenced to cardinal directions

Background

This study was conducted within the BMZ/GIZ project "Improved stress-tolerant potato varieties and water management technologies to enhance water use efficiency, resilience, cost-effectiveness, and productivity of potato producing smallholder farms in stress-prone Central Asian environments". Aim of the project is to increase potato productivity, heat and drought tolerance and yield stability. In addition competitiveness and family income of resource-poor farmers in Central Asia will be strengthened.

The field experiment for this master thesis was embedded in a larger experiment of a PhD study that in total consisted of 13 potato clones from the advanced breeding population developed at the International Potato Center. However, this study only concentrates on five contrasting genotypes.

1. Introduction

1.1. The impact of climate change on potato production

World food production increasingly faces problems due to changing environmental conditions. Increasing temperature, altered rainfall patterns, extreme weather events and seasonal water scarcity can be observed globally (IPCC, 2002).Till the next mid-century, predicted increase of global average temperature due to climate change will be 2.1 to 3.2 °C, and 1.6 to 3.0 °C in potato growing areas. Estimated impact of such temperature change is an 18-32 % decrease in global potato yield. Predicted yield losses will be highest (up to > -50%) in the potato growing areas of the (sub) tropics. In the large potato-growing regions of southeast Europe, Russia, Kazakhstan, India and China, potato yields could decline by 10 to > 50%. Adaptions in terms of a shift of one to two months in planting time and use of suitable varieties could mitigate a large part of the predicted climate change induced yield loss in potato (Hijmans, 2003).

1.2. The role of potato

During the last decades, the world potato production has experienced major changes. In the early 1960s potato production was highest in the formers Soviet Union, Europe and the United States (App. Figure 67). In 2012, China and India were the top potato producing countries, with 86 and 45 MT (App. Figure 68).

Due to its advantageous characteristics in terms of productivity and nutritional value (see below), the potato is on the increase in developing countries (FAO, 2008). In Asia, Africa and South America, production has almost tripled in the period from 1990 to 2012, whereas production in Western Europe and North America stagnated (Table 1). However, with 16.6 t/ha, productivity in Asia, Africa and South America is still considerably lower than in Europe and North America, where yields of about 40 t ha^{-1} were achieved (Table 1) Low soil fertility, pests and diseases, frost and water stress and the lack of good quality seeds are reasons for then low potato yields in developing countries (FAO, 2009a, b)

Table 1: Harvested Area, Production quantity and Yield per hectare of Potato in 1990 and 2012 by region (Statistical Division (FAOSTAT, 1990 and 2012)).

	Area harvested (ha)		Production quantity (MT)		Yield per hectare (t/ha)	
	1990	**2012**	**1990**	**2012**	**1990**	**2012**
Western Europe	999,031	640,211	29,629,540	27,839,341	29.7	43.5
North America	674,445	606,433	21,244,423	23,757,261	31.5	39.2
South America	808,419	902,079	9,643,025	15,164,658	12.0	16.8
Asia	4,811,539	9,664,920	64,181,929	176,653,699	13.3	18.3
Africa	763,008	1,894,075	8,221,617	28,169,519	10.8	14.9
World	**17,656,487**	**19,202,082**	**266,825,273**	**364,808,768**	**15.1**	**19.0**

The potato is a food crop of high value. Potato plants not only consist by 85 % of edible food (FAO, 2009b), it also produces more food per m^3 water than major crops like wheat, maize, rice (Renault and Wallender, 1999). With 5600 kcal per m^3 of water, potato is much more productive than wheat (2300 kcal per m^3 of water), maize (3860 kcal per m^3 of water) and rice (2000 kcal per m^3 of water). In terms of protein production per m^3 water, potato also ranks first among main food crops (Renault and Wallender, 1999). Additively, potatoes contain high quality protein and are rich in Vitamin C (FAO, 2009b). Due to its high nutritional value and high productivity, potato becomes an increasingly important food crop to ensure food security in present and future, particularly for growing population and decreasing resources (FAO, 2009b). In the case of Central Asia, well-adapted potato cultivars could be a vital alternative to diversify cotton-wheat rotations and help to deal with food shortage and the consequences of climate change (Carli, 2008).

1.3. Potato production in Central Asia

The magnitude of climate change induced environmental changes is not homogeneous, therefore differs for every region in the world (Walther *et al.*, 2002). For Central Asia, projected warming will exceed global mean temperature increase by 40 % (IPCC, 2002). Rainfall is unreliable and scarce in this region, and drought appears periodically (Carli, 2008). Average annual rainfall in Central Asia is 273 mm, and ranges from less than 70 to over 2400 mm, depending on landscape (Fig. 1; FAO, 2013a). Due to the arid climate,

irrigation plays an important role in central Asia, as 26 % of cultivated cropland is irrigated. However, water is used highly inefficiently as 12,000 – 14,000 m^3 water is used for irrigation per hectare. In Egypt and Pakistan only 9,000 – 10,000 m^3 ha^{-1} are withdrawn (World Bank, 2003). The excessive irrigation and the use of saline irrigation water from the Syr-Darya and Amu-Darya basin (Central Asia's main rivers) has the consequence that nearly half of the irrigated area is already affected by salinization (Funakawa *et al.*, 2006; World Bank, 2003). Moreover, irrigation systems themselves are in a bad condition because of poor investment in operation and maintenance (Gupta *et al.*, 2009).

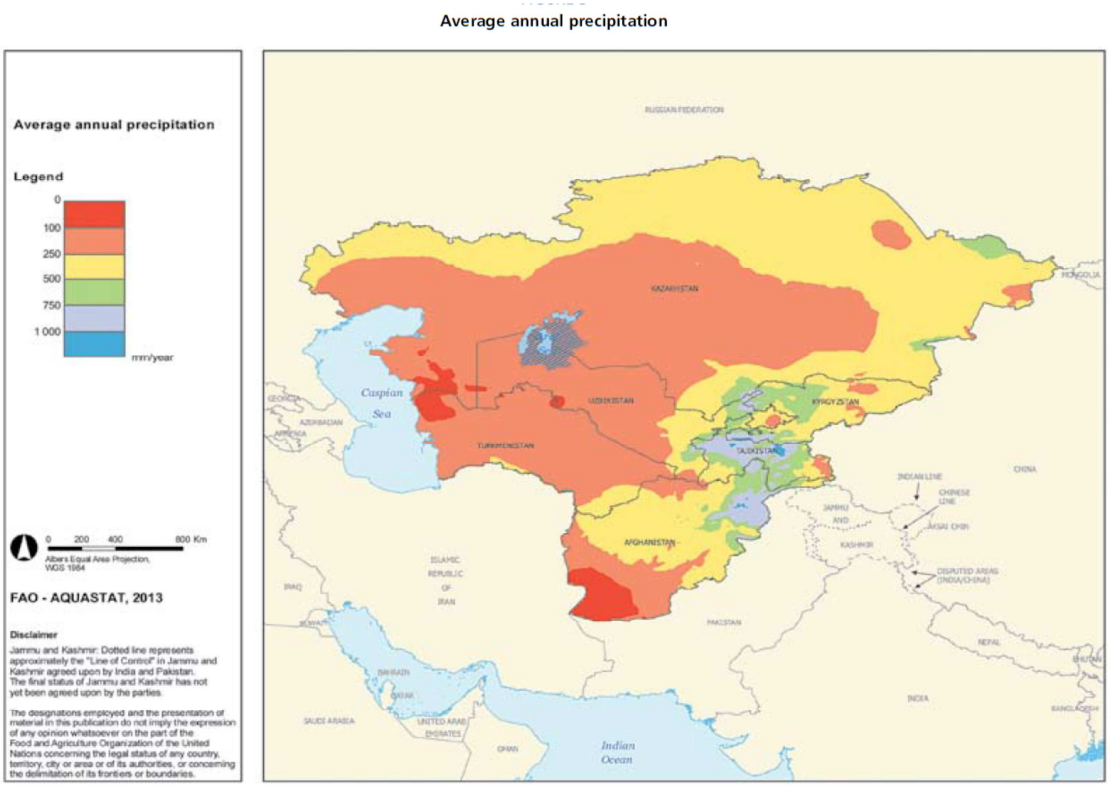


Figure 1: Average annual precipitation of Central Asia in 2013 (FAO-AQUASTAT (2013)).

The availability of sufficient water for irrigation during the vegetative period will become more and more uncertain: The two main rivers in the region, the Syr-Darya and Amu-Darya have their origin the mountains of Central Asia, where they are fed by glacier and snow-melt-run-off (IWMI, 2003). However, global warming will increase glacier-melt and a shift of run-off-peak from summer to spring is predicted. Such a shift would lead to

serious irrigation water deficit during vegetative period from April to September (Siegfried *et al.*, 2011).

In Central Asia, wheat and cotton are dominating the agricultural landscape, being grown on 16.0 and 2.3 million hectare (FAO, 2013b), respectively. But in terms of production quantity (MT), potato ranks second after wheat (Table 2, FAOSTAT, 2012), with 7.6 million tons in 2012.

Table 2: Production quantity of wheat, cotton and potato in Central Asia for 2012 (Statistical Division (FAOSTAT, 2012)).

	Production (MT)		
	Wheat	Potato	Cotton seed
Kazakhstan	9,841,100	3,126,400	218,700
Kyrgyzstan	540,531	1,312,699	55,900
Tajikistan	852,000	990,200	220,000
Turkmenistan	1,200,000	280,000	396,000
Uzbekistan	6,512,400	1,900,000	1,980,000
Central Asia	**18,946,031**	**7,609,299**	**2,870,600**

However, situation for potato production in Central Asia is by far not optimal. Owing to the breakdown of the Soviet Union, supply of quality seed tubers stayed out and research on potato has been neglected. As a consequence many traditional, locally adapted potato varieties have been lost and seed potatoes needed to be imported from Europe. Thus, farmers in Central Asia have to rely on expensive European cultivars that are not adapted to local conditions, and have high yield losses under the arid climate of the region (Carli, 2008).

1.4. Origin and genetic potential

The genetic origin of potato is located in Peru with more than 4.000 varieties originated from the Andes (cipotato.org). In South America potatoes are grown in a large range of environmental conditions, from coastal regions up to 4200 m above sea level. Due to their cultivation and selection by Andean farmers, these potato varieties carry high potential for resistances against biotic and abiotic stresses (Ritter *et al.*, 2008; Schafleitner *et al.*, 2007; Watkinson *et al.*, 2006; Vasquez-Robinet *et al.*, 2008). Traits associated with drought tolerance in potato include high growth rate and high stomatal conductance, delayed leaf senescence, high capacity of energy dissipation and high osmotic adjustment (Monneveux *et al.*, 2013).

To safeguard biodiversity of potato, the "International Potato Center" (CIP) in Lima, Peru maintains a gene bank containing over 7,000 accessions of native, wild and improved varieties. Varieties are explored in order to identify traits that help the breeding process to develop improved varieties with biotic and abiotic resistances. Improved varieties and innovative technologies are used to ensure food security, improve incomes of the poor and help farmers cope with the ongoing climate change all over the world (ciptato.org).

To be able to detect mechanisms for drought resistance within the broad range of potato varieties, powerful screening tools are vital to identify promising candidates. Reactions and adaptions of potato plants under drought stress and the underlying mechanisms must be examined, to identify traits that could be used as a screening tool. In addition, identifying drought resistance traits will help the breeding process to sustain potato production.

1.5. Potato and Drought

However, potato is reported to be sensitive to drought stress, in comparison to other crops (van Loon, 1980; Weisz *et al.*, 1994). This sensitivity is mainly attributed to its low capacity to extract soil water (compared to other crops) due to its shallow root system (Weisz *et al.*, 1994). Even short period of water deficit can significantly reduce tuber yields (Levy, 1983), but the extent of yield reduction depends on the phenological stage in which it occurs (Spitters and Schapendonk, 1990). Tuber initiation stage was reported to be

much more sensitive to drought stress in terms of yield reduction than early and late tuber bulking (Costa *et al.*, 1997).

Drought affects multiple traits: 1. Drought stress reduces overall plant growth (Van Loon, 1980), 2. induces leaf senescence (Van Loon, 1980) and 3. decreases tuber number (Anithakumari *et al.*, 2012). 4. Root dry mass, root and stolon length and stolon number have been shown to be sensitive to soil water deficit (Lahlou and Ledent, 2004). 5. Specific leaf area (SLA), a measure of leaf thickness, is modified by environmental factors, such as light intensity, temperature, drought and CO_2 concentration, as well as physiological aspects such as leaf age and source-sink characteristics (Marcelis *et al.*, 1997; Marron *et al.*, 2003). Under drought, SLA typically decreases due to a higher effect of drought on leaf expansion than on photosynthesis (Tardieu *et al.*, 1999) and due to an accumulation of soluble compounds (Marron *et al.*, 2003). 6. Chlorophyll fluorescence of plant leaves is another parameter that is sensitive to drought stress. It can be used to investigate the impact of drought on the performance of the photosynthetic apparatus. The chlorophyll fluorescence parameter Fv/Fm is a measure of the efficiency of photosystem II photochemistry (maximum quantum yield of PS II), that typically decreases under drought stress, due to inhibition of photosynthetic metabolism (Baker and Rosenqvist, 2004; Anithakumari *et al.*, 2012). In leaves of *Acer pseudoplatanus, Fagus silvatica* and *Quercus robur* Fv/Fm values have been shown to be highly correlated to changes in leaf relative chlorophyll content (Percival *et al.*, 2008), an indicator of photosynthetic capability (Nageswara *et al.*, 2001). 7. The maintenance of leaf relative chlorophyll content ("stay-green") under drought is considered as an important trait in potato (Ramírez *et al.*, 2014). Higher relative chlorophyll contents under deficit irrigation compared to fully-irrigated control under both, greenhouse and field conditions were reported by Yactayo *et al.*, 2013 and Ramírez *et al.*, 2014. 8. In maize, triticale and rice the maintenance of high leaf water potential (LWP) under drought stress is associated with drought tolerance (Grzesiak *et al.*, 2006; Jongdee *et al.*, 2002). In potato, the water capacity of leaves is relatively low, as small changes in leave water content strongly reduce leave water potential (Vos and Groenwold, 1988). According to Maxwell and Redmann (1978) the rate of change in leaf water content for a given reduction in leaf water potential could be used to identify drought resistance.

1.6. Hypotheses and Objectives

Changes in growth and partitioning patterns constitute an important component in the adaption strategies of potato under water deficit conditions.

Additionally, drought responses vary as a function of the phenological stages. Furthermore, sensitivity of various physiological and morphological parameters of potato to drought stress will be tested.

The objectives of this study are, therefore to investigate a) the effects of drought stress on plant growth and on carbohydrate partitioning, and b) the phenological responses of five contrasting potato genotypes, to drought depending on the development stages.

2. Materials and Methods

2.1. Location

The experiment was conducted from 19th of July till 1st of November 2013. Experiments were carried out on the experimental research station of the "National Agricultural Research Institute" (Instituto Nacional de Investigación Agraria). The station is located at 16 ° 29`27`` S (latitude) and 72° 05`33`` E (longitude), 1.265 m above sea level in Majes, Arequipa, the costal arid region in southern Peru.

2.2. Experiment

2.2.1. Design

The experiment design was a completely randomized "split-split plot" design with three replications, four treatments, five genotypes and four different harvest dates for each treatment. Treatments, as the main plots were randomized within replications, genotypes (plots) within treatments and harvest plants (sub plots) within genotypes (App. Figure 69).

To prevent interactions between treatments or genotypes, every plant row was accompanied by a row of border plants of the same genotype on each side (Figure 2). Plots also contained border plants. Every second plant in the row was a border plant, so that the removal of one plant at a harvest date did not have any influence on the growing conditions of the other harvest plants (Figure 2). Additionally, border plants were planted in every first and last plot of a row (App. Figure 69).

Before the start of the treatments, in each plot plants were labeled for the destructive measurements at the three harvest dates. These plants further will be referred to as "harvest plants". The position of harvest plants within the plot was previously randomized. For all none-destructive measurements, another plant per plot was selected and measurements were always repeated on this plant. When choosing that plant (prior to treatment start), care was taken that it will be accompanied by two border plants throughout treatment duration to avoid distorted results (Figure 2). Furthermore, this plant needed to be representative for the whole plot. This plant further will be referred to as "physiological plant".

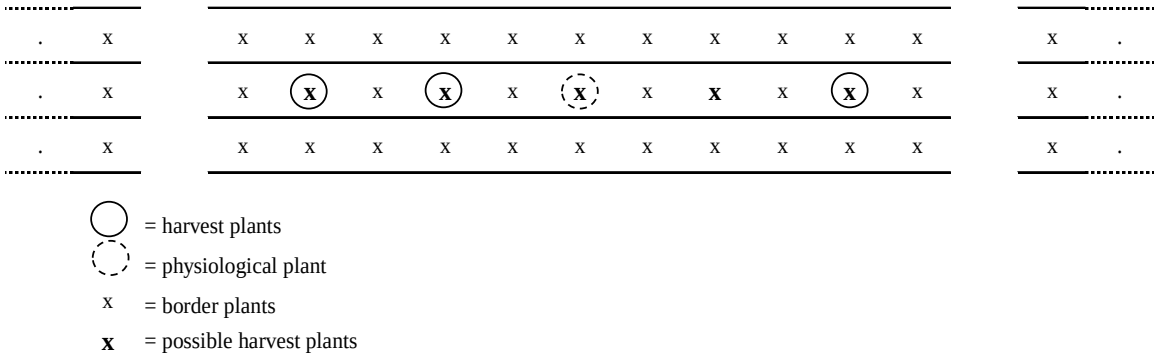


Figure 2: Example of randomization and border plant scheme within one plot. Plots were accompanied by one row of border plants on each side. Position of harvest plants, marked with solid circles, among possible harvest plants was randomly distributed.

2.2.2. Treatments

Five different potato genotypes, CIP 392797.22, CIP 301040.63, CIP 392025.7, CIP 397073.16, CIP 397078.12, were investigated. The treatments consisted of three drought stress treatments, implemented at different development stages of potato. In the first treatment (T54), irrigation was withheld 54 days after planting (DAP) (Figure 3). In treatment two (T67) and three (T80), at 67 and 80 DAP, respectively. Corresponding control plants were well-watered throughout growing time. Harvests were conducted in each treatment and corresponding control plots 6, 16 and 26 days after withholding irrigation (DAWI). Three plants per treatment were harvested each time. At the end of the growing cycle, a final harvest was conducted 125 DAP for all three treatments.

Control	Harvest 1	Harvest 2	Harvest 3	Final Harvest
T54	Harvest 1	Harvest 2	Harvest 3	Final Harvest
DAP	*60*	*70*	*80*	*125*
DAWI	*6*	*16*	*26*	*71*

54 DAP

Control	Harvest 1	Harvest 2	Harvest 3	Final Harvest
T67	Harvest 1	Harvest 2	Harvest 3	Final Harvest
DAP	*73*	*83*	*93*	*125*
DAWI	*6*	*16*	*26*	*58*

67 DAP

Control	Harvest 1	Harvest 2	Harvest 3	Final Harvest
T80	Harvest 1	Harvest 2	Harvest 3	Final Harvest
DAP	*86*	*96*	*106*	*125*
DAWI	*6*	*16*	*26*	*45*

80 DAP

Figure 3: Treatment design. Water was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Control plots were well-watered throughout. Harvests were conducted 6, 16 and 26 days after withholding irrigation (DAWI) in all three treatments and corresponding control plots. Final harvest was conducted 125 DAP in all tree treatments (71 DAWI (T54), 58 DAWI (T67), 45 DAWI (T80)).

2.3. Planting

Presprouted seed tubers of the five potato genotypes were planted on the 17th/ 18th of July, on the 2300 m^2 experimental field.

The required dams were formed mechanically two days before planting. The field was divided into 3 m long and 0.8 m wide plots (Figure 6). In total, eleven seed tubers were planted in each plot with a distance of approximately 27 cm. Every plot was followed by a 1 m gap, supposed to ease handling.

For planting, pre-sprouted seed tubers were carefully placed by hand on the left side of the ridge with sprout upturned (Figure 4). Mineral fertilizer mixture (162 kg/ha potassium sulfate (50 % K_2O, 18 % S; INTI), 81 kg/ha Urea (46 % N, Misti Fertilizer) and 244 kg/ha Fertiphos®-Plus (20 % P_2O_5; 36 % CaO; 6 % S, 17 % SiO_2; 1.08 % Fe_2O_3; 0.9 % MgO; Micronutrients Zn, Mn, Cu, B)) was placed manually in between the seed tubers. As an organic nutrient source, Guano (1.6 ton/ha) was used and applied on the bottom of the furrows (Figure 5). With shovels seed tubers were covered with the fertilizer-soil-mixture from the furrow. Mixing the soil with the fertilizer instead of applying it directly on the seed tubers was done to protect sprouts and roots from burning.

Figure 4: Seed tubers placed on the side of the ridge with sprouts upturned.

Figure 5: Ridges with mineral fertilizer applied between seed tubers and organic fertilizer on the bottom of the furrow.

Figure 6: Marked plots with different seed tubers.

2.4. Irrigation

A drip line irrigation system was installed on the 19th of July. This system was chosen because of its advantages in terms of irrigation homogeneity in comparison to other irrigation systems, e.g. sprinkler irrigation.

Drip lines (John Deere Water; Row Drip; 16 mm ID, 5 mm wall, 20 cm spacing, 500 LPH/100m @ 0.55 bar) were positioned for every row in the middle of the ridge, with every row having one drip line. On one end, drip lines were connected to a water source and on the other end sealed. Weighing down the drip lines with soil at the gaps in between plots ensured that lines were not slipping off the dams.

On day after planting, field was irrigated initially for 180 min with 33 m^3 h^{-1} ha^{-1} to ensure water availability for sprouting. Thereafter filed was irrigated daily for 45 min. At 12 DAP irrigation time was further restricted to 20 minutes per day. To meet the water demand of the plants, irrigation time was increased to 40 and 60 min 31 and 40 DAP, respectively. For a period of eight days, irrigation time was decreased to 30 min, 67 DAP. Thereafter, plants were watered for one hour till the end of experiment.

After hilling, 42 DAP, a second irrigation drip line was installed for each row, to avoid one-sided tuber growth and ensure homogeneous water supply to the root zone.

2.5. Soil

For soil analysis, samples were taken one week before the start of the experiment. Soil samples were taken from 0 - 15 cm and 15 - 30 cm soil layer at five different locations evenly distributed over the experimental field.

Samples were analyses in the analytical laboratory for soils, plants, water and fertilizers at the National Agrarian University La Molina, Lima. Physiochemical properties (means of five sample locations) of the soil from the experimental field are presented in Table 3.

Table 3: Mean physiochemical soil properties and soil characteristics for Majes (n=5).

Depth	**pH** (1:1)	**EC** (1:1) dS/m	**$CaCO_3$** %	**Organic matter** %	**P** ppm	**K** ppm	**Sand** %	**Silt** %	**Clay** %	**Textural class**
0 - 15 cm	8.0	0.8	0.1	1.5	16.9	499.2	80.8	11.2	8.0	loamy sand/ sandy loam
15 - 30 cm	7.9	0.6	0.1	1.0	3.5	321.4	81.6	10.0	8.4	loamy sand/ sandy loam

Depth	**CEC** meq / 100 g	**Exchangable Cations**					**Sum of Cations**	**Sum of Bases**	**% of saturated Bases**
		Ca^{+2} meq / 100 g	**Mg^{+2}** meq / 100 g	**K^{+}** meq / 100 g	**Na^{+}** meq / 100 g	**Al^{+3} + H** meq / 100 g			
0 - 15 cm	6.8	3.4	1.7	1.3	0.4	0.0	6.8	6.8	100.0
15 - 30 cm	6.1	3.3	1.4	0.9	0.5	0.0	6.1	6.1	100.0

The soil was a loamy sandy /sandy loam with averagely 81.2 % sand, 10.6 % silt and 8.2 % clay. With values of 8.0 and 7.9, the pH of the 0 - 15 cm and 15 - 30 cm layer was neutral to alkaline. For phosphorus, potassium, $CaCO_3$ and organic matter, higher concentrations were always found in the upper soil layer (0 – 15 cm). The same pattern was found for the amount of exchangeable cations, except for Na^{+} and Al^{+3} + H.

2.6. Crop management

2.6.1. Weeding

To minimize competition between weeds and the potato plant, weed control measures were regularly performed during the crop cycle. At hilling (40 DAP), weeds were buried with soil. Furthermore, weeds were pulled up manually 56, 77 and 89 DAP. Weed control was done manually and not chemically to avoid negative impacts on potato plants.

2.6.2. Pesticide application

Pest control measures were carried out at planting (0 DAP), after hilling (42 DAP), 49 and 84 DAP, to control pest like gall midge (*Prodiplosis longifila*), thrips (*Thysanoptera*), cutworm (*Agrotis* ssp.) etc. (Table 4). Pesticides were either applied via backpack sprayer or distributed via the irrigation system. Foliar micronutrient fertilizers were applied in combination with insecticides, 49 and 84 DAP.

Table 4: Pest control measures conducted during the experiment.

DAP	Product name		Mode of application	Dose
0	FURADAN® 4F	Insecticide/ Nematicide	spread in soil before tubers are covered	12 kg ha^{-1}
	PENTACHLORO FARMEX	Fungicide	spread over tubers before they are covered	30 g x 15 Lt
42	ROVRAR	Fungicide	by irrigation system	50 g x 200 Lt
	PENTACHLORO FARMEX	Fungicide	by irrigation system	350 g x 200 Lt
	SOBRA 50 EC	Insecticide	by foliar spraying	200 cc x 200 Lt
	CONFIDOR 350 SC	Insecticide	by foliar spraying	150 cc x 200 Lt
49	SOBRA 50 EC	Insecticide	by foliar spraying	200 cc x 200 Lt
	CONFIDOR 350 SC	Insecticide	by foliar spraying	150 cc x 200 Lt
	QUIMIFOL	Fertilizer	by foliar spraying	400 g x 200 Lt
84	SOBRA 50 EC	Insecticide	by foliar spraying	250 cc x 200 Lt
	CONFIDOR 350 SC	Insecticide	by foliar spraying	150 cc x 200 Lt
	BAYFOLAN	Fertilizer	by foliar spraying	500 cc x 200 Lt

2.6.3. Hilling

Hilling is a standard cultural practice in potato production that aims at protecting tubers from sunlight, improves weed control and helps at controlling temperature and drainage. Hilling was done manually with shovels 40 DAP. The lower third of the plants thereafter was covered with soil (Figure 7) and dam height was increased by about 10 cm. As plant height was not homogeneous, care was taken not to bury small plants. To ensure a sufficient nutrient supply, mineral fertilizer (244 kg/ha Ammonium nitrate (33% N_{total}; 16.5 % NO_2^-; 16.5 % NH_4^+; 3.0 % P_2O_5), was spread in the furrows before hilling.

Figure 7: Plant rows after hilling.

2.7. Weather conditions

Before planting, a weather station (HOBO® Weather station) was set up at the experimental field to record temperature (°C), relative humidity (rH; %), photosynthetically active radiation (PAR; µE m^{-2} s^{-1}), wind direction (Ø), wind speed (m s^{-1}) and gust speed (m s^{-1}) in ten minute intervals. Additionally, two sensors were used to detect soil temperature in 10 cm depth, once between two fully irrigated rows, the other one between two drought stressed rows.

Daily mean temperature and relative air humidity are presented in Figure 8/Figure 9. Because of technical problems data from 21st of September till the 4th of October is not available.

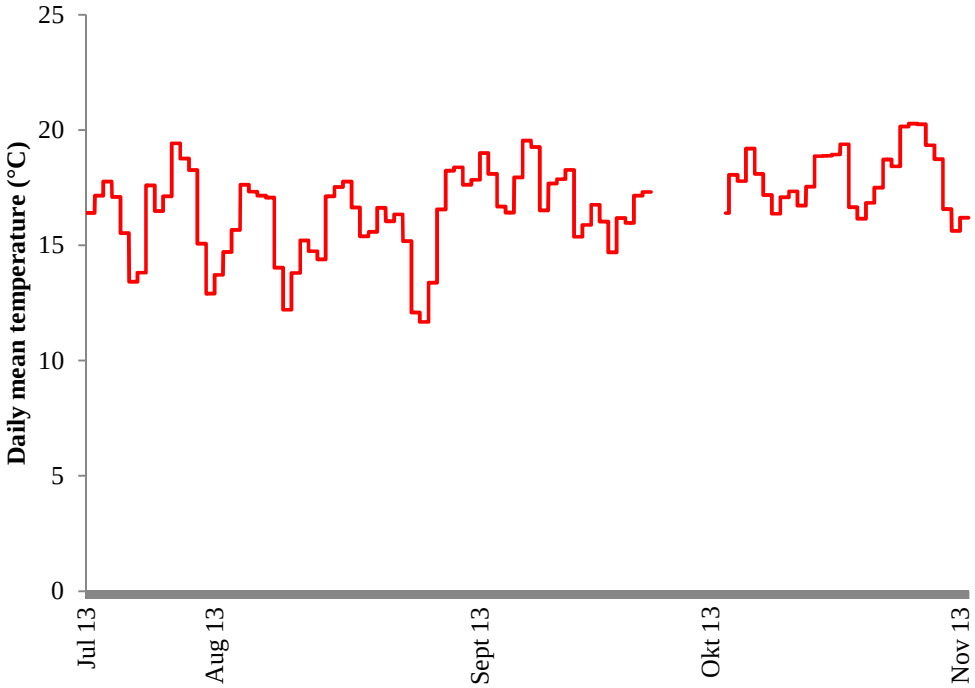


Figure 8: Daily mean temperature calculated from recorded data of air temperature (°C) taken by HOBO weather station.

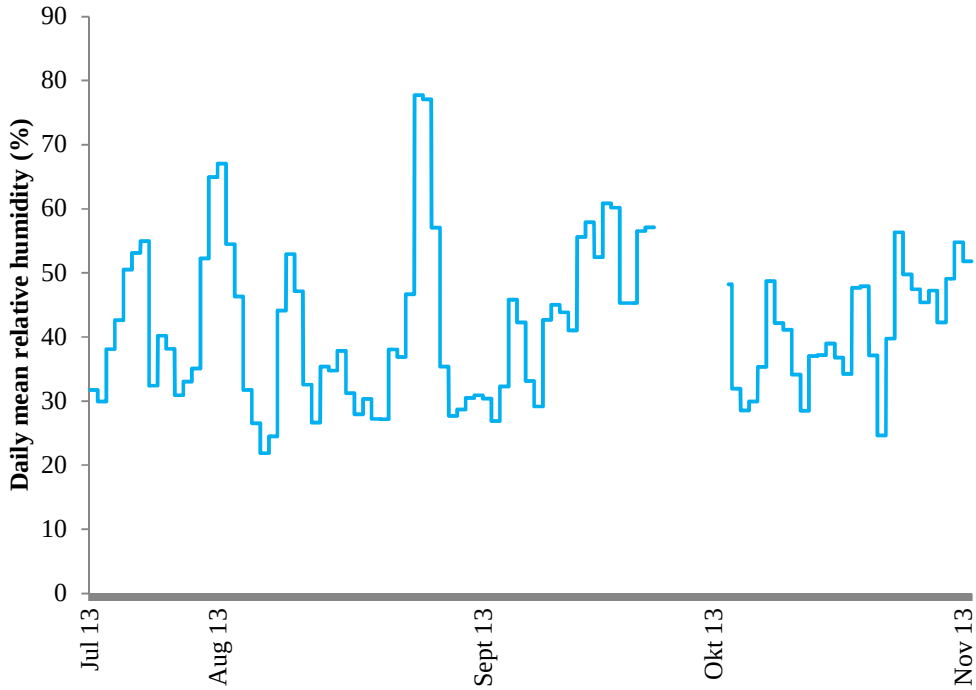


Figure 9: Daily mean relative humidity in % calculated from recorded data of relative air humidity taken by HOBO weather station.

Monthly mean air temperature as well as soil temperature in wet and dry soil increased during the experiment (Table 5). Air temperature ranged from 15.7 °C in August to 18.0 °C in October. Average temperature in wet and dry soil was 20.5 and 21.9 °C, respectively. During the period from July to November, relative humidity increased by 10.7 %. Photosynthetically active radiation (PAR) constantly intensified, with values increasing from 396.9 to 677.7 µE m^{-2} s^{-1}. Wind and gust speed increased from 0.4 and 1.1 m s^{-1} in July to 1.0 and 2.2 m s^{-1} in November.

Table 5: Monthly mean weather data for the month July to November, 2013.

	Temperature soil (dry), °C	Temperature soil (wet), °C	Temperature air, °C	Relative humidity (rH) %	PAR, µE m^{-2} s^{-1}	Wind Direction, ø	Wind Speed, m s^{-1}	Gust Speed, m s^{-1}
Jul 13	20.4	20.2	17.0	37.7	396.9	216.8	0.4	1.1
Aug 13	19.4	19.6	15.7	39.2	494.1	160.7	0.7	1.7
Sept 13	20.6	19.8	17.2	44.7	593.6	152.2	0.8	1.9
Oct 13	25.9	20.9	18.0	40.6	635.1	187.6	0.7	1.7
Nov 13	23.2	22.0	17.3	48.4	677.7	183.6	1.0	2.2

2.8. Genotype characterization

As already mentioned above, all five genotypes are part of an advanced breeding population from the International Potato Center. Selection of genotypes for this experiment was based on a drought susceptibility index (DSI) assessment derived from a prior-year experiment (2012). Choice of genotypes was done in order to get an assortment of contrasting genotypes.

The drought susceptibility index is a measure of relative drought tolerance and allows comparing genotypes across location and time. It is calculated according to the formula presented by Fischer and Maurer (1978):

$$DSI = (1 - Y_D / Y_w) / D$$

Where Y_D = fresh tuber yield of the genotype under drought conditions, Y_W = fresh tuber yield of the genotype under well-watered conditions and D = (1- mean fresh tuber yield of all genotypes under drought conditions / mean fresh tuber yield of all genotypes under

well-watered conditions). DSI values lower than 1.0 point to a lower than average drought susceptibility, while values higher than 1.0 indicate higher drought susceptibility.

Till now, the only commercially available potato clone from these five clones is Unica, with CIP code: 392797.22. All other potato clones are no varieties yet. To simplify handling, genotypes further will be denoted with their field code. Therefore, CIP 392797.22, CIP 301040.63, CIP 392025.7, CIP 397073.16 and CIP 397078.12 will be further referred to as Genotype A, B, C, D, E.

2.8.1. Genotype A (CIP 392797.22)

In 2012 (prior-year experiment), genotype A (Gen A) (Population LTVR, Breeders Code C92.140) showed a low drought susceptibility with a DSI of 0.535.Plants of this genotype had a small canopy with a radial distribution growth. During development, on some plants inflorescences were formed, but those were only rarely further developed into flowers (Figure 11). Plants neither carried berries and therefore nor seed. Compared to other genotypes, this genotype had an early stolon and tuber development (Figure 10), but also showed early wilting under drought in this experiment (Figure 12).

Figure 10: Tuber and stolon development status of genotype A, 36 DAP.

Figure 11: Flowering status in control plot of genotype A, 79 DAP.

Figure 12: Above-ground biomass of genotype A, 25 DAWI (T67).

2.8.2. Genotype B (CIP 301040.63)

Genotype B (Gen B) (Population Intermediate LT-LB; Breeders Code C01.154) had a bad DSI assessment in 2012 with a Drought Susceptibility Index of 1.497.

Emergence of plants took place much later in time than that of the other genotypes, which resulted in delayed growth and development. Nevertheless, plants of this genotype in the end had largest canopies with an erect growth habitat and a large share of biomass located in stems. Stolons and tubers developed set in much later compared to the other genotypes (Figure 13), but also wilting under drought conditions set in late (Figure 15). Nearly all plants of this genotype formed flowers (Figure 14) and often berries were built.

Figure 13: Tuber and stolon development status of genotype B, 36 DAP.

Figure 14: Flowering status in control plot of genotype B, 79 DAP.

Figure 15: Above ground biomass of genotype B, 25 DAWI (T67).

2.8.3. Genotype C (CIP 392025.7)

With a Drought Susceptibility Index of 0.568, genotype C (Gen C) (Population LTVR; Breeders Code LR-93.221) showed a similarly good performance under drought stress in 2012 like Gen A. Also here stolon and tuber development set in early (Figure 16), but plants were a little bit taller and plant habitus was more bush like. Under drought stress, wilting of the above-ground biomass set in early (Figure 18). In terms of inflorescences, flowering and berry-formation plants of Gen C act in a similar manner as those of Gen A (Figure 17). Only very few plants formed inflorescences and flowers and berries none existed.

Figure 16: Tuber and stolon development status of genotype C, 36 DAP.

Figure 17: Flowering status in control plot of genotype C, 79 DAP.

Figure 18: Above-ground biomass of genotype C, 25 DAWI (T67).

2.8.4. Genotype D (CIP 397073.16)

Genotype D (Gen D) (Breeder Code WA.104) had a relatively high Drought Susceptibility Index of 1.487 in 2012. This medium-sized genotype had a bush-like plant habitat and exhibited early wilting under drought stress (Figure 21). Compared with the other genotypes, start of stolon and tuber development was later, but not as late as in Gen B (Figure 19) Blooming started early in this genotypes with many plants forming berries. At 79 DAP flowering was already over in this genotype (Figure 20).

Figure 19: Tuber and stolon development status in genotype D, 36 DAP.

Figure 20: Flowering status in control plot of genotype D, 79 DAP.

Figure 21: Above-ground biomass of genotype D, 25 DAWI (T67).

2.8.5. Genotype E (CIP 397078.12)

In the experiment of the year 2012, the performance of genotype E (Gen E) (Population LTVR; Breeders Code 314.12) resulted in an intermediate Drought Susceptibility Index of 0.922. Plants of this genotype had tall canopies with an erect to bush-like growth habitat. Comparable to genotype D, also here, a high share of flowers were open at an early stage and many plants formed berries (Figure 23). Stolon and tuber development was later, compared to the other genotypes (Figure 22). Wilting of the above ground biomass under drought stress was detected at a late stage (Figure 24).

Figure 22: Tuber and stolon development status in genotype E, 36 DAP.

Figure 23: Flowering status in control plot of genotype E, 79 DAP.

Figure 24: Above-ground biomass of genotype E, 25 DAWI (T67).

2.9. Experimental parameters

2.9.1. Soil water content

Soil water content was measured by a Time Domain Reflectometer (Profile Probe; Type PR2; Delta-T Devices Ltd.). Therefore, 40 cm long access tubes were installed in the field providing information about soil water content in different soil layers.

In total 195 tubes (for 13 clones) were installed, each plot receiving one. If possible, access tubes were set right in the middle of the plot (Figure 25) in between two plants (Figure 26), to ensure reliable information about soil moisture in the root zone. With an installation kit, access tubes were installed 42 DAP. Attention needed to be paid that tubes were strictly vertical, that there was no dirt or moisture in the tubes, and that tubes had close contact with soil matrix over the whole outer surface.

Soil moisture content was measure every three days from start of treatment on by using the TDR-probe (Figure 27). The probe recorded soil moisture in Vol % for soil layers 0 – 10 cm, 10 - 20 cm and 20 - 30 cm (App. Figure 70). To improve information quality and to minimize the influence of inhomogeneous soil zones, for each tube measurements were done in total three times at 0, 90, and 120 ° and mean was calculated.

Figure 25: Position of access tube within one plot.

Figure 26: Access tube installed between two plants.

Figure 27: Soil water content measurement with TDR-probe.

2.9.2. Leaf area expansion rate

To determine leaf area expansion rate of the different potato clones, potato leaves of the physiological plant were measured with a tapeline every three days after withholding irrigation in each treatment. Examined parameters were leaf length and width.

Measurements started on leaf number two on the main stem and were continued on then new leaves that have developed during the treatment period (new second leaf). The corresponding leaves were marked with labels giving the order of development (Figure 30). Leaf length was measured from insertion on stem till tip of terminal leaflet (Figure 28). Width of the compound leaf was measured by determining length in cm from tip of leaflet two (Figure 29/Figure 31) till tip of leaflet three. Leaf expansion rate was derived by calculating leaf area (leaf length x leaf width) and computing the increment in leaf area on a daily basis.

Figure 28: Measurement of leaf length.

Figure 29: Measurement of leaf width.

Figure 30: LER labels giving the order of development.

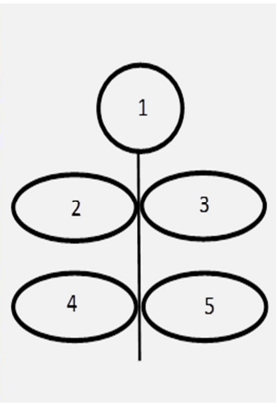


Figure 31: Scheme of potato leaf with numbered leaflets.

2.9.3. Leaf area index

Leaf area index (LAI) was measured in seven day intervals after withholding irrigation by using the Decagon Device AccuPar (modelLP-80 PAR/LAI conceptiometer). This device allows simultaneous above and below canopy PAR readings from which LAI can be estimated.

Calculation of LAI is based on the following parameters: zenith angle (z), fractional beam radiation (F_b), Tau (τ), leaf area distribution parameter (χ). Fractional beam radiation and Tau are automatically calculated. For a correct zenith angle it is necessary to enter date and time, longitude and latitude of the location and select daylight saving time or standard time. The leaf distribution parameter (χ) depends on the structure of the canopy and therefore varies for species and genotypes. For potato, typical χ-values range between 1.70 and 2.47, and can be adapted according to the structure of the canopy. For more horizontally growing canopies higher χ-values must be set than for canopies of a vertical nature.

The measurements were taken on three representative plants in a row per plot and on three different positions: under the right side of the canopy, in the canopy and under the left side of the canopy for mean calculation. The light sensing segment was placed horizontal in the different positions (see Figure 32; Figure 33; Figure 34) while the external sensor was mounted vertically on a 2 m high wooden stand which was placed close to the measured

plants. All measurements were done at clear sky conditions between 9:00 and 15:00 h. Measurements were replicated three times in each treatment.

Figure 32: Leaf area index measurement under right side of the canopy.

Figure 33: Leaf area index measurement in the canopy.

Figure 34: Leaf area index measurement under left side of the canopy.

2.9.4. Chlorophyll content

Every seven days after withholding water, relative chlorophyll content (SPAD) of potato leaves was measured, using a Chlorophyll Meter (SPAD-502Plus, Konica Minolta). Prior to SPAD measurements, the device was calibrated by closing the measuring head without having a sample inside.

On three leaflets of the potato leaf (excluding leaflet no. one (see Figure 31)), three measurements were taken and averaged. This was done by placing the attached leaflet in the sample slot and closing it until SPAD values were displayed (Figure 35). When placing the leaflet in the slot, care must be taken, that the leaflet vein was not in the range of the sensor, to avoid incorrect readings. To get an impression of the whole plant and not just from a single leaf, in total five leaves from different positions (bottom, upper bottom, middle, upper middle and top leaf) on the main stem were measured and mean was calculated. This was repeated three times per treatment and always done on the physiological plant.

Figure 35: Measurement of chlorophyll content of potato leaves with Chlorophyll Meter

2.9.5. Chlorophyll fluorescence

Chlorophyll fluorescence was measured every seven days after withholding water in control and stressed plants by using the portable Chlorophyll Fluorometer (OS1p; OPTI SCIENCE). Fluorescence data recorded included minimal (Fo) and maximal fluorescence (Fm) and the ratio of variable to maximal fluorescence (Fv/Fm). The variable fluorescence Fv is calculated as Fv = Fm – Fo.

Since the appropriate time for dark-adaption varies between and within species, a test needed to be performed prior to measurements, to figure out how long potato plant leaves should be dark-adapted.

To test that, a leaf clip was places on a leaflet of a boarder plant and allowed to dark-adapt for five minutes. Then a measurement was taken with the Chlorophyll Fluorometer with record set to one second at full intensity. The measured Fv/m value was noted and the sample was re-dark adapted, this time for ten minutes. Another measurement of Fv/m was conducted and the value also noted. This procedure was repeated. Every time, dark adaption time was extended by five minutes. When the Fv/m value did not increase any further, adaption time where the highest Fv/m value was found gave the appropriate time for dark-adapting potato leaves. In this case twenty minutes seemed to be suitable (see Table 6).

Table 6: Fv/Fm values for dark-adaption test. Leaflet was dark-adapted for 5, 10, 15, 20, 25, 30 and 35 minutes before measurement with portable Chlorophyll Fluorometer.

Time (min)	5	10	15	20	25	30	35
Fv/Fm	0.767	0.764	0.772	0.798	0.768	0.755	0.772

Chlorophyll fluorescence was measured on the physiological plant, at the third-fully expanded leaf of the main stem. Measurements were done always on the same leaflet. This was ensured by attaching labels on the leaf, giving the number of the leaflet to be measured (Figure 39).

Chlorophyll fluorescence was measured in the dark-adapted state. For dark-adaptation leaf clips were mounted on the respective leaflet for 20 minutes with the dark slide of the clip closed (Figure 37). To produce reliable data, it was important not to move the clip again after once being placed on the leaflet, and that the leaflet vein was not part of the measured

area. Fv/Fm was measured on the dark-adapted leaves by inserting the fiber optic bundle into the leaf clip, opening the dark slide (Figure 36) and pressing the trigger switch on the far end of the bundle to take measurements (Figure 38).

As only ten leaf clips were available for dark adaption, it took a lot of time to finish measurements. To handle that workload, decision was made to perform prospective dark adapted fluorescence measurements at night. Measurements started after 22:30 h and were only done at low moonlight.

Figure 36: Dark clip mounted on leaflet with dark slide open.

Figure 37: Dark clip mounted on leaflet with dark slide closed for dark adaptation.

Figure 38: Measurement of Fv/Fm. Fiber optic bundle is inserted into dark clip and dark slide is open.

Figure 39: Label attached to potato leaf, giving the number of leaflet to be measured.

2.10. Harvest

Harvests were conducted 6, 16 and 26 DAIS in all three treatments. At each harvest, three replicates for each genotype in treatment and control were harvested by hand. Analyzed parameters were: Leaf water potential, specific leaf area, stolon number and length, stem number, tuber number, tuber average size, root architecture, fresh weight of tubers and dry weights of leaves, stems, below-ground biomass (roots + stolons) and tubers.

Plants were harvested genotype wise and the order in which the genotypes were harvested was changed at each harvest to minimize effects of diurnal variation. Plants were harvested with a pitch fork that was set about on hand´s length below dam ridge to dig out the plant (Figure 40). Only two to three plants were removed from the soil at once and were then stored in big plastic bags to keep water losses low until analysis. A final harvest was conducted 125 DAP in all three treatments to determine final tuber yield.

Figure 40: Manual harvest of a potato plant.

2.10.1. Stolon number and length

Length of stolons was measured on three representative stolons per plant. Length in cm was measured with a common ruler (Artesco, plastic) from the insertion on the root till stolon`s tip.

Stolon number was determined by simply counting the stolons per plant.

2.10.2. Tuber number and size

To study the effect of drought stress on tuber number of the contrasting genotypes, number of tubers per plant was counted. Criterion for tuber initials (stolon swellings) to be counted as tubers was to have twice the diameter of the stolon (Walworth and Carling, 2002).

When harvesting the plants by hand, care needed to be taken that no tuber remained in the soil.

To get further information about the development of the tubers /tuber initials, tuber length and width were measured with a vernir caliper on three representatives (Figure 41).

Figure 41: Measurement of tuber length (left picture) and tuber width (right picture) with a vernir caliper.

2.10.3. Dry weights of biomass

Dry weights of leaves, stems, tubers and below-ground biomass (roots and stolons) were determined in this study.

At harvest, leaves were separated from stems, stems were cut into short pieces to better fit into the measuring vessel and tubers were cleaned from adhering soil. Total tuber fresh weight was investigated as well as fresh weight of the three representatives. Tuber fresh weight was determined in the field by using an industrial balance (Jadever; JWG Series Weighing Scale; JWG-15K; d=e=0,001 kg) that was put into a cardboard box to avoid the influence of windy conditions. Fresh weight determination was necessary for total tuber dry weight calculation, as only subsamples were dried.

After weighing, the three representative tubers were cut into thin slices to facilitate the drying process. All samples were separately packed into paper bags (Unline; #12/25 hardware paper bag; Model No. 6914/7631) for drying (Figure 42).

Figure 42: For tuber dry weight determination, tubers are cut into slices (left picture) and are then stored in paper bags (right picture).

Since no drying oven was available during harvesting period, samples were air-dried. The paper bags with plant material were evenly distributed on a concreted area of the research

station. The concreted area was chosen because of its favorable conditions for drying: the concreted ground in combination with direct sunlight promoted the development of high temperatures (around 45 °C), and the good wind circulation avoided rotting of the samples.

The samples were allowed to dry at least for three weeks before dry weights of leaves, stems and below-ground biomass were taken with an analytical balance. Below-ground biomass was put on a fine-meshed net and gently shaken to get rid of still adhering soil particles before dry weight determination.
In the middle of November a drying oven was available on the research station that allowed checking whether the air-dried samples contained any residual moisture. Subsamples of below-ground biomass, stems and leaves were dried in an oven for 24 hours at 80 °C and weight again.
Calculated residual moisture in air dried subsamples was 8.99 % (below-ground-biomass), 8.79 % (stem) and 7.36 % (leaf). Dry weights of the air-dried biomass are corrected by these percentages.
Tuber samples were dried in an oven for 72 hours at 80 °C and weighted.

2.10.4. Root architecture

To get further information about the root architecture, several parameters were examined at each harvest: root system width, maximum root length, average root length.
Parameters were measured with a 50 cm ruler (Artesco, plastic). To measure root system width, root was held straight, and width was measured on the widest side. Average root length was measured from root crown up to the point where the majority of the roots ended (defined as average root length). Maximal root length was measured from root crown till the tip of the longest root.

2.10.5. Predawn leaf water potential

At each harvest leaf water potential of the five genotypes was determined by using a Scholander pressure chamber. Leaf water potentials were taken predawn, from approximately 4.30 - 5.30 a.m.. The third-fully expanded leaf on the main stem was detached from the harvest plant with a razor blade, to get a clear cut and avoid tissue injury. To minimize water losses, the detached leaf then was stored in a multi-lock plastic bag and cooled with ice until analysis.

Figure 43: Predawn leaf water potential measurement with a pressure chamber (Scholander type).

Leaf water potential of detached leaves was measured according to the method of Scholander *et al.*, 1965 (Figure 43). After analysis, leaves were put back into the multi-lock plastic bags and cooled with ice, as they were further used for SLA determination.

2.10.6. Specific Leaf Area

To study the specific leaf area (SLA) of potato plant leaves under drought stress conditions, SLA was determined at each harvest date. To investigate whether SLA varies for different levels of leaves, the third-, sixth- and ninth-fully expanded leaf of main stem from the harvest plant were sampled.

SLA-leaves were detached shortly before the plant was harvested, stored in multi-lock-plastic bags (Rubin, 1liter) and cooled with ice to minimize the effects of shrinkage and respiration. Since leaf water potential and specific leaf area needed to be examined on the third-fully expanded leaf, both of them were taken from the same leaf.

Prior to leaf area scanning, leaflets were separated from stems. Leaf area was compiled by using a Scanner (CanonScan LiDe 110; Canon). Each leaf was analyzed separately, by placing the separated leaflets on a blank paper in a transparent plastic folder (Figure 44). At this, care needed to be taken that there was no overlapping between the leaflets to gain full leaf area. The plastic sheeting was necessary to flatten curled leaves. When the arrangement of the leaflets was satisfying, the plastic sheet was put on the contact surface

of the scanner and scanned. Scanned Images of leaflets are later analysis with the analytical software ImageJ. Thereafter samples were stored in paper bags (# 5 50LB Hardware bags, 250/BD; Unline) for drying. After at least 3 weeks of air drying, leaf dry weight was measured with an analytical balance (MRC Ltd., model ASB-220-C2; d = 0.1 mg) (Figure 45).

Figure 44: Leaf area for SLA calculation was measured by placing the separated leaflets in a plastic sheet and scanning the sample.

Figure 45: Leaf dry weight measurement for SLA calculation.

2.11. Determination of phenological stage

Genotypes did not only differ in morphological aspects but also in the rate of development. Therefore, it was important to regularly determine the current development status of the respective genotype.

Based on a Data Scale Sheet by CIP and the BBCH Scale of Hack *et al.* (1993), an evaluation scale was defined to determine the different development stages of the potato genotypes (App. Table 8).

Parameters like plant growth habitat, canopy cover, tuber development and tuber size, status of inflorescences, flowering, formation of berries and senescence were evaluated. Parameters were evaluated on all plants of one plot, except the two parameters concerning tuber development. To avoid injury of below-ground plant parts, tuber development and tuber size were determined on two representative border plants of the plot .Determination of the current phenological development was conducted always one day before harvest (5, 15, 25 DAWI).

2.12. Stress severity index

Since irrigation was withheld at different development stages, plants' transpirational capacity was different and thus stress severity experienced by the plant varied with the treatments. A stress severity index was developed relating the soil water deficit to the treatments and the genotypes relative to fully watered conditions.

For the calculation of the stress severity index, only water that is available for plants is considered. Therefore, the useable field capacity is determined by estimating the field capacity (FC) and the permanent wilting point (PWP) by using the retention curve of Schröder (1984).

Retention curves usually consist of three slopes for sand, silt and clay, respectively. FC and PWP for these three main soil types can be figured out by simply reading the volumetric water content values at pF 4.2 (PWP) and at pF 1.8 (FC) on the three slopes. Usable field capacity is then derived by subtracting volumetric soil water content at PWP from that at field capacity (1). Volumetric water content values at FC obtained from the retention curve of Schröder (2008) are 48 Vol % (clay), 38 Vol % (silt) and 11 Vol % (sand). At PWP, values for clay, silt and sand were 32, 17, 3 Vol %.

Usable field capacity = field capacity – permanent wilting point (1)

In this study, the soil was a loamy sand with averagely 81.2 % sand, 10.6 % silt and 8.2 % clay. To estimate FC and PWP for this soil, the formulas (2, 3) together with the values received from the retention curve of Schröder (2008) was used.

Vol % (**FC**) = **x** * (Vol % (FC) sand) + **y** * (Vol% (FC) silt) + **z** * (Vol% (FC) clay) (2)

Vol % (**PWP**) = **x** * (Vol % (PWP) sand) + **y** * (Vol% (PWP) silt) + **z** * (Vol% (PWP) clay) (3)

The variables x, y, z represent the percentage of sand, silt and clay in the soil. Adding these percentages into the formula results in an estimated volumetric water content at FC of 16.9 Vol % and at PWP of 6.9 Vol %.

In order to consider only soil water that is available for plants, soil water content data need to be transformed. As soil water below PWP cannot be extracted by plants, the estimated volumetric water content at PWP (6.9 Vol %) is subtracted from the soil water content. The adjusted water content values are then added to the formula (4)

$$\textbf{Stress value} = \frac{(e^{((10.034-xadj)/10.034)}-1)}{(e^{1}-1)} \quad (4)$$

to calculate stress values, where *xadj* are the adjusted soil water content values in Vol % and 10.034 the usable field capacity (16.9 Vol % (FC) – 6.9 Vol % (PWP)). Stress values range between 0 and 1, with 1 meaning highest stress intensity, and 0 meaning no stress. When soil water content exceeds usable field capacity (values > 10.0), stress values become negative. These values are then set zero, because this water is part of percolating water.

During treatments, soil water content was determined in three day intervals. To be able to calculate stress values for 0 to 26 DAWI, data set was complemented via linear interpolation.

Stress severity index for a specific day is then calculated according to formula (5) as the sum of stress values from 0 days after initiation of stress (d= 0) to the desired day after initiation of stress (dn).

$$\textbf{Stress severity index} = \sum_{d=0}^{dn} \frac{(e^{((10.034-xadj)/10.034)}-1)}{(e^{1}-1)} \quad (5)$$

2.13. Statistical analysis

To be able to compare the effect of drought on the investigated parameter of the five genotypes, data was normalized by calculating relative values. Relative values were derived by relating mean parameter values (mean of three replications) under drought conditions to that under fully-irrigated conditions and by this obtaining % of control values:

$$\mathbf{X}\ \%\ \text{of control} = (\ \mathbf{X}_{\text{Control}} / \mathbf{X}_{\text{Drought}}) \times 100$$

where **X** is the parameter investigated, either under control ($\mathbf{X}_{\text{Control}}$) or drought condition ($\mathbf{X}_{\text{Drought}}$).

To further relate changes under drought conditions to drought stress severity, relative values were plot against calculated stress severity index, and regression lines were fit, using Microsoft Office program Excel (Version 2007). The significance of the coefficient of determination (R^2) was tested by using the formula:

$$t_{Vers} = \frac{|r|}{\sqrt{1 - r^2}} \sqrt{(n-2)}$$

where r^2 is the coefficient of determination and n is the number of data points. The calculated value t_{Vers} is then compared to a critical t-value (two-sided) at $\alpha = 0.05$ significance level.

When data is presented in absolute values, mean of three replication and standard error of the means is calculates.

3. Results

3.1. Phenological development

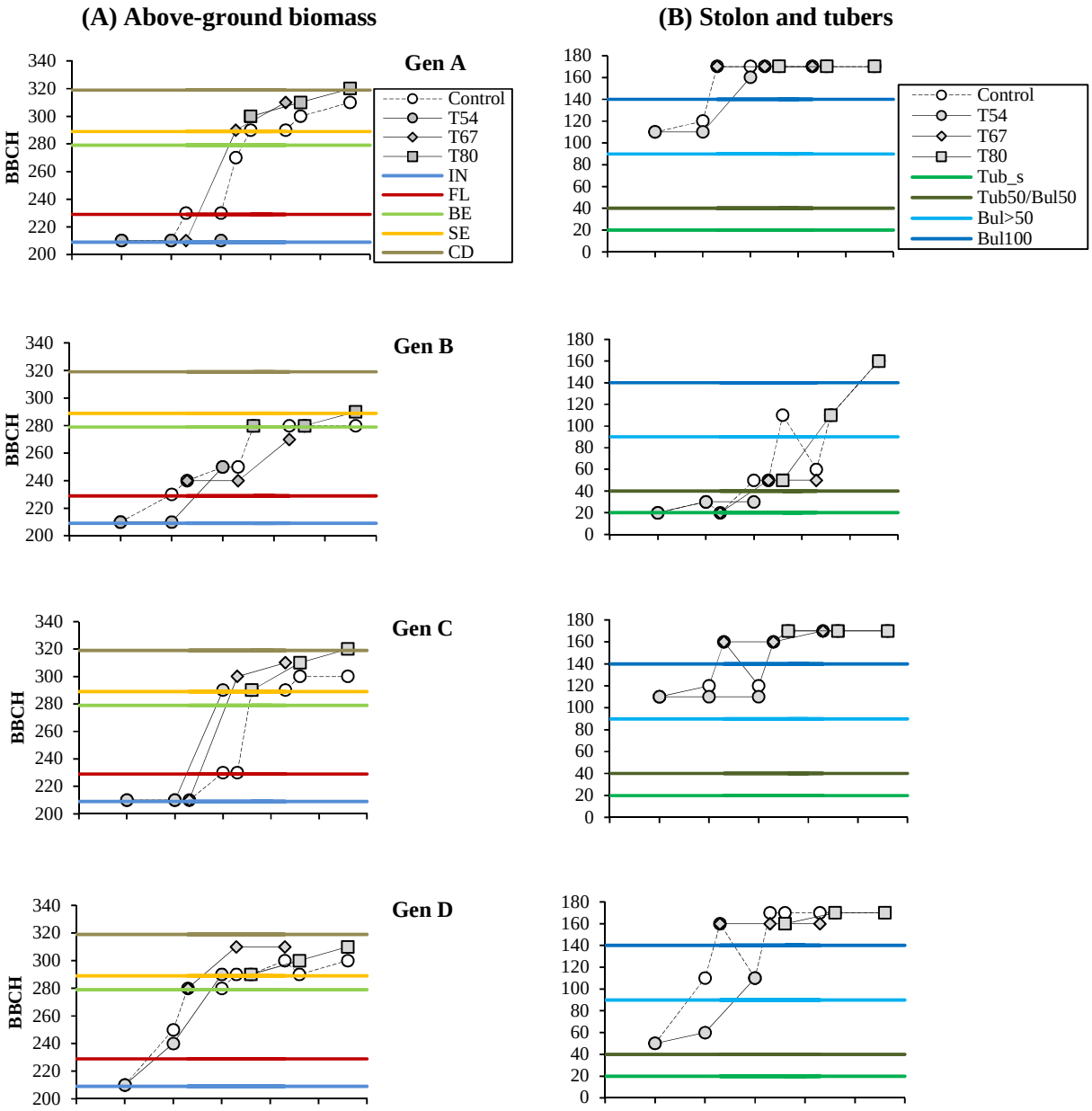
Based on the evaluation scale used for phenological development determination, a BBCH code was established to classify the different development stages of the five potato clones. Detailed BBCH code for classification is provided in the appendix in Table 9. BBCH code labeled with “A” refers to development stage of the above-ground biomass and code labeled with “B” describes below-ground parameters like stolons and tubers.

Genotypic differences in terms of phenological development were observed among all five genotypes (Figure 46). Gen A and C did not form berries under well-watered conditions nor drought, although some flowers were built under well-watered condition. Flowering was weak in control plants of these two genotypes and often only 1-3 plants per plot formed flowers. Under fully-irrigated conditions, Gen A, C and D showed senescence of above-ground biomass earlier than Gen B and E. Control plants of Gen A and C displayed senescent characters at 86 DAP and Gen D at 83 DAP, whereas in Gen E, start of senescence was evaluated at 96 DAP. In control plants of Gen B, yellowing of leaves occurred later than 106 DAP as no senescence was detected during the experimental period. At the first harvest (6 DAWI, T54), control plants of Gen A and C already had more than 50 % of tubers/tuber initials at bulking stage (B110) whereas Gen D and E had 50 % of tubers /tuber initials at tuberization stage and 50 % at bulking stage (B50/B60). Plants of Gen B germinated much later than plants of the other genotypes. At 6 DAWI in T54, tuberization had only started in this genotype.

Drought stress slowed down phenological plant development in potato genotypes. In Gen B, D, E drought delayed development during formation of inflorescences, flowering as well as in stolons and tubers. After termination of flowering, plant development was found to be accelerated by drought in comparison to control. Owing to dry out of inflorescences, flowering in plants of Gen A and C was inhibited by drought and plant development was found to be accelerated by drought earlier than in Gen B, D and E. Under drought stress, start of senescence was recorded earlier than in control plots, at 83 DAP (16 DAWI; T67)

in Gen A, at 80 DAP (26 DAWI; T54) in Gen C and D and at 93 and 106 DAP (26 DAWI; T54; T67) in Gen E and B.

In the following sections, genotypes will be grouped according to the senescence characteristics. Gen A, C, and D will further be referred to as early senescencing genotypes, and Gen B and E as late senescencing genotypes.



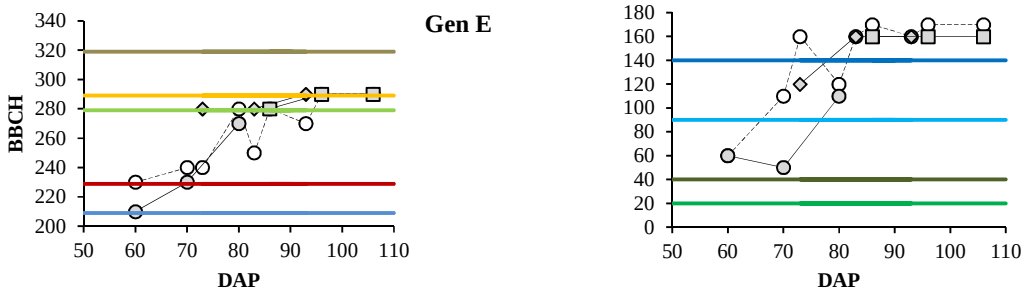


Figure 46: Phenological development of A) above-ground biomass and B) stolons and tubers of five potato genotypes under fully-irrigated and drought stress conditions. Irrigation was withheld 54 (T54), 67 (T67), and 80 (T80) days after planting (DAP). Colored horizontal lines represent start of principal growth stages (IN= inflorescences; FL= flowering; BE= Berries; SE= senescence; CD= canopy death; Tub_s= tuberization start; Tub50/Bul50= 50% of tubers at tuberization stage and 50% at tuber bulking stage; Bul>50= more than 50% of tubers at tuber bulking stage; Bul100= all tubers at bulking stage).

3.2. Stress severity index

Drought stress severity experienced by the potato plants varied between treatments and genotypes (Figure 47). Calculated SSI values were higher in T67 and T80 compared to T54. The higher water use probably resulted from the higher evaporative demand (higher temperatures, lower rH) in the late treatments and increased canopy size/transpirational surface.

In the early drought treatment water usage patterns were similar among the five potato genotypes (Figure 47 a)). However, at treatment end, highest SSI was calculated for plants of Gen C, and lowest for plants of Gen B and D. In T67, late senescencing genotypes were highly depleting soil water and suffered highest stress severity 26 DAWI (Figure 47 b)). Water usage in early senescencing genotypes was lower. By far highest soil water depletion in late drought treatment (T80) was found in late senescencing Gen E (Figure 47 c)). Right from treatment start, water usage in plants of this genotype was clearly higher compared to the other genotypes. Lowest water use in T80 was found in Gen A and B.

In all treatments, SSI was very low in the first days after withholding irrigation. Therefore stress severity was not high at first sampling occasion (6 DAWI) but then considerably increased with time. However, SSI development of potato genotypes varied between treatments, indicating that soil water usage patterns were genotype and development stage dependent.

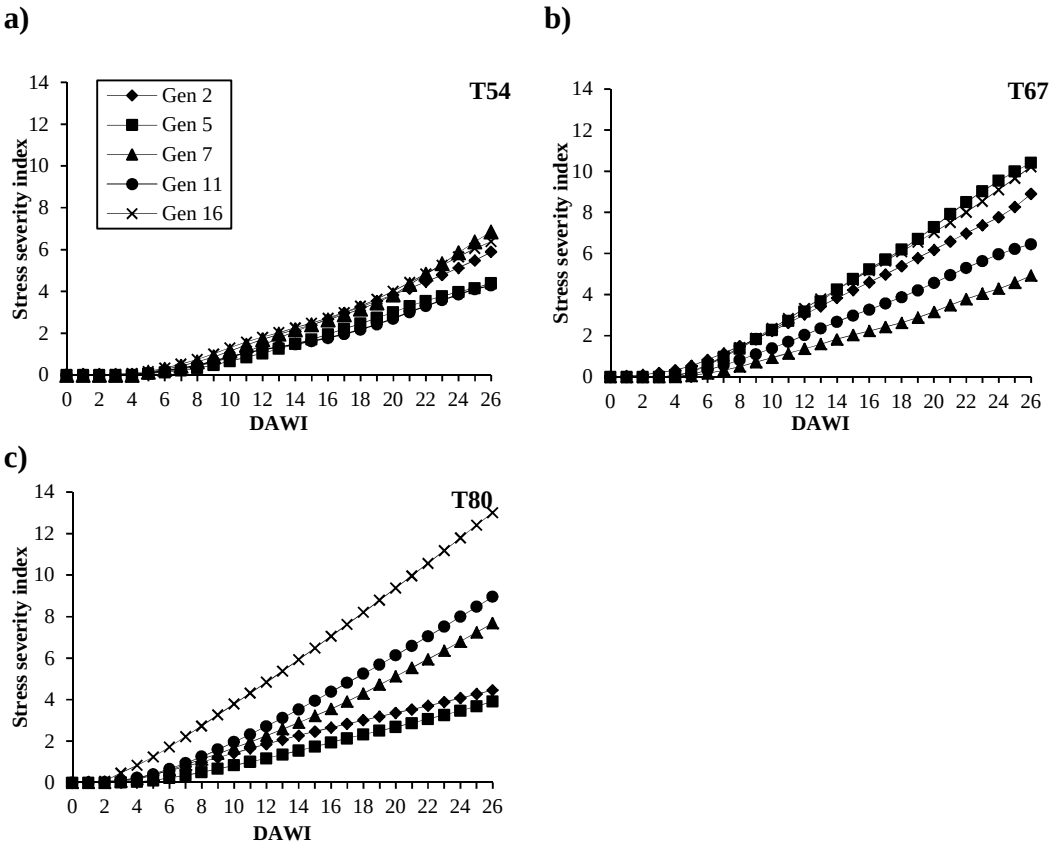


Figure 47: Increment of stress severity index over time (in days after withholding irrigation (DAWI)) in five potato genotypes. Irrigation was withheld a) 54 DAP (T54), b) 67 DAP (T67) and c) 80 DAP (T80).

3.3. Biomass

The five potato genotypes differed in weighting of their plant components (Figure 48): Across sampling occasions, mean leaf dry weight (DW) under fully-irrigated conditions was 18.6±1.9 and 19.6±2.1g plant^{-1} in the early senescencing genotypes A and C, and 31.8±3.9, 34.8±2.2 and 31.1±3.9 g plant^{-1} in Gen B, E and D (Table 10). With 31.5±4.6 (Gen B) and 22.2±2.1g plant^{-1}(Gen E), late senescencing genotypes produced on average higher stem dry weight (DW) under fully irrigated conditions than early senescencing genotypes, where mean stem DW was 9.0±1.0 (Gen A), 8.2±1.2 (Gen C), 13.4±1.5 g plant^{-1}(Gen D). Below-ground biomass (BGB) in control plots, on average, was highest in in late senescencing Gen B with 10.5±1.1 g plant^{-1}, followed by Gen E and D with averagely 7.4±0.5 and 6.9±0.9 g plant^{-1}. The early senescencing genotypes A and C produced lowest BGB under fully-irrigated conditions among genotypes of averagely 3.5±0.4 and 4.7±0.5 g plant^{-1}. Tuber dry weight (tuber DW) typically increased throughout experimental period in all genotypes (Figure 72, App.). Mean tuber dry weight in control plots was 121.5±15.9, 127.5±22.9 and 140.4±30.0 g plant^{-1} in early senescencing genotypes A, C, D and 50.4±16.3 and 121.8±15.7 g plant^{-1} in late senescencing genotypes B and E.

Drought diminished plant biomass and their components. When comparing effect of drought at 26 DAWI in T54, T67 and T80 plant total biomass (PTB) was most affected in T54 and least in T67 (Table 11). Across genotypes, PTB was reduced by 53 % of control at 26 DAWI in T54 and by 25 and 38 % in T67, T80, respectively. Drought stress at 26 DAWI in T54 most affected tuber DW in comparison to fully-irrigated control, and reduced tuber DW by 65 % of control. Leaf DW was the component that was reduced most by drought at 26 DAWI in T67 and T80.

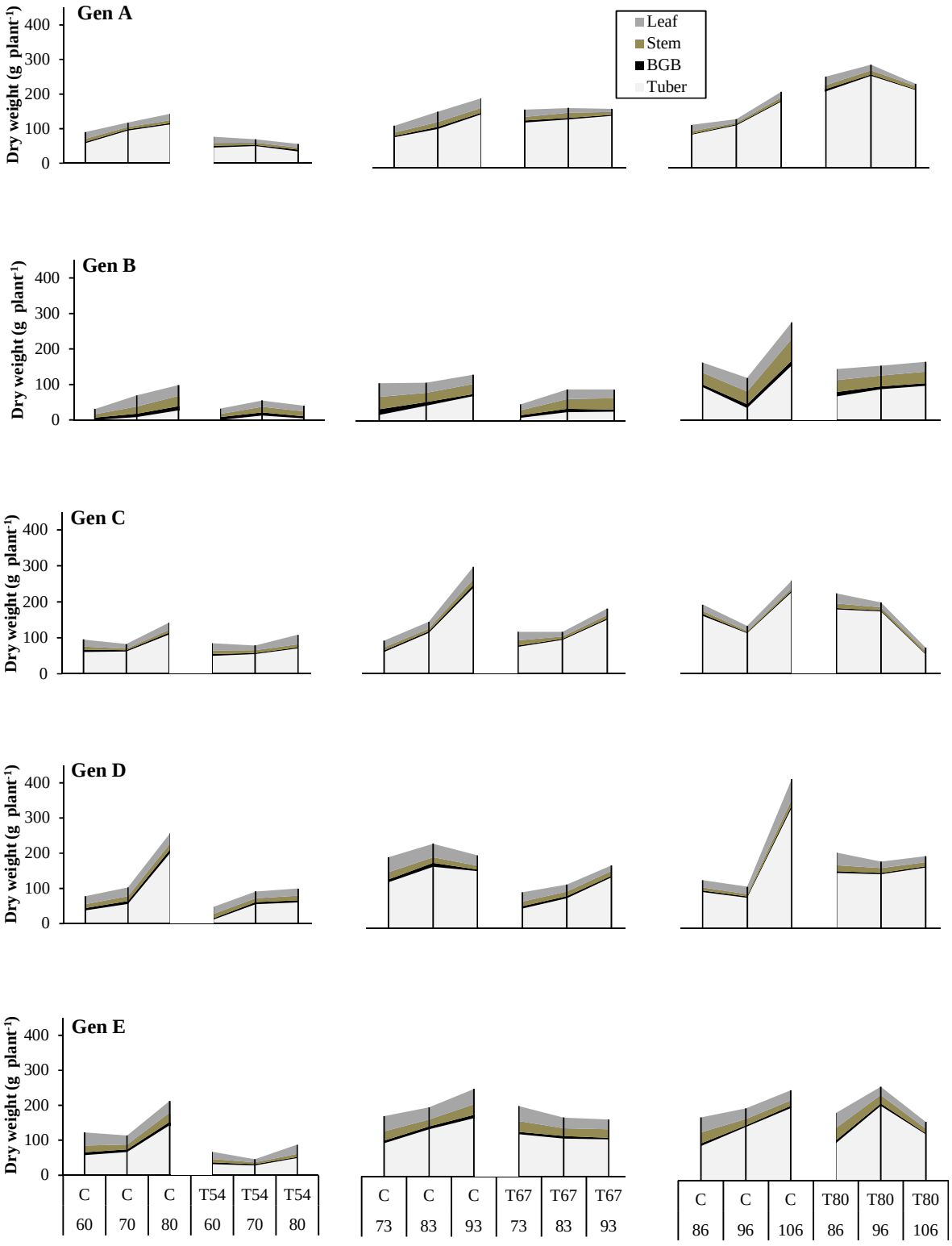


Figure 48: Changes in leaf, stem, below-ground biomass (BGB) and tuber dry weight (g plant^{-1}) over time under fully-irrigated (C) and drought stress conditions (T54, T67; T80)) of five potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting. Graphs represent mean values (n=3).

3.4. Dry mass partitioning and Harvest index

Harvest index ranged from 0.00 (Gen B) to 0.93 (Gen A) and increased throughout the experimental period, in control plots as well as in drought stress plots (Figure 49). Mean HI in control plots of early senescencing genotypes was 0.79±0.02 in Gen A, 0.77±0.07 in Gen C and 0.69±0.09 in Gen D. In late senescencing genotypes, mean harvest index in control plots was 0.33±0.04 in Gen B and 0.63±0.04 in Gen E and therefore lower than in early senescencing genotypes. Mean share of leaves and stems under fully irrigated conditions was lowest in the early senescencing genotypes A and C, with 13±1.5 and 14±1.5 % of biomass allocated in leafs and 6±0.7 and 6±0.8 % allocated in stems. Gen D and E on average allocated 14±1.5 and 20±2.0% in leaves and 8±1.2 and 13±1.4 % in stems under fully irrigated conditions.

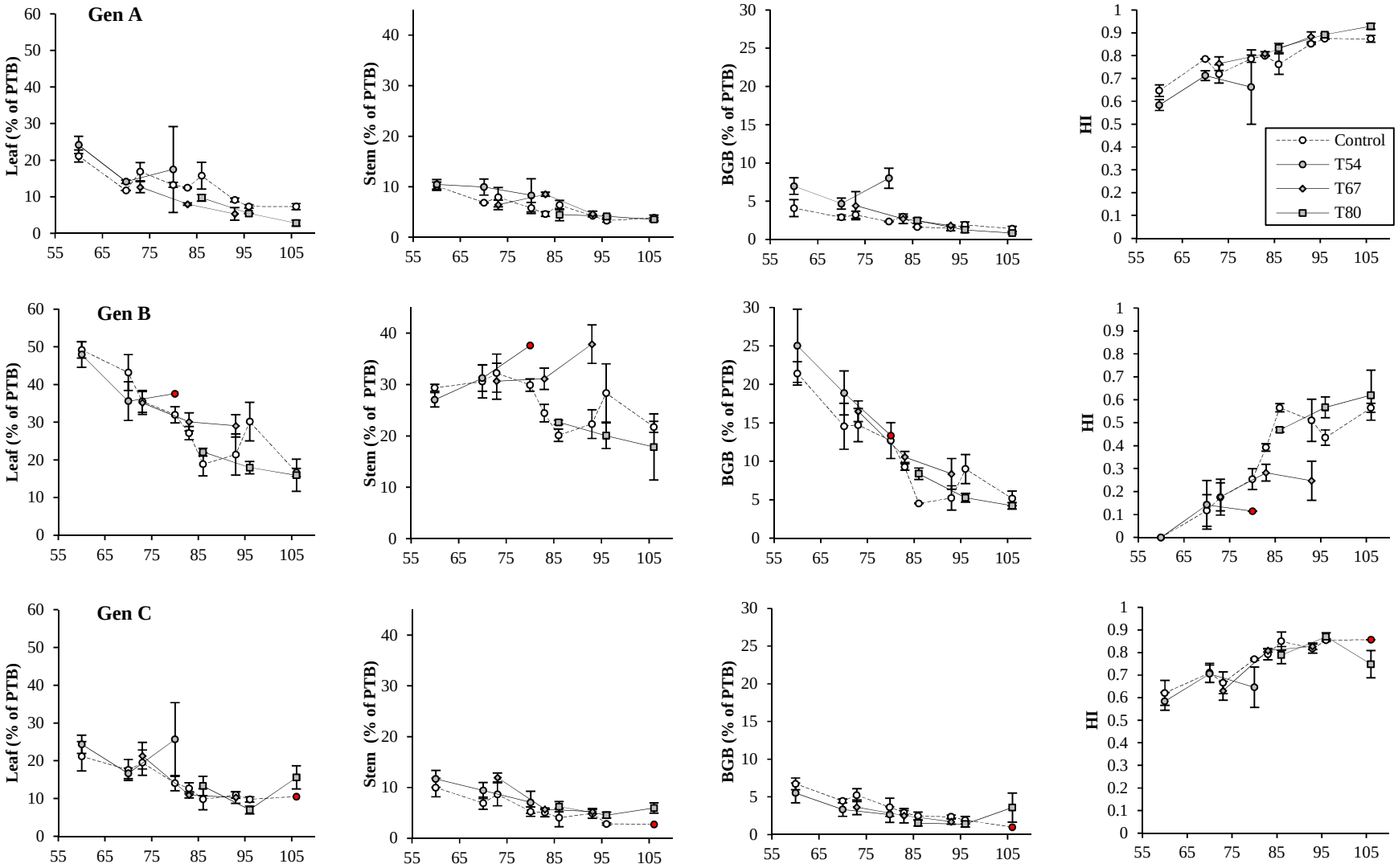
Drought stress affected partitioning of photosynthates in all genotypes, but the effect of drought varied depending on the time in which it occurred.

Early drought stress in T54 decreased HI in all genotypes compared to fully-watered conditions, except in Gen E. However, differences between treatments became often only apparent at SSI ≥ 4.3 at 26 DAWI (Figure 49; Figure 71 a), App.). HI was reduced by 55 % in Gen B, and by 16 and 19 % compared to control in Gen C and D. In Gen B, leaf and stem ration was increased by 6 and 8 % and in Gen D partitioning into stems and BGB was increased by 5 and 3 %. At 26 DAWI, Gen C and D were at development stage B110 (Bul>50), which indicates susceptibility to high SSI when part of tubers were still at tuberization stage and redirection of assimilates away from tubers. The high reduction of HI in Gen B 26 DAWI indicates high susceptibility to drought during tuberization (B30) and competition for assimilates during flowering (A250). In the early senescencing Gen A, HI was reduced by 9-10 % of control already under lower SSI at 6 and 16 DAWI, but not at 26 DAWI. At all three sampling occasions partitioning in BGB was increased by 2-5 % and at 16 DAWI partitioning into leaves and stems increased by 2 and 3 %. Results might indicate lower sink strength of tubers at B110 (6, 16 DAWI) in comparison to B160 at 26 DAWI.

When irrigation was withheld 67 DAP (Figure 49; Figure 71 b); App.), reduction in HI was calculated for Gen E at low SSI at 6 DAWI and Gen B at higher drought stress level at 16

and 26 DAWI. In Gen E, HI was reduced by 9 % compared to control and in Gen B by 28 and 52 % of control at 16, 26 DAWI, respectively. The decrease in HI in Gen E at 6 DAWI again indicates higher susceptibility to drought, when part of tubers are still at tuberization (B120) compared to the situation when all tuber are at bulking stage (> B140). In addition, plants of Gen E were forming berries (A280) at 6 DAWI, and leaf and stem ratio increased by 3 and 4%, indicating competition for assimilates during berry formation. Early senescencing genotypes displayed senescence characteristics (A≥290) at 16 DAWI. HI was unaffected by drought stress in these genotypes and in Gen A, partitioning into leaves was reduced by 4 - 5% at all sampling occasions. High reduction in HI and the increase in stem ratio (7 and 16 %) under drought in Gen B again indicates susceptibility to water shortage during flowering (A240-A270) and tuberization (B50 (50% at tuberization stage)). Additionally, high SSI at 26 DAWI had a stronger effect on HI than stress severity level at 16 DAWI.

Late drought stress (T80) increased assimilate supply to tubers in early senescencing Gen A and D by 6 and 14 % in comparison to control at SSI ~ 4.4 (26, 16 DAWI) (Figure 71 c), App.; Figure 49). Plants of these genotypes were at development stage B170, i.e. all tubers were at bulking stage and at development stage A310/A320 (senescence). Increased partitioning to tubers under drought stress indicates high sink strength of tubers and remobilization of assimilates during senescence, as leaf ratio was reduced by 2 % (Gen A) and 9 % (Gen D). In Gen B, HI decrease under drought stress by 17 % of control when 50% of tubers/tuber initial were at tuberization stage (B50) (6 DAWI) and increased by 30 % when more than 50 % of tubers were at bulking stage (B110) (16 DAWI). Relatively low sink strength at B50 in combination with preferential assimilate supply to BGB (increased by 4 %) might be reasons for reduction in HI at 6 DAWI. Increase in HI at 16 DAWI came along with a strong reduction in leaf and BGB ratio of 12% and 4%, respectively, and less tubers at tuberization stage compared to 6 DAWI. In Gen C, HI was reduced by 13% compared to control at SSI= 7.7 (26 DAWI) and partitioning into leaves, stems and BGB was increased by 5, 3 and 3% despite the fact that all tubers were at bulking stage (B170).


Gen A
Gen B
Gen C
Leaf (% of PTB)
Stem (% of PTB)
BGB (% of PTB)
HI
Control
T54
T67
T80

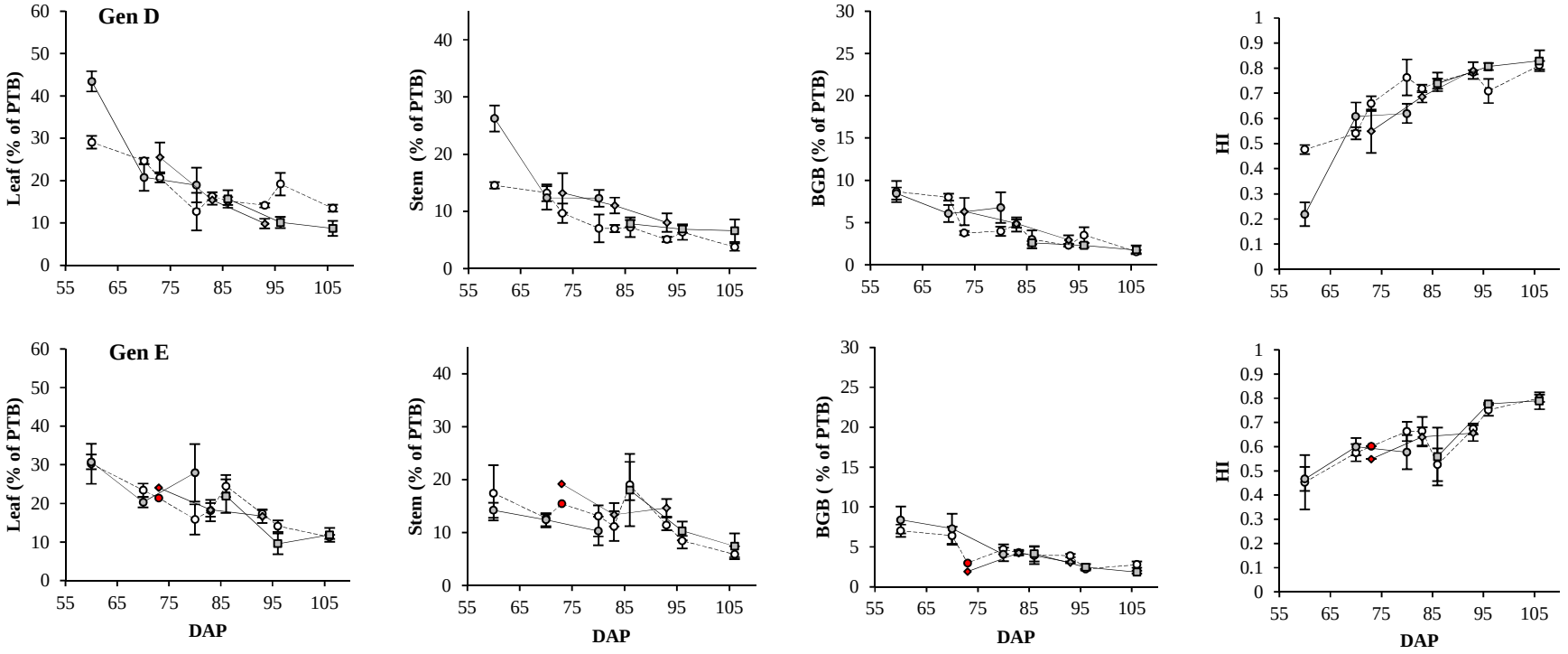


Figure 49: Time-course of dry mass partitioning (% of plant total biomass (PTB)) in leaves, stems and below-ground biomass (BGB= roots and stolons) and harvest index (HI) of five potato genotypes under fully-irrigated (control) and drought stress conditions. Irrigation was withheld at 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean ±S.E. of n=3. Data points marked with red color represents data from one replication

Across genotypes, relative harvest index (HI) decreased under drought (Figure 50). Relative HI was most affected by early drought (T54) and least by late induced drought (T80). Data in Figure 50 shows a decrease in relative HI with increasing level of drought in T67, but when comparing with relative HI on genotype level (Figure 71 b); App.), it gets clear that this trend is mainly due to the high reduction of HI in Gen B.

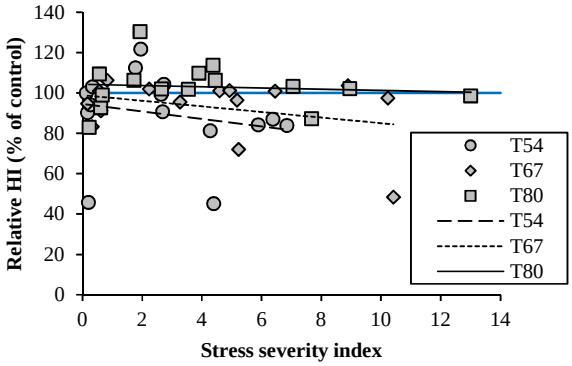


Figure 50: Relationship between drought stress severity index (SSI) and relative harvest index (HI). Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3.

Linear regression equations:
T54: y= - 1.86x + 94.62 R^2= 0.04
T67: y= - 1.40x + 98.97 R^2= 0.11
T80: y= - 0.30x + 104.28 R^2= 0.01

3.5. Effect of drought on tuber parameters

3.5.1. Tuber dry weight

Withholding irrigation at 54 DAP reduced tuber DW in all five genotypes (Figure 51; Figure 72, App.). At 26 DAWI, reduction of tuber DW under drought stress was clearly lower in Gen C than in the other genotypes (Figure 51 a)). In Gen C, tuber DW was reduced by 36 % and by 66-83 % compared to control in the remaining genotypes at SSI≥ 4.3. In Gen A and E, reduction in tuber DW under drought already became apparent at lower SSI of ~ 2.7 (16 DAWI). Tuber DW was reduced by 48 (Gen A) and 58 % compared to control (Gen E). However, at 26 DAWI, reduction of tuber DW was highest in Gen B, but under lower stress severity at 16 DAWI, tuber DW was unaffected by drought in this genotype. This strong response to drought relative to control plots at 26 DAWI might be due to delayed development of BGB, as stressed plants of Gen B were still in tuberization during that time.

Drought stress in T67, affected only tuber DW of genotypes that were flowering under drought and were forming berries, i.e. Gen B; E; D (Figure 51 b); Figure 72, App.). Tuber DW in late senescencing genotypes was reduced by 63 % (Gen B) and 37 % (Gen E) at 26 DAWI, by 58 and 52 % compared to control in Gen D at 6 and 16 DAWI. Gen B was at development stage A270 (end of flowering), Gen E at A280 (Berries) and Gen D at A280 and at A310 (berries/senescence) at 6 and 16 DAWI. Reduction in tuber DW under drought at flowering/berry formation might indicate a change in the assimilate supply in favor of flowers and berries.

Drought stress in T80 increased tuber DW by 40-117% compared to control at 16 DAWI in all genotypes, except Gen C (Figure 51 c); Figure 72, App.)). The increase in tuber DW was highest in genotypes that were exposed to lowest SSI at that sampling occasion. Withholding irrigation at 80 DAP accelerated plant development and speed up or induced senescence in potato plants. In combination with intermediate drought stress at 16 DAWI, this might have led to the strong increase in tuber DW. This can also be seen in Gen A at 6 DAWI, where tuber DW increased by 130 % compared to control as most leaves were yellowish (A300). However, tuber DW decreased substantially in all genotypes, except Gen A, as drought stress became more severe at 26 DAWI. Tuber DW decreased by 37 and 36 % in late senescencing genotypes and by 76 and 50 % compared to control in Gen C and D.

As can be seen in Figure 51 d), drought stress had different effect on tuber DW depending on the time in which it occurred. Tuber DW reduction was highest under the early drought (T54) and lowest under the late induced drought (T80). This indicates higher sensitivity of potato genotypes to drought stress applied at tuber initiation/early tuber bulking stage. The increased tuber DW under drought stress relative to control in T80 was accompanied by highest reduction in relative tuber DW per increase in SSI among all three drought stress treatments.

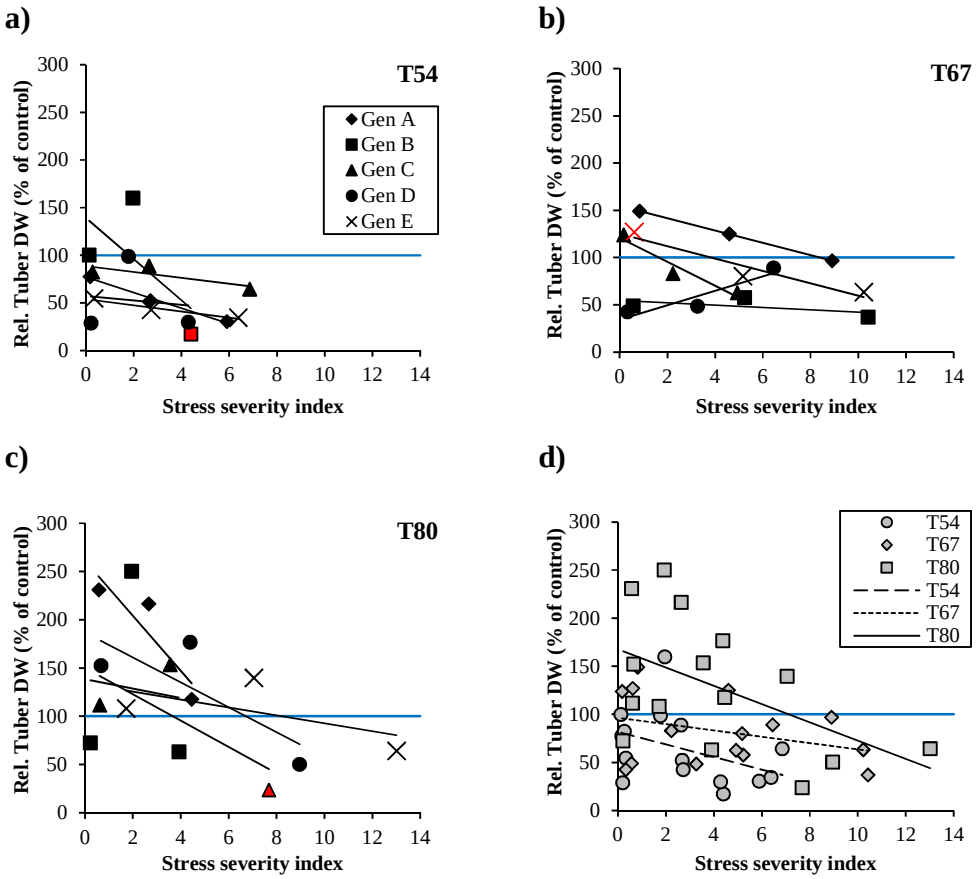


Figure 51: Relationship between drought stress severity index (SSI) and relative tuber dry weight (DW) in five potato genotypes. Irrigation was withheld a) 54 (T54), b) 67 (T67) and c) 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. In d) linear regression lines were fit to relative values of all genotypes in T54, T67 and T80. Significance level of regression coefficient: *P< 0.05. Data points marked with red color represent data from one replication.

Linear regression equations:

a)
Gen A: y= -8.17x + 77.24 R^2=0.99;
Gen B: y= -21.54x + 138.94 R^2= 0.41;
Gen C: y= -3.08x + 88.51 R^2=0.66;
Gen D: y= -2.29x + 57.24 R^2=0.01;
Gen E: y= -3.24x + 53.96 R^2=0.95

b)
Gen A: y= -6.50x + 154.81 R^2=1.00*;
Gen B: y= -1.26x + 54.79 R^2= 0.36;
Gen C: y= -12.62x + 120.78 R^2=0.93;
Gen D: y= 7.69x + 34.21 R^2=0.86;
Gen E: y= -5.894x + 127.65 R^2=0.96

c)
Gen A: y= -28.59x + 261.46 R^2=0.81;
Gen B: y= -4.894x + 138.50 R^2= 0.01;
Gen C: y= -13.658x + 150.08 R^2=0.54;
Gen D: y= -12.89x + 186.63 R^2=0.64;
Gen E: y= -4.07x + 133.59 R^2=0.37

d)
T54: y= - 6.55x + 81.89 R^2= 0.17
T67: y= - 3.28x + 96.36 R^2= 0.11
T80: y= - 9.51x + 167.63 R^2= 0.26

3.5.2. Final tuber dry weight

Drought stress reduced final tuber DW in all genotypes. Reduction was highest in T54 (Table 7), what is not surprising, as potato genotypes were exposed to longest period without irrigation in this treatment. Final tuber dry weight of control plants at 125 DAWI ranged between 144.2±34.9 (Gen C) and 232.3±16.6 g plant^{-1} (Gen D) (Figure 52).

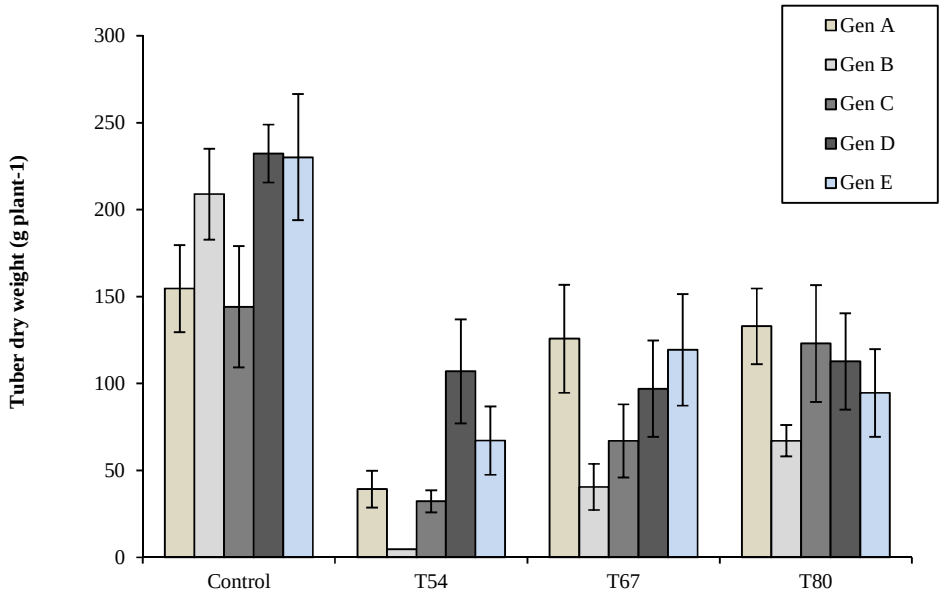


Figure 52: Final tuber dry weight (g plant^{-1}) of five potato genotypes at 125 days after planting (DAP) under fully-irrigated (Control) and drought stress conditions. Irrigation was withheld 54 (T54), 67 (T67) and 80 DAP (T80). Bars represent mean value ±S.E. (n=9).

Among genotypes, reduction under drought stress in comparison to control was highest in the genotype that was at tuberization stage during treatment start, i.e. Gen B. Withholding irrigation at 54 DAP reduced final tuber DW by 98 % compared to control in Gen B, by 71-78 % in Gen A, C and E and by 54 % in Gen D. In T67 lowest reduction of 19 % compared to control was found in Gen A and highest again in Gen B (reduction of 81% compared to control). In Gen C, D and E, tuber DW was reduced by 48-58 % of control. Withholding irrigation at 80 DAP did not have a strong

Table 7: Relative tuber dry weight of five potato genotypes 125 days after planting (DAP). Irrigation was withhold 54 (T54), 67 (T67) and 80 DAP (T80).

	Relative tuber dry weight (% of control)		
Genotype	**T54**	**T67**	**T80**
A	25	81	86
B	2	19	32
C	22	46	85
D	46	42	49
E	29	52	41

impact on final tuber DW of Gen A and C, as final tuber DW was only reduced by 14 and 15 % compared to control. In Gen B, D and E final tuber DW was reduced by 68, 51 and 59 % compared to control, and therefore reduction was clearly higher than in Gen A and C.

3.5.3. Tuber number and area

Under fully irrigated as well as under drought stress conditions, plants of early senescencing genotypes produced larger tuber than plants of late senescencing genotypes (Figure 53). Mean tuber area in control plots was 35.2±2.1, 25.7±1.9 and 26.4±2.5 cm^2 $plant^{-1}$ in Gen A, C, D and 11.4±2.3 and 22.4±1.6 cm^2 $plant^{-1}$ in Gen B and D. Mean tuber number in control plots was highest in Gen E with 24±2.5 tubers $plant^{-1}$. Tuber number was lower in Gen A, B, C and D, as plants of these genotypes produced on average 12±0.9 (Gen A) - 16±0.8 (Gen D) tubers $plant^{-1}$ under fully-irrigated conditions.

Drought stress during relatively early development stage (T54), did not clearly affect tuber number of early senescencing genotypes (Figure 53; App. Figure 76). In late senescencing genotypes, tuber number was reduced by drought, but tuber number was only clearly lower than control at high stress intensity at 26 DAWI. Under drought stress, plants of all genotypes produced smaller tubers and reduction in tuber area was found already at 6 or 16 DAWI. Effect of drought on tuber number and area was strongest in Gen B as tuber number and area decreased both by 82 % compared to control.

Withholding water at 67 DAP (T67) did not have high impact on tuber number of the five genotypes. Only among early senescencing genotypes response to drought could be detected. At 16 DAWI tuber number in Gen C was reduced by 26 % compared to control, and at 26 DAWI by 49 % in Gen C and by 19 % in Gen D (Figure 53; App. Figure 76). Contrary, tuber area was only affected by drought in late senescencing genotypes and Gen D. Tuber area in late senescencing genotypes was reduced by 39 % (Gen B) and 32 % (Gen E) compared to control at 16 DAWI and by 68 % (Gen B) and 28 % compared to control (Gen E) at 26 DAWI . In Gen D tuber area was reduced by 26 % compared to control at 26 DAWI. The high reduction in tuber area of Gen B in comparison to Gen E might again shows the higher sensitivity of early development stages to drought stress. At

26 DAWI, Gen 5 had 50 % of tubers/tuber initials at bulking stage (B50) and 50% at tuberization, whereas Gen E was completely in tuber bulking (B160).

In T80, only high drought stress severity at 26 DAWI reduced tuber number, and just in early senescencing genotypes A and D (Figure 53; App. Figure 76). Tuber number was reduced by 53% in Gen A and by 32 % of control in Gen D. Tuber area was decreased by 37 % in Gen C, by 29 % in Gen D, by 30 % in Gen B and by 42 % compared to control in Gen E by high drought stress severity at 26 DAWI.

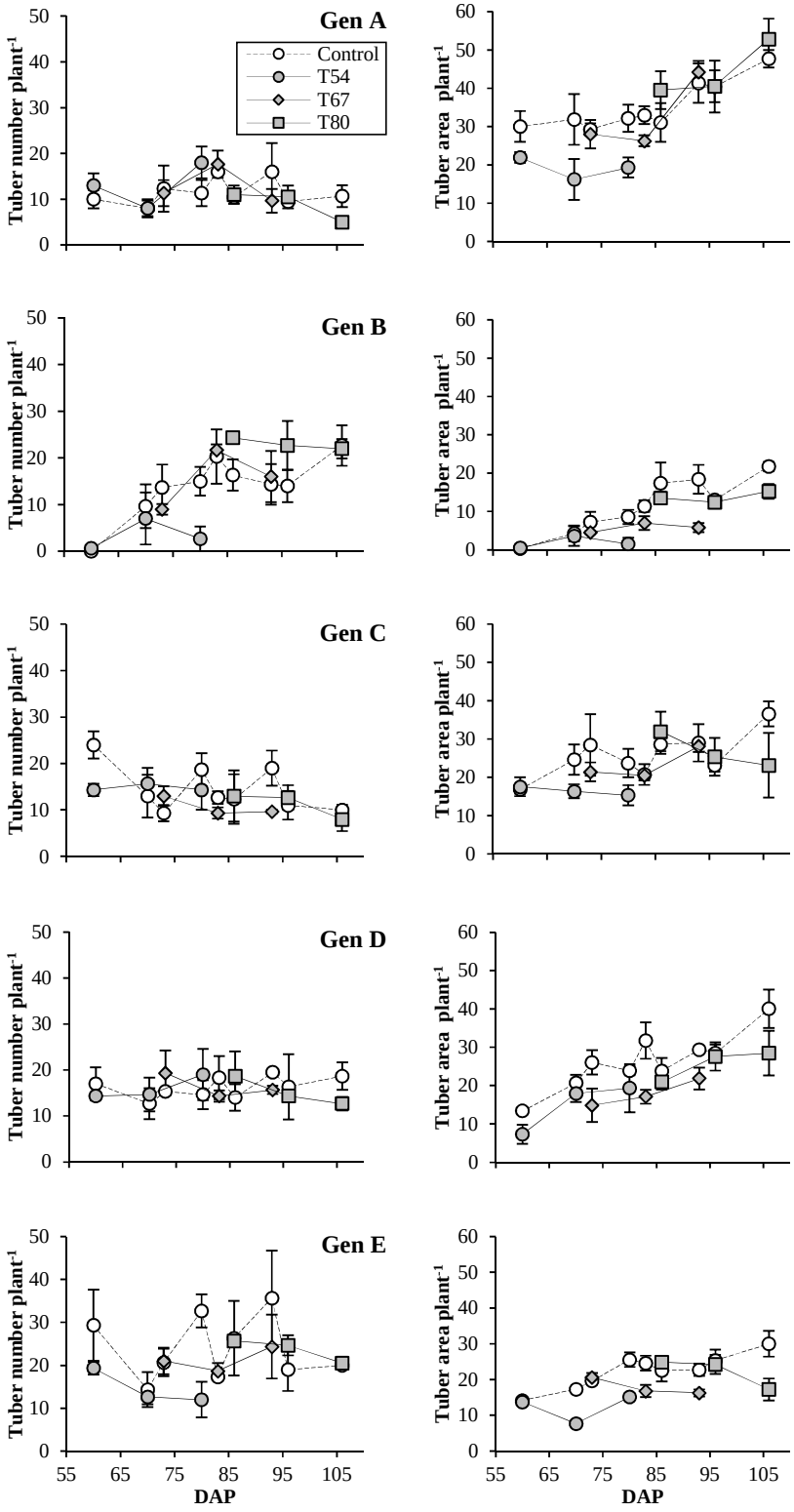


Figure 53: Changes of tuber number (plant^{-1}) and tuber area (cm^{-2} plant^{-1}) over time in fully-irrigated and droughted plants of five potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. (n=3).

As can be seen in Figure 53 and Figure 54 in all treatments, tuber area was more affected by drought stress than tuber number. Across genotypes, tuber number in T54 was already reduced by drought at low SSI, whereas during late drought stress in T80, tuber number was only reduced at SSI>4.0 (Figure 54 a)). However, response to drought (reduction per increase in SSI) was strongest in T80. Also tuber area (across genotypes) was strongest affected by early drought stress in T54 (Figure 54 b)). Here, tuber area was already reduced at low SSI and further declined with increasing SSI. In T67, tuber area was also shown to be reduced at low SSI but response to drought was weak. Across genotypes, tuber area under late drought stress (T80) was reduced at SSI> 2.0, but response to drought was lower than in T54. However, relative tuber size in T80 decreased linearly with increasing SSI.

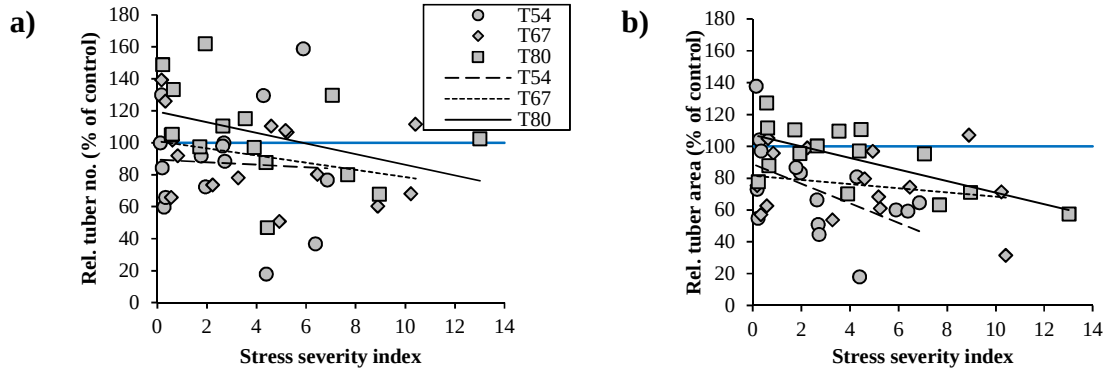


Figure 54: Relationship between drought stress severity (SSI) and relative tuber number and tuber area in potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. Significance level of regression coefficient: ** P<0.01.

Linear regression equations:

a)
T54: y= -0.79x + 89.48 R2= 0.00
T67: y= -2.25x +101.10 R2= 0.10
T80: y= -3.33x + 119.59 R2= 0.17

b)
T54: y= -6.31x + 88.73 R2= 0.26
T67: y= -1.33x +81.61 R2= 0.05
T80: y= -3.63x + 107.21 R2= 0.42**

3.6. Leaf area index

LAI was reduced under drought stress in all genotypes and treatments (App. Figure 73). Mean LAI in control plots ranged between 2.4±0.1 and 3.1±0.1. Highest LAI of 3.9 was found in control plots of the two late senescencing genotypes B and E at 76 and 69 DAP. Under drought stress, lowest LAI (>1.2) was found in the early senescencing genotypes A, C and D at the end of T80.

When irrigation was withheld 54 DAP (T54), LAI reduction under drought did not differ substantially between genotypes (Figure 55 a)). At the end of T54 (22 DAWI), LAI was reduced by about 40% compared to control in all genotypes.

During T67, LAI of early senescencing genotypes (A, C, D) were more affected by drought stress than LAI of late senescencing genotypes and declined more rapidly with increasing stress severity (Figure 55 b)). LAI of early senescencing genotypes was reduced by about 60 % compared to control at 22 DAWI, whereas in late senescencing genotypes, LAI was only reduced by 32 % (Gen B) and 25 % in comparison to control (Gen E). As soil water content influences canopy expansion and vice versa, genotypes that maintained LAI (high transpiration surface) under drought stress suffered higher stress severity (higher SSI) than genotypes that reduced LAI. This also can be seen under drought stress in T80 (Figure 55 c)), in late senescencing Gen E, but not in Gen B.

When irrigation was withheld at 80 DAP, a high reduction in LAI by 47-59 % compared to control was found in early senescencing genotypes, already at low SSI of ~1.1. LAI of early senescencing genotypes was further reduced at highest SSI at 22 DAWI, by 73 (Gen A), 65 (Gen C) and 62 % compared to control (Gen D). 22 DAWI, highest reduction of LAI resulted in lowest depletion of soil water (lowest SSI). In late senescencing genotypes, LAI was reduced by about 40 % of control, but only at SSI≥ 3.0.

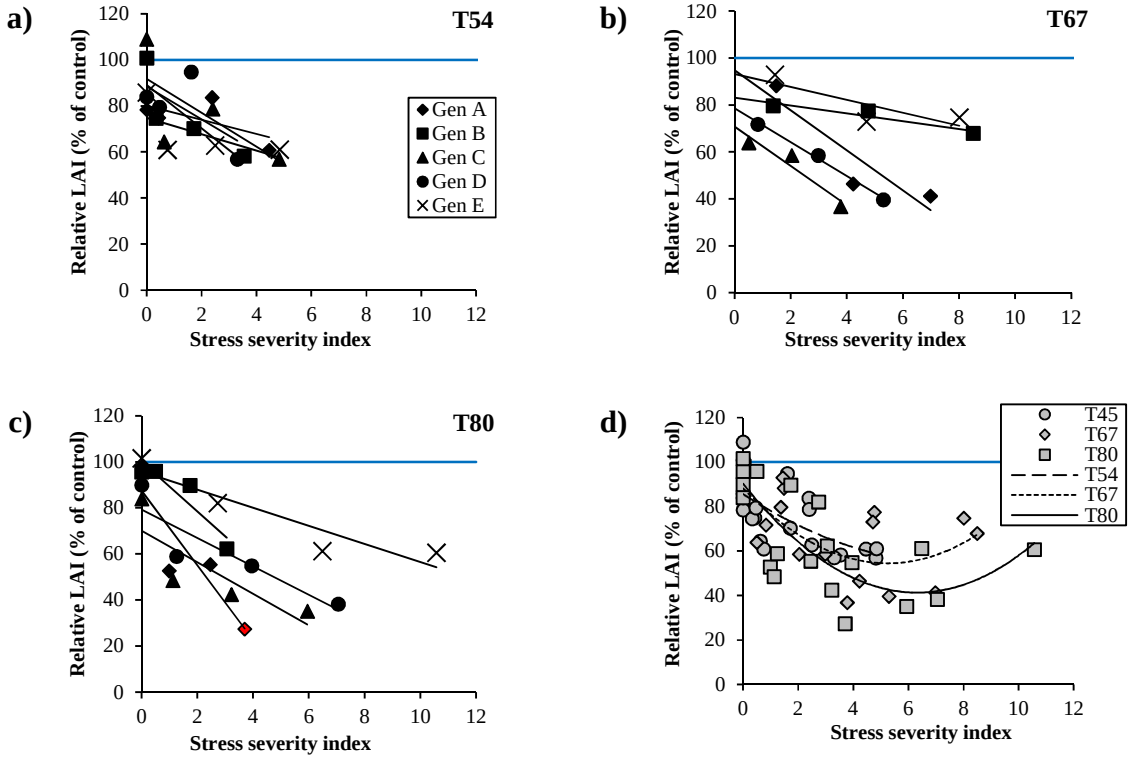


Figure 55: Relationship between drought stress severity (SSI) and relative leaf area index (LAI) in five potato genotypes. Irrigation was withheld a) 54 (T54), b) 67 (T67) and c) 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. In d) polynomial regression lines were fit to relative values of all genotypes in T54, T67 and T80. Data points marked with red color represent data from one replication.

Linear regression equations:

a)
Gen A: y= -3.06x + 80.0 R^2=0.41;
Gen B: y= -9.39x + 89.0 R^2= 0.71;
Gen C: y= -7.34x + 91.6 R^2=0.78;
Gen D: y= -7.08x + 88.3 R^2=0.43;
Gen E: y= -3.52x + 74.8 R^2=0.39

b)
Gen A: y= -8.54x + 94.84 R^2= 0.83;
Gen B: y= -1.67x + 83.20 R^2= 0.90;
Gen C: y= -8.37x + 70.74 R^2=0.91;
Gen D: y= -7.18x +78.46 R^2= 0.98;
Gen E: y= -2.76x + 93.30 R^2= 0.68.

c)
Gen A: y= -16.18x + 87.51 R^2= 0.79;
Gen B: y= -10.78x +100.11 R^2= 0.85;
Gen C: y= -6.84x + 70.07 R^2= 0.68;
Gen D: y= -6:16x +79.31 R^2= 0.80;
Gen E: y= -3.93x +95.76 R^2= 0.86

d)
Polynomial regression equations:
T54: y= 0.51x^2 - 8.03x + 85.60 R^2= 0.43
T67: y= 1.22x^2 - 12.83x + 88.16 R^2= 0.27
T80: y= 1.23x^2 - 15.49x + 90.24 R^2= 0.60

Across genotypes, LAI under drought stress was most affected under late drought in T80, and least under the early induced drought in T54 (Figure 55 d)). Further, LAI in T80 declined more rapidly with increasing stress severity than in T67 and T54, indicating the influence of larger canopies and higher temperatures. At SSI value of 4.0 LAI in T54, T67 and T80 was reduced by 38, 44 and 52 % compared to control, respectively. Vice versa, SSI must reach values of 4.5, 3.1 and 2.4 in T54, T67 and T80, to decrease LAI by 40%.

3.7. Leaf expansion rate

Leaf expansion of individual potato leaves declined under drought stress in all genotypes (Figure 56). Moreover, drought delayed or inhibited the formation of new leaves. Under drought stress conditions, less new leafs were formed and new leaves generally appeared at a later point in time during treatment period (Figure 56). Across treatments, more new leaves were formed in late than in early senescencing genotypes. Most new leaves appeared in control plants of Gen B between 55 and 77 DAP, the genotype that showed delayed germination.

During T54, highest reduction in leaf area expansion was found in two late senescencing genotypes B and E and in the early senescencing Gen D. These genotypes showed highest mean leaf expansion under fully-irrigated conditions of 11.0±2.4 cm^{-2} d^{-1} (Gen B), 7.3±1.7 cm^{-2} d^{-1} (Gen D) and 7.2±1.4 cm^{-2} d^{-1} (Gen E). However, under drought stress mean leaf area expansion was markedly reduced to 4.9±0.7 cm^{-2} d^{-1} (Gen B), 4.2±1.1 cm^{-2} d^{-1} (Gen D) and 2.0±0.4 cm^{-2} d^{-1} (Gen E), respectively, which corresponds to a reduction by 56, 43 and 73 % compared to control. In the early senescencing Gen A and C, which exhibited lower mean leaf area expansion under control condition of 4.1±0.8 cm^{-2} d^{-1} (Gen A) and 5.0±0.7 cm^{-2} d^{-1} (Gen C) leaf area expansion decreased by 37 % compared to control (2.6±0.8 cm^{-2} d^{-1}) in Gen A, and by 16 % compared to control (4.2±1.4 cm^{-2} d^{-1}) in Gen C.

In T67, similar pattern were found. The late senescencing genotypes and early senescencing Gen D showed on average highest reduction of leaf expansion rate under drought stress, and the early senescencing genotypes lowest reduction. Mean leaf expansion was reduced by 72 % (Gen B), 75 % (Gen E) and 87 % of control (Gen D) and by 65 and 53 % of control in Gen A and C. Under fully irrigated conditions, mean leaf expansion rate ranged from 2.4±0.5 in Gen C up to 6.7±2.0 in Gen B.

Leaf area expansion under fully-irrigated conditions slowed down/ decreased throughout the experiment as an effect of aging and development stage. In late senescencing genotypes expansion under fully irrigated conditions decreased to very low level (< 1 cm^{-2} d^{-1}) at 99 DAP (19 DAWI; T80). In early senescencing genotypes leaf area expansion in control plots was reduced to very low levels at 96 DAP in Gen A, and totally ceased (0 cm^{-2} d^{-1}) at 96 and 89 DAP in Gen C and Gen D, respectively, which coincided with leaf senescence

(most leaves yellowish). In late senescencing genotypes that development stage (most leaves yellowish) set in later (> 106 DAP). Mean leaf area expansion under fully irrigated conditions ranged between 0.6±0.3 cm^{-2} d^{-1} in Gen C and 2.2±0.9 cm^{-2} d^{-1} in Gen E. Under late induced drought in T80, leaf area expansion of early senescencing Gen C and D ceased completely 7 DAWI (87 DAP). In Gen A, leaf area expansion in drought stressed plants ceased already 3 DAWI (83 DAP) which might indicate a higher sensitivity to changes in soil water content due to an earlier start of senescence (at 86 DAWI at A300 and at A290 in Gen C, D). Though leaf expansion under drought was low in the late senescencing genotypes, leaves (primarily younger leaves) of these genotypes were expanding until 12 DAWI (92 DAP) in Gen E and 16 DAWI (96DAP) in Gen B.

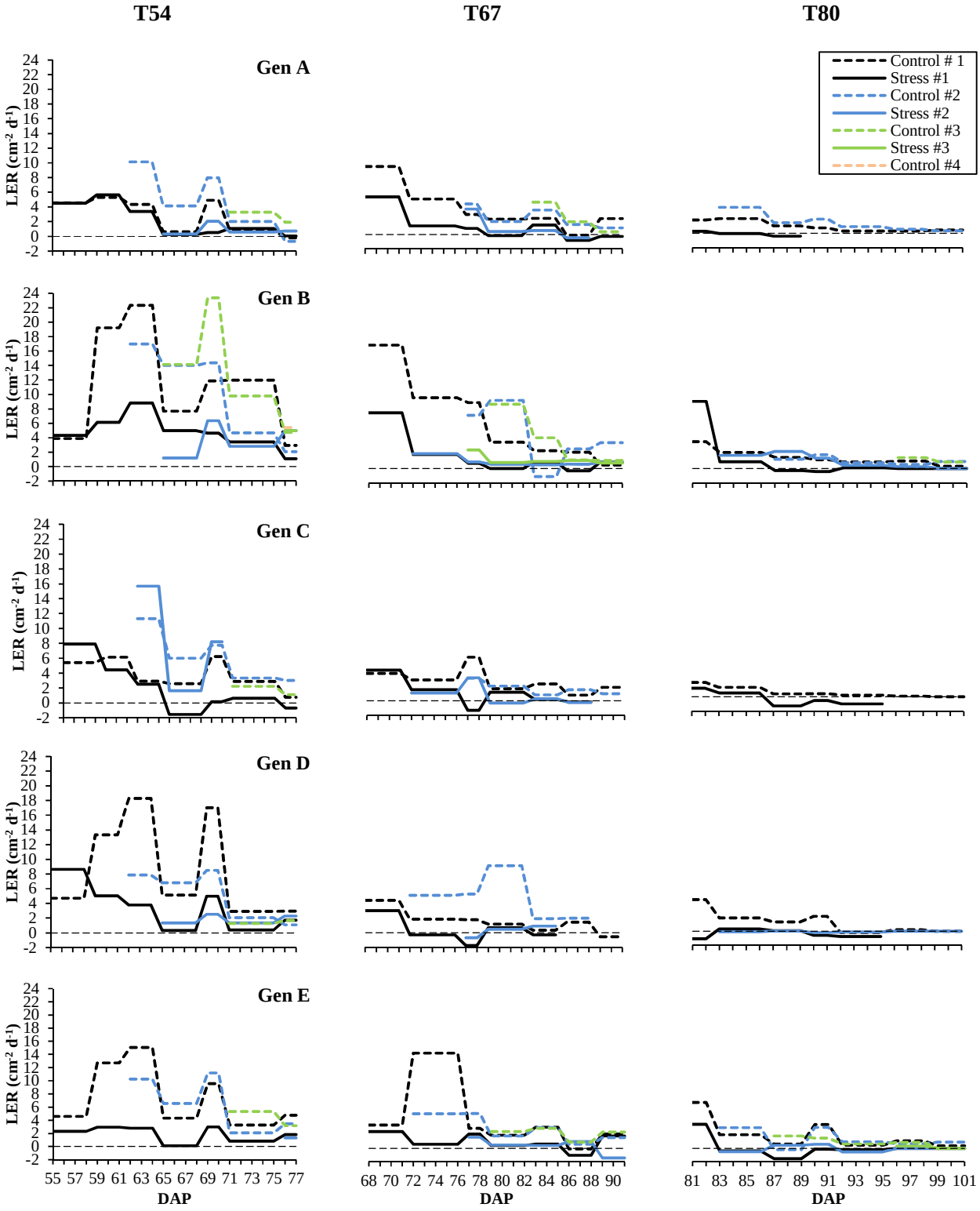


Figure 56: Leaf area expansion rate (LER; cm^{-2} d^{-1}) of potato leaves under fully irrigated (- - - -) and drought stress conditions (——). The LER for five potato genotypes at 4 different leaf positions is presented. Irrigation was withheld at 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean of n= 3.

Under water deficit, expansion of potato leaves declined linearly with decreasing LWP (Figure 57). During early drought (T54), expansion rate ceased completely at LWP of -0.5MPa (Figure 57 a)). During mid (T67) and late induced drought stress (T80), expansion rate of potato leaves ceased at higher LWP of -0.45 and -0.40 MPa (Figure 57 b), c)).

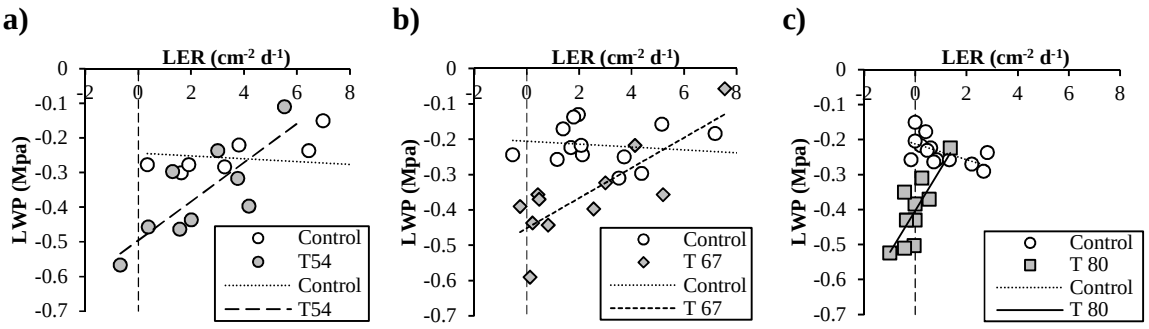


Figure 57: Relationship between mean leaf area expansion rate (LER; cm^{-2} d^{-1}) of leaf #1, 2, 3, 4 and predawn LWP in potato genotypes. Irrigation was withheld a) 54 (T54), b) 67 (T67) and c) 80 (T80) days after planting. Linear regression lines were fit to mean values of n=3. Significance level of regression coefficient: ** P<0.01.

Linear regression equations:

a)	b)	c)
Control: y= -0.00x – 0.24 R^2= 0.13	Control: y= -0.00x – 0.21 R^2= 0.09	Control: y= -0.02x – 0.21 R^2= 0.34*
T54: y= 0.06x -0.50 R^2=0.63**	T67: y= 0.04x -0.45 R^2=0.65**	T67: y= 0.12x -0.40 R^2=0.65**

3.8. Leaf water potential (predawn)

In T54 leaf water potential (LWP) in control and drought stress treatments was very low at 6 DAWI and substantially increased at 16 DAWI in all five genotypes (App. Figure 75). At time of LWP determination (6 DAWI, T54), potato plants were not exposed to drought stress in control plots (soil water content ≥ FC) and stress level was low in drought stressed plots compared to values at 16 DAWI. It seems that the low LWP in control and stress treatment at 6 DAWI are probably due to an error in measurement, and values therefore are excluded in Figure 58 a) and d).

In fully watered control, predawn LWP ranged from -0.15 to -0.34 MPa and in drought stress treatments from -0.21 to -0.62 MPa (Figure 58). LWP decreased with increasing stress severity in all three treatments (Figure 58).

In 54 DAP (T54), potato genotypes maintained LWP at level of control under mild and intermediate drought stress at 6 and 16 DAWI (Figure 58 a); App. Figure 75). However, at 26 DAWI (SSI≥ 4.3) a clear reduction in LWP by 17 – 21 % in comparison to control could be detected in all genotypes, except Gen D, but LWP did not differ among the five genotypes. Gen D could maintain LWP in droughted plants at level of control until 26 DAWI. In early senescencing Gen C, LWP was reduced by 26 % compared to control already at SSI= 2.6 (16 DAWI). Contrary, late senescencing Gen B showed a higher LWP under drought stress (SSI= 2.0) at 16 DAWI than under fully-irrigated conditions.

When irrigation was withheld 67 DAP (T67), LWP in plants of early senescencing Gen A and C already decreased at 16 DAWI by 45 % (Gen A) and 26 % (Gen C) compared to control (Figure 58 b); App. Figure 75). Plants of early senescencing Gen D again could maintain LWP at level of control throughout the whole treatment period. Late senescencing Gen B and E could maintain LWP for a longer period than early senescencing Gen A and C, as a decrease under drought stress by 44 % (Gen B) and 20 % (Gen E) in comparison to control could only be detected at 26 DAWI. The two late senescencing genotypes consumed more soil water during the treatment period than early senescencing genotypes, reflected in higher SSI values at 16 and 26 DAWI.

Withholding irrigation at 80 DAP (T80) decreased LWP in Gen C and D by 24 % and 20 % compared to fully-irrigated conditions at SSI≥ 3.5 (16 DAWI) (Figure 58 c); Figure 75, App.). At higher stress severity at 26 DAWI, LWP was reduced by 36 % (Gen C) and 21 % (Gen D) compared to control. In early senescencing Gen A, a reduction in LWP already was detected at low stress severity (SSI= 0.7) at 6 DAWI. In late maturing Gen E, a reduction by 27 % compared to control could be found at highest SSI of 13.0 (26 DAWI) and not at all in Gen B.

Across genotypes, response of LWP to increasing stress severity was strongest in T54 and T80 (Figure 58, d)). When water was withheld 67 DAP (T67), decrease of LWP per increase of SSI was lower compared to T54 and T80. That indicates that plants could maintain LWP at higher level, when drought stress was applied during that stage of development, compared to the early and late induced drought.

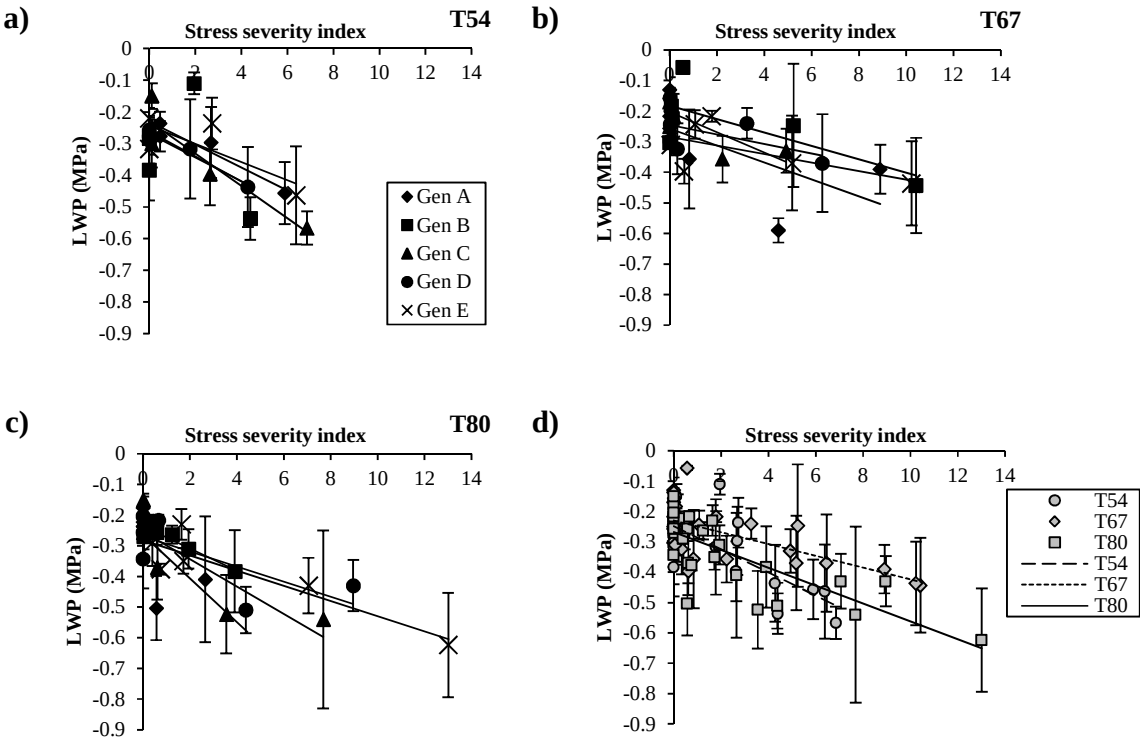


Figure 58: Relationship between drought stress severity (SSI) and leaf water potential (LWP) in five potato genotypes. Irrigation was withheld a) 54 (T54), b) 67 (T67) and c) 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. In d) linear regression lines were fit to relative values of all genotypes in T54, T67 and T80. Significance level of regression coefficient: *P<0.05; ***P<0.001.

Linear regression equations:

a)
Gen A: y= -0.04x – 0.23 R^2= 0.93*;
Gen B: y= -0.04x – 0.27 R^2= 0.19;
Gen C: = -0.05x – 0.23 R^2= 0.86;
Gen D: y= -0.04x – 0.26 R^2= 0.97*;
Gen E: y= -0.03x – 0.24 R^2= 0.61.

b)
Gen A: y= -0.03x – 0.26 R^2= 0.39;
Gen B: y= -0.02x – 0.18 R^2= 0.53;
Gen C: y= -0.03x – 0.20 R^2= 0.59;
Gen D: y= -0.02x – 0.25 R^2= 0.30;
Gen E: y= - 0.01x -0.28 R^2= 0.39.

c)
Gen A: y= -0.07x - 0.26 R^2= 0.34;
Gen B: y= -0.04x – 0.24 R^2= 0.88*;
Gen C: y= -0.04x – 0.25 R^2= 0.73*;
Gen D: y= -0.02x – 0.27 R^2= 0.53;
Gen E: y= -0.02x – 0.28 R^2= 0.83*.

d)
T54: y= -0.04x – 0.25 R^2= 0.56***
T67: y= -0.02x – 0.23 R^2= 0.44***
T80: y= -0.03x – 0.27 R^2= 0.59***

3.9. Specific leaf area

Specific leaf area (SLA) from 3rd, 6th and 9th fully-expanded potato leaves is presented in Figure 80 (App.). No clear differences in SLA were found between the different leaf positions. In Figure 79 (App.) mean SLA of 3rd, 6th and 9th fully-expanded leaf at the different sampling occasions is shown for the five genotypes. SLA varied between the

different sampling occasions under fully irrigated as well as under drought stress conditions, but drought had no clear effect on SLA of the five potato genotypes.

3.10. Relative chlorophyll content

Average SPAD values in control plants of early senescencing genotypes ranged between 42.8±1.0 (Gen C) and 47.8±1.2 (Gen B) (App. Figure 74). Across sampling occasions and treatments, plants of early senescencing genotypes showed lower mean SPAD values (41.2 (Gen A), 39.2(Gen C), 43.1(Gen D)) under drought stress than the two late senescencing genotypes (50.0 (Gen B), 49.1 (Gen E)). In late senescencing genotypes, average SPAD values under drought stress were even higher than under control conditions.

Increasing SPAD values in comparison to control with increasing stress severity during early drought treatment (T54) were found in late senescencing genotypes and early senescencing Gen A. (Figure 59 a)). 21 DAWI, relative chlorophyll content (SPAD) was increased by 19 % (Gen A), 9 % (Gen B) and 15 % compared to control (Gen E).In early senescencing Gen C and D, changes in SPAD values with increasing stress severity were small, however, relative SPAD followed an increasing trend in Gen D and decreasing trend in Gen C.

Under drought in T67 SPAD values increased compared to control only in late senescencing genotypes as drought stress intensified, but to a lesser extent than in T54 (Figure 59 b)). In early senescencing genotypes SPAD decreased in comparison to control (Gen C) or remained at level of control (Gen A; D). At 21 DAWI, SPAD values in Gen C were decreased by 13 % of control at SSI= 3.5.

In T80, relative SPAD of late senescencing genotypes increased (Gen B) or remained at level of control (Gen E) and decreased in early senescencing genotypes as drought stress intensified (Figure 59 c)). SPAD values were reduced by 75 %, 37 % and 50 % of control 21 DAWI in Gen A, C, D, respectively.

When irrigation was withheld 67 DAP, in Gen C, SPAD values under water deficit were decreased by 13 % compared to control at SSI value of 3.5, and only by 4 % at SSI value of 4.3 when water was withheld 54 DAP. Similar pattern were also found for Gen A and B.

Changes in SPAD are therefore not necessarily related to drought stress severity alone. Rather the effect of drought stress on SPAD of potato plants might depend on the respective development stage in which it occurs, as 50% of plant leaves in Gen C were already brownish at SSI=3.5 in T67 and at SSI=4.3 in T54 senescence had only started.

Drought stress applied at different stages during crop development had diverse effects on SPAD of the five potato genotypes (Figure 59 d)). Across genotypes, drought stress in T54 and T67 resulted in increasing relative SPAD values, with increasing stress severity, whereas the increase was higher during early drought stress. In T54, SPAD values increased linearly with increasing SSI. However, only when drought stress was applied during a late development stage (T80), relative SPAD values were clearly reduced with increasing stress severity.

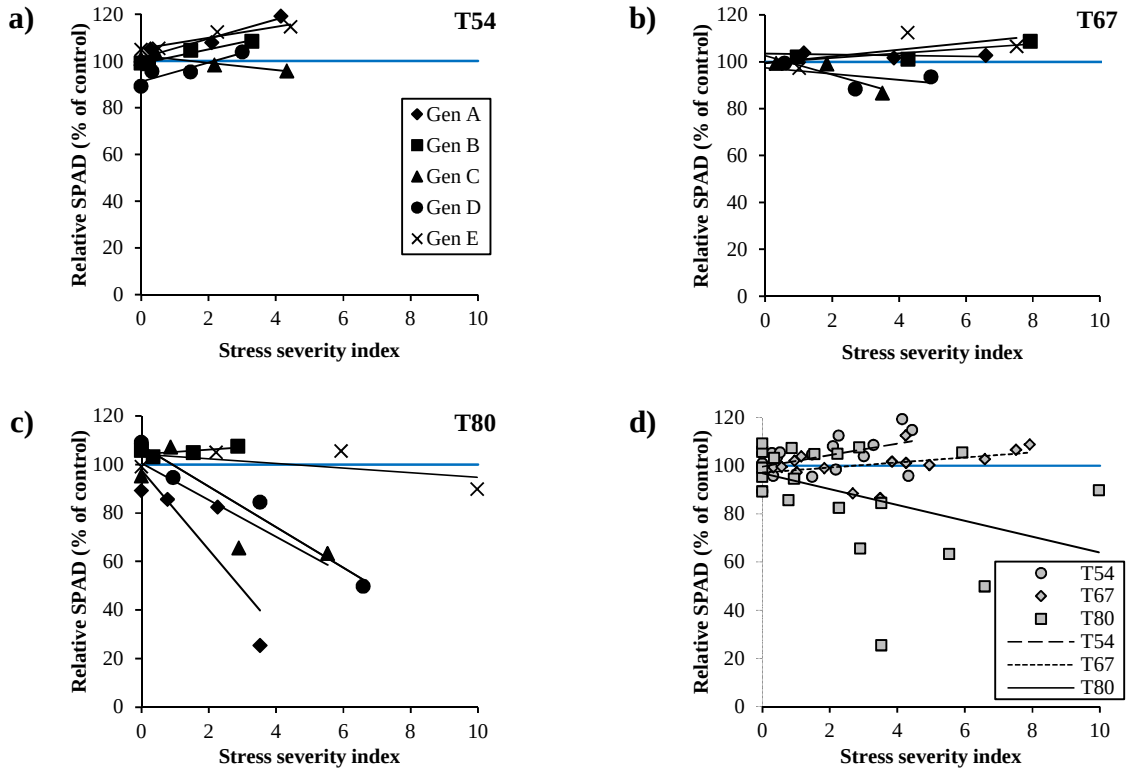


Figure 59: Relationship between drought stress severity (SSI) and relative SPAD in five potato genotypes. Irrigation was withheld a) 54 (T54), b) 67 (T67) and c) 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. In d) linear regression lines were fit to relative values of all genotypes in T54, T67 and T80. Significance level of regression coefficient: *P< 0.05.

Linear regression equations:

a)
Gen A: y= 04.14x + 101.34 R^2=0.93*;
Gen B: y= 3.30x + 99.05 R^2= 0.97*;
Gen C: y= -1.55x +102.37 R^2= 0.82;
Gen D: y= 4.06x +91.27 R^2= 0.84;
Gen E: y= 2.37x + 105.20 R^2= 0.93*.

b)
Gen A: y= -0.20x + 103.58 R^2= 0.25;
Gen B: y= 0.98x + 99.74 R^2= 0.67;
Gen C: y= -4.06x +102.67 R^2= 0.79;
Gen D: y= -1.30x + 97.45 R^2=0.27;
Gen E: y= 1.42x + 99.46 R^2= 0.36.

c)
Gen A: y= -16,43x + 97.71 R^2= 0.72;
Gen B: y= 0.95x + 104.24 R^2= 0.46;
Gen C: -7,5508x +100.44 R^2= 0.72;
Gen D: y= -8.38x + 107.69 R^2= 0.96*;
Gen E: y= -0.96x + 104.24 R^2= 0.33.

d)
T54: y= 2.38x + 99.62 R^2=0.28*
T67: y= 1.05x +97.12 R^2=0.16
T80: y= -3.28x + 96.87 R^2= 0.16

3.11. Chlorophyll fluorescence

As can be seen in Figure 61, minimal fluorescence as well as maximal and variable fluorescence was considerably higher during the first three sampling occasion (DAP≤ 69), compared to data collected later in time. Reason for this is an accidental reduction in modulation intensity during measurement of light-adapted Fv'/m'. Therefore it is not possible to compare chlorophyll fluorescence data from before and after 69 DAP.

However, drought stress reduced minimal fluorescence (Fo), but had no effect on maximal (Fm) and variable fluorescence (Fv) (Figure 61). Averaged over genotypes and treatments, drought reduced Fo by 10 % compared to control. However, mean Fv/m (maximum quantum yield of PS II in the dark-adapted state) of all genotypes varied between sampling occasions (Figure 60). Considering only Fv/m data after 69 DAP, Fv/m in control plots increased from 0.76 at 74 DAP to 0.82 at 88 DAP and remained unchanged thereafter. Drought stress during T54, T67 and T80 did not reduced maximum quantum yield of PSII relative to control.

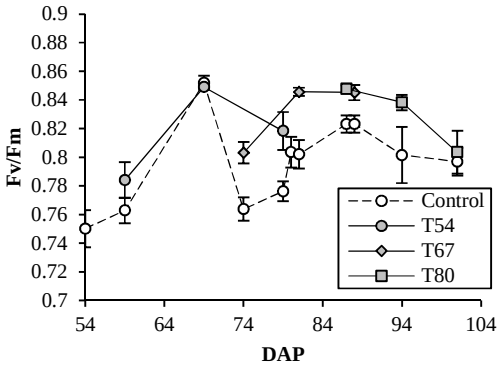


Figure 60: Changes in quantum yield of PS II after dark adaption (Fv/m) over time in fully-irrigated (Control) and droughted plants of five potato genotypes. Irrigation was withheld at 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. of five potato genotypes (n=5).

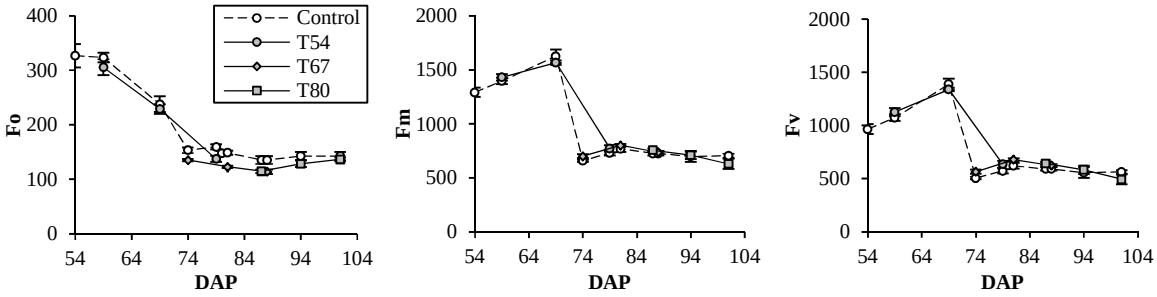


Figure 61: Changes of minimal (Fo), maximal (Fm) and variable fluorescence (Fv) of dark-adapted samples over time in fully-irrigated and droughted plants of five potato genotypes. Irrigation was withheld at 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. of five potato genotypes (n=5).

On genotype level, higher Fv/m under drought compared to control conditions were found in late senescencing genotypes and in Gen D (Figure 62). Fv/m in plants of early senescencing genotype remained largely at level of control. Therefore, maximum quantum efficiency of PS II reaction centers was not affected by drought in these five potato genotypes, indicating the existance of efficient adaption mechanisms.

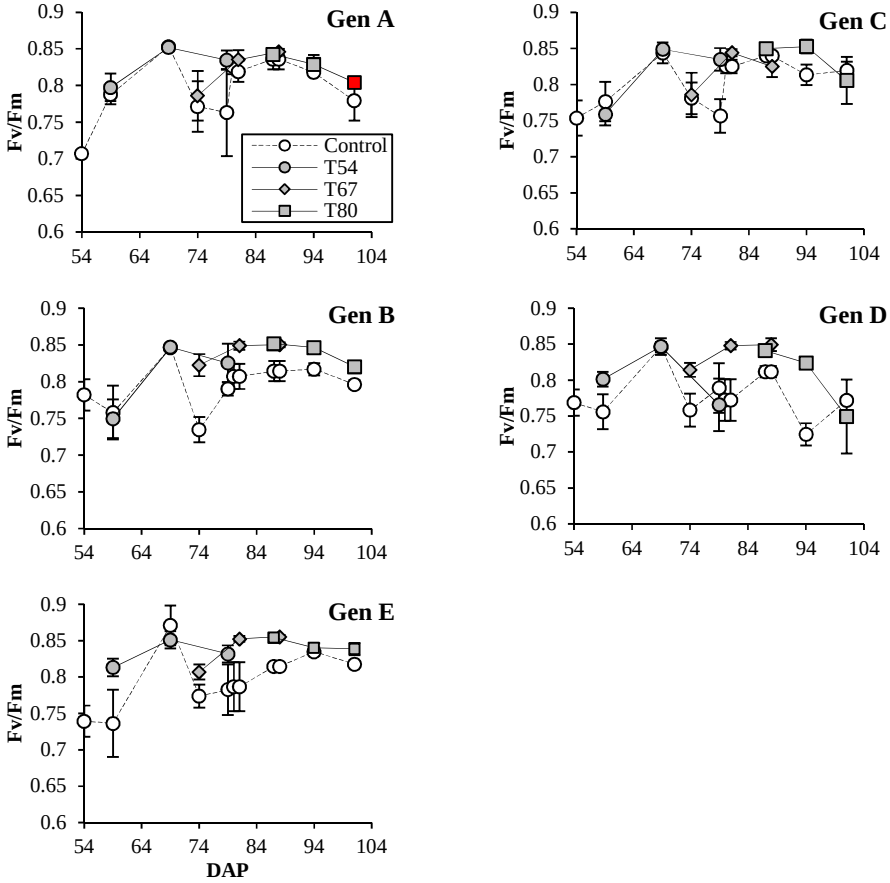


Figure 62: Changes in quantum yield of PS II after dark adaption (Fv/m) over time in fully-irrigated and droughted plants of five potato genotypes. . Irrigation was withheld at 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. of (n=3).Data points marked with red color represent data from one replication.

3.12. Root architecture

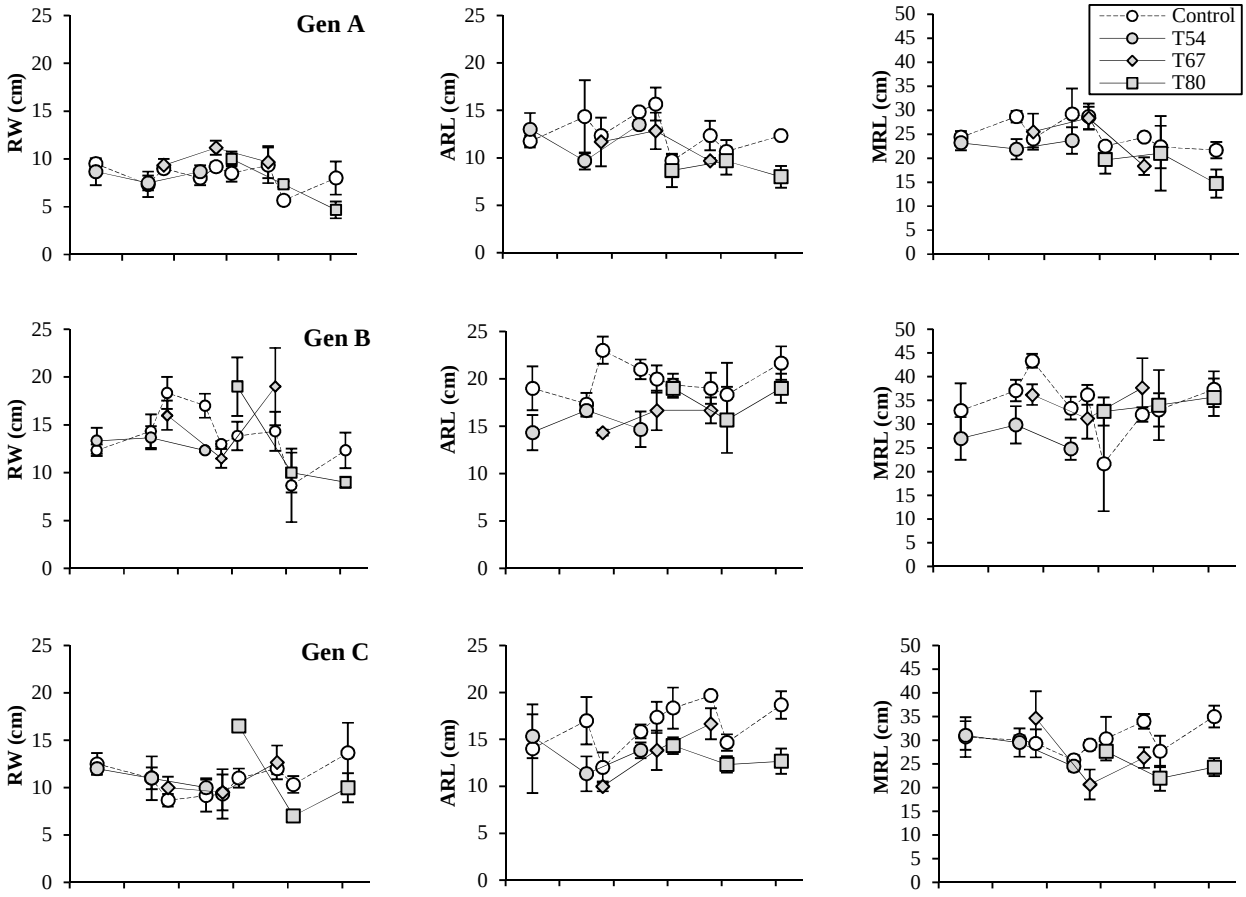
Mean root system width (RW) under fully-irrigated condition was 14±0.9 and 14±1.1 cm plant^{-1} in the late senescencing genotypes B and E (Figure 63). Early senescencing genotypes, in comparison, had lower mean RW, with 8±0.4cm (Gen A), 11±0.5 cm (Gen C) and 12±0.5 cm (Gen D). With 34±1.9 cm (Gen B) and 35±1.0 cm (Gen E), late senescencing genotypes also showed higher maximum root length (MRL) under fully-irrigated conditions, than early senescencing genotypes, where mean MRL ranged between 25±1.0 cm (Gen A) and 31±1.2 cm (Gen D). Highest average root length (ARL) in control plots of 20±0.6 cm was found in late senescencing genotype B, followed by Gen D, E and C with 17±1.0 cm, 16±0.6 cm and 16±0.8 cm. Early senescencing Gen A showed lowest ARL among genotypes, of 13±0.7 cm.

Drought stress in T54 did not have a strong impact on RW of the five potato genotypes. However, early senescencing Gen D reduced RW by 37 % compared to control at 6 DAWI and late senescencing Gen B by 27 % compared to control at 26 DAWI (Figure 63; App. Figure 78). In nearly all genotypes, ARL as well as MRL (MRL not in Gen C) was reduced by drought stress. In late senescencing genotypes and reduction in ARL was already observed under mild drought stress at 6 DAWI and at higher drought stress level at 16, 26 DAWI in early senescencing genotypes. At 26 DAWI, reduction of ARL was highest in Gen D and B. ARL was reduced by 30 % (Gen B) and 34 % compared to control (Gen D), whereas MRL was reduced by 25 % in both genotypes. In late genotypes, MRL was reduced relative to control at all three sampling occasions. MRL was also least affected in Gen A and C. Lower MRL under drought stress was only found at 16 DAWI in Gen A and not at all in Gen C.

In T67, differences in root system width were recorded at 16 DAWI in most genotypes. RW decreased by 40 % compared to control in D and increased by 22 and 25 % in Gen A and E (Figure 63; App. Figure 78). Changes in ARL and MRL under drought were found in all genotypes, except Gen E. In early senescencing genotypes MRL was on average reduced by 28 % compared to control at 26 DAWI, and ARL decreased (Gen A, C) by 19

% in comparison to control. Late senescencing Gen B showed smaller root length at 6 DAWI, with higher reduction in ARL than in MRL.

Withholding irrigation at 80 DAP (T80) increased RW in Gen B and C at low stress severity at 6 DAWI by 37 and 50 %, and in Gen E at higher stress severity at 16 DAWI by 38 % compared to control (Figure 63; App. Figure 78). At about SSI = 4.0, RW decreased in Gen A, B and C by 27 – 42 % compared to control. ARL in Gen C was lower under drought condition at all three sampling occasions, whereas the reduction became higher with increasing stress severity. However, 26 DAWI ARL in early senescencing genotypes was reduced by 32-36% in comparison to control. MRL was also reduced by drought at that time by 29 – 32 % compared to control in Gen A, C and E.



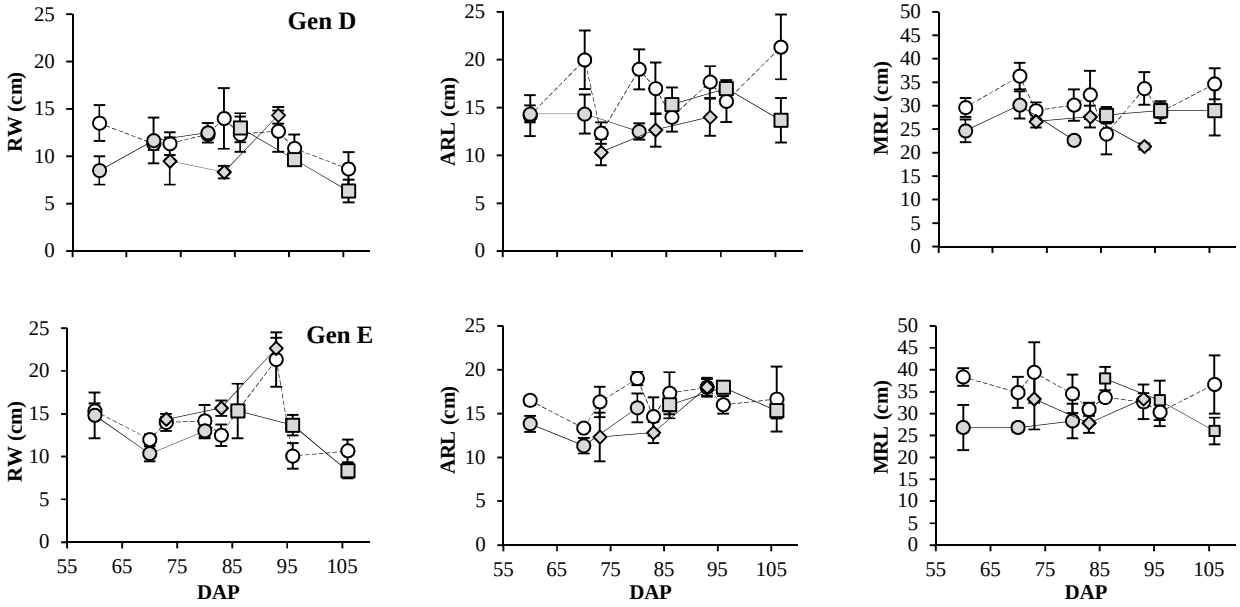


Figure 63: Changes of root system width (RW; cm), average root length (ARL; cm) and maximum root length (MRL; cm) over time in fully-irrigated and droughted plants of five potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. of n=3.

Across genotypes, drought stress in T54 had almost no effect on RW in T54, but in T80, relative RW decreased linearly with increasing SSI (Figure 64 a)). Root average length was slightly reduced by drought stress (Figure 64 b)), whereas the decrease was strongest in T54. Average genotype response of MRL to drought was strongest in T80, where relative MRL decreased linearly with increasing SSI (Figure 64 c)).

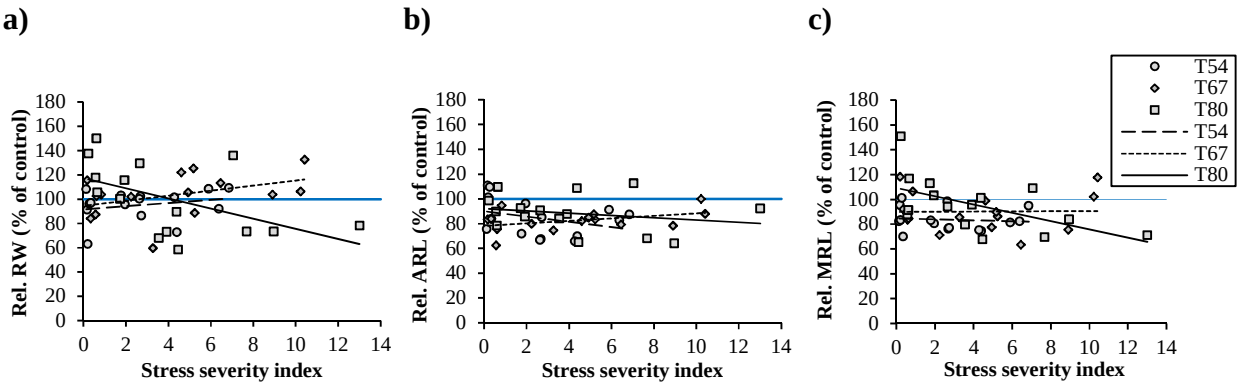


Figure 64: Relationship between drought stress severity (SSI) and a) relative root system width (Rel. RW) b) relative average root length (Rel. ARL) and c) relative maximum root length (Rel. MRL). Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting. Linear regression lines were fit to relative values calculated from means of n= 3. Significance of regression coefficient: *P< 0.05.

Linear regression equations:

a)	b)	c)
T54: y= 1.30x + 91.46 R^2= 0.06	T54: y= -2.15x + 90.11 R^2= 0.11	T54: y= -0.36x + 84.60 R^2= 0.01
T67: y= 2.07x + 94.54 R^2= 0.16	T67: y= 1.01x + 78.12 R^2= 0.17	T67: y= 0.08x + 89.79 R^2= 0.00
T80: y= -4.16x + 117.27 R^2= 0.27*	T80: y= -0.92x + 92.15 R^2= 0.05	T80: y= -3.33x + 109.12 R^2=0.32*

3.13. Stolon number and length

Under fully irrigated conditions, the late senescencing genotype E had highest number of stolons among the five genotypes with averagely 23±1.8 stolons plant^{-1}, followed by Gen D (18±1.4 stolon plant^{-1}), Gen C (18±1.1 stolons plant^{-1}) and Gen B (17±1.3 stolons plant^{-1}) (Figure 65). Lowest stolon number under fully-irrigated conditions occurred in plants of Gen A, with averagely 12.6±1.2 stolons plant^{-1}. The two late senescencing genotypes on average had longest stolons under fully-irrigated conditions, with 11±1.0 cm plant^{-1} (Gen B) and 11±1.1 cm plant^{-1}. In the early senescencing genotypes, stolons were shorter. Compared to Gen D with averagely 9±0.9 cm plant^{-1} and Gen C with 7±0.8 cm plant^{-1}, stolons were shortest in Gen A (3±0.2 cm plant^{-1}) under fully-irrigated conditions.

When irrigation was withheld 54 DAP, clear differences in stolon number were only detected in Gen A at 26 DAWI. Stolon number increased by 104 % in Gen A (Figure 65; App. Figure 77). Change in stolon length was only found in late senescencing Gen B at 26 DAWI, where stolon length was decreased by 49 % compared to control.

Drought stress in T67 had a variable effect on stolon length of the five genotypes. Plants of Gen A and E displayed longer stolon under drought stress at 6 and 16 DAWI and Gen B produced shorter stolons at 6 DAWI. Stolon number was reduced by drought in Gen C, D and E, but often only at single sampling occasions

Withholding irrigation at 80 DAP (T80) reduced number of stolons per plant in early senescencing genotypes, but only at 26 DAWI. Stolon number was reduced by 58 % in Gen A and by 27 % compared to control in Gen C and D. The genotypes A, C, E displayed an increase in stolon length under mild drought stress at 6 DAWI and at 16 DAWI.

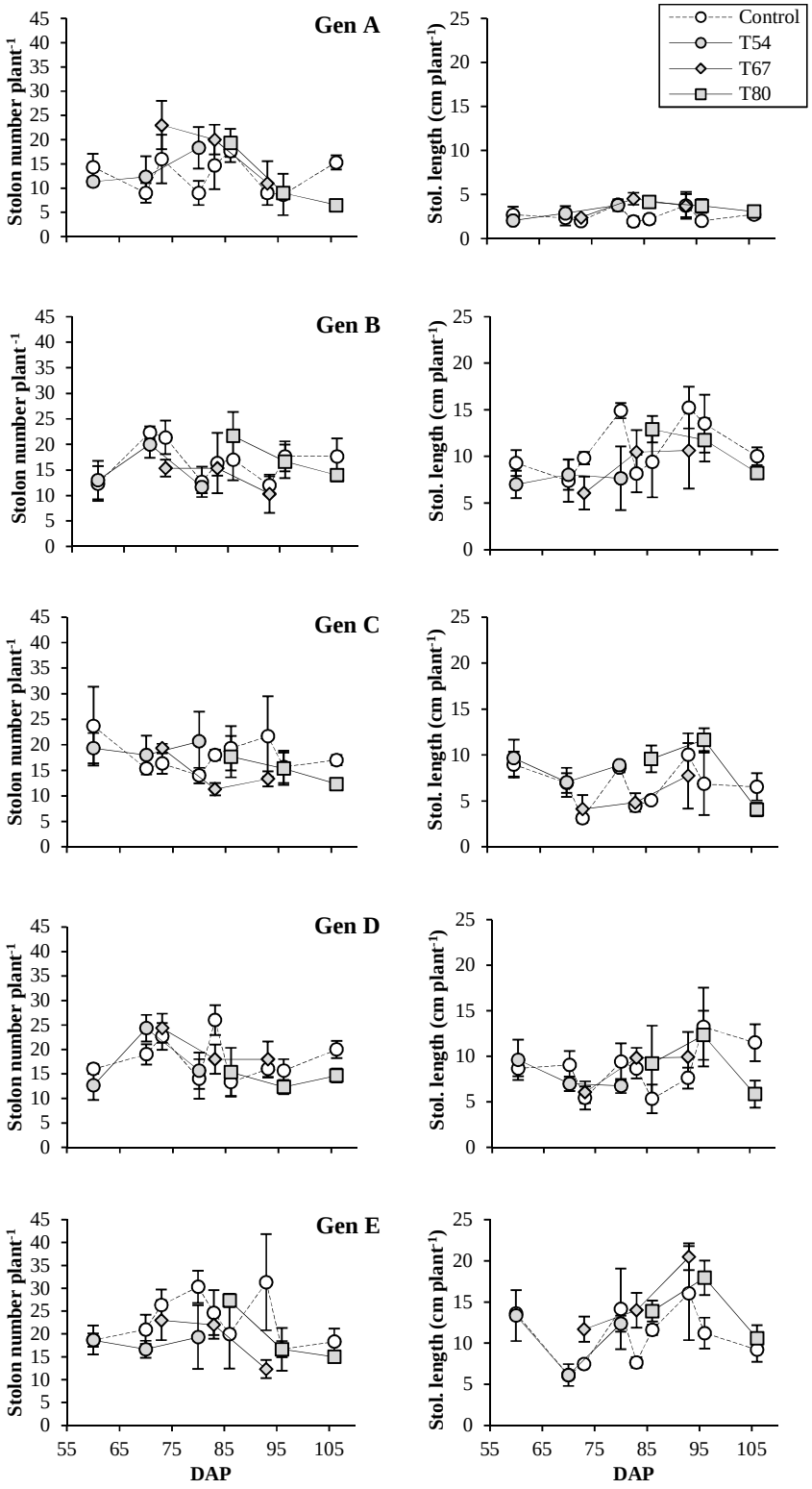


Figure 65: Changes of stolon number (plant^{-1}) and stolon length (Stol. length; cm plant^{-1}) over time, in fully-irrigated and droughted plants of five potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) days after planting (DAP). Graphs represent mean value ±S.E. of n=3.

In all five genotypes stolon number and stolon length was affected by drought stress. Across genotypes (Figure 66 a)), relative stolon number increased during the early drought stress (T54) and was only slightly affected by drought stress in T67. Under late drought stress in T80 relative stolon number decreased linearly with increasing SSI. No clear response of stolon length to increasing drought stress was found in T54 and T67 (Figure 66 b)). In T80, relative stolon length decreased with increasing SSI, but stolon length was only reduced at SSI>8.0.

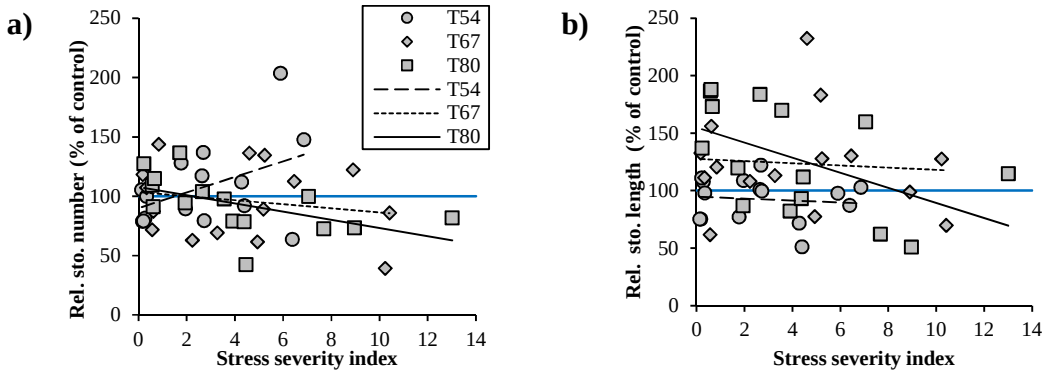


Figure 66: Relationship between drought stress severity (SSI) and a) relative stolon number and b) relative stolon length in potato genotypes. Irrigation was withheld 54 (T54), 67 (T67) and 80 (T80) DAP. Linear regression lines were fit to relative values calculated from means of n= 3. Significance level of regression coefficient: *P< 0.05.

Linear regression equations:

a)
T54: y= 6.55x + 89.95 R^2= 0.19
T67: y= -1.71x +103.48 R^2= 0.04
T80: y= -3.46x + 107.74 R^2= 0.29*

b)
T54: y= -0.87x + 94.88 R^2= 0.01
T67: y= -0.95x +127.51 R^2= 0.01
T80: y= -6.56x + 154.83 R^2= 0.26

4. Discussion

Drought affected all parameters investigated in this study. However, the impact of drought differed among parameters, treatments and genotypes.

The ability to maintain yield under drought conditions has a multiple trait nature, thus in influenced by many different aspects. The impact of different plant traits on drought tolerance depends on the development stage in which drought occurs and on stress severity (Spitters and Schapendonk, 1990). This study tries to analyze the effects of drought on various plant parameters and their contribution to yield maintenance with respect to phenological development stage and stress severity in five contrasting potato genotypes.

4.1. Effect of soil moisture availability on phenological development

The effect of drought on phenological development of the five potato genotypes varied depending on genotype and on the development stage in which it occurred. Drought during inflorescence formation and flowering slowed down development, although just in late senescencing genotypes and Gen D. In upland rice, Asch *et al.* (2004) also reported that severe constant drought stress (constant soil moisture content of 10 %) lengthens the vegetative phase; however, under progressive drought stress development was not delayed. Asch *et al.* (2004) suggested that such development pattern under drought stress might constitute kind of resistance strategy. However, in potato genotypes, phenological development was already found to be delayed under low stress severity 6 and 16 DAWI, indicating the high sensitivity of potato genotypes to soil water deficits. Early senescencing Gen A and C did not flower under drought, but quickly induced premature senescence. In four *Festuca* grasses, Wang and Bughrara (2007) also found that flowering just occurred in well-watered plants and not under drought stress conditions and therefore, drought prevented reproductive development. However, in potato the primary source of reproduction are tubers. In early senescencing Gen A and C, the development of stolons and tubers under drought conditions was delayed to a minor extent than in genotypes that flowered under drought, indicating that non-flowering can help to escape drought.

After flowering, drought accelerated phenological development and induced premature senescence in all genotypes. This is a common observation made in plants under drought

stress (Haverkort and Goudriaan, 1994; Spitters and Schapendonk, 1990; Dalirie *et al.*, 2010) and is a mechanism by which plants can escape drought and complete their life cycle as will be discussed below.

4.2. Effect of soil moisture availability on plant total biomass

Plant total biomass was most affected by the early drought treatment and least by drought in T67 and T80. The huge effect of the early drought on plant total biomass was due to the high reduction in tuber DW under drought in T54. As tuber DW constitutes the largest fraction within potato plants, the high reduction in plant total biomass in T54 is not surprising. Contrary, drought in T67 and T80 most affected leaf DW, which is also confirmed by the fact that LAI reduction was highest in T80. As vegetative growth or canopy expansion (LER) was very low in the late drought treatment, leaf DW reduction probably occurred mainly due to leaf shedding or nutrient reallocation during senescence (Haverkort and Goudriaan, 1994; Jefferies, 1989; Munné-Bosch and Alegre, 2004).

4.3. Effect of soil moisture availability on dry mass partitioning

Partitioning of assimilates into the different plant components, especially the allocation between vegetative and reproductive organs , plays an important role in determining crop yield under adverse growing conditions like drought stress (Kage *et al.*, 2003). The partitioning of assimilates to harvested reproductive organs, i.e. the harvest index (HI) of crops is one important component that determines yield (Araus *et al.*, 2001). A reduction in HI under drought stress therefore negatively affects crop yields. HI in potato typically decreases under drought conditions (Evers *et al.*, 2010), and the relative maintenance of HI is associated with drought tolerance (Deshmukh and Mate, 2013).

Relative HI of potato genotypes was most affected by early drought (T54) and least by late induced drought (T80). Likewise, tuber DW was reduced most under early drought and least under late induced drought. As potato genotypes were at tuberization /early tuber bulking stage during T54, results indicated higher susceptibility to drought during this development stage, which was also reported by Costa *et al.* (1997).

4.3.1. Drought in T54

Under early induced drought (T54), almost all genotypes showed reduced partitioning to tubers when part of tubers/tuber initials was still at tuberization stage, but only at highest SSI, 26 DAWI. Jefferies (1992) concluded that early drought adversely affects tuberization and shift partitioning to non-tuber biomass. A preferential supply of assimilates to leaves, stems or BGB on the expense of tubers was observes in Gen A, B, C and D, whereas the effect was highest in Gen B (highest HI reduction). In Gen B, all tubers were at tuberization stage and plants were flowering, 26 DAWI. That probably created competition for assimilates between tubers and above-ground reproductive organs (Rodrigues *et al.*, 1995), especially, when development of tubers was that weakly proceeded. However, also under fully-irrigated conditions, plants of Gen B exhibited a low HI. In a study of Tourneux *et al.* (2002), six potato genotypes were well-watered until tuber initiation (54 DAP) and were then subjected to progressive water shortage. Among the investigated cultivars, genotype *Luky* showed similar morphological characteristics like Gen B of the present study. Both genotypes were tall in size, maintained their LAI under drought and showed a low HI in well-watered and drought conditions. Under drought conditions, in both genotypes tuber dry biomass and HI strongly decreased.

Like in Gen A, B and D, a reduction in HI was also found in Gen C at 26 DAWI. However, tuber DW at 26 DAWI was least affect in Gen C which might be due to relatively high depletion of soil water, as highest SSI at 26 DAWI among genotypes was found in Gen C. The relatively high usage of soil water might be due to the low reduction in leaf expansion (mainly in the upper canopy: will be discussed below) resulting in high canopy water losses. LWP was already reduced in comparison to control at 16 DAWI in this genotype, whereas LWP was maintained for a longer period in the remaining genotypes. The decrease in LWP might have decreased stomatal conduction by partial stomata closure. However, as stomatal conductance in potato is reduced earlier than assimilation rate (assimilation rate less sensitive to soil water deficit), and transpiration efficiency is increased due to water stress (Ahmadi *et al.*, 2010) indicates, that the early reduction in LWP in Gen C not necessarily decreased C-capture, but rather increased the efficiency of water use.

Development of stolons and tubers was fastest in Gen A. At 26 DAWI all tubers/tuber initial were at bulking stage which might explain why HI in this genotype was unaffected by drought. However, at 6 and 16 DAWI, part of tubers were still at tuberization stage, and partitioning of assimilates to tubers was reduced by 9 – 10 % in comparison to control in favor of non-tuber biomass, particularly BGB. When assuming that the increase in BGB ratio at least partly constitutes an increased partitioning to roots, this increase might be kind of avoidance strategy to assure water access (Blum, 2005). Root system width or length under drought conditions was not increased, thus the increased partitioning to BGB could have increased root density or stolon dry mass. As plants of Gen A were able to extract a large proportion of soil water (SSI) it seems probable, that root density was enhanced under drought. Since SSI was at low level at 6 DAWI, plants of Gen A were able to detect small changes in soil water content and quickly induced measures to cope with the impending drought situation. The increased partitioning into BGB under drought stress at all three sampling occasions is reflected in tuber area, as plants of Gen A produced smaller tubers in comparison to fully-irrigated conditions. Reduction in tuber DW compared to control by 48 and 70 % was detected 16 and 26 DAWI in this genotype. As drought diminished plant growth (LAI, LER) tuber DW was reduced 26 DAWI although HI was not affected, probably due to a restriction in C-accumulation resulting from LAI reduction (Dalirie *et al.*, 2010).

The differences in susceptibility of potato plants during tuberization and tuber bulking in terms of HI reduction under drought conditions might result from variations in sink strength. Sink strength means the capacity of a storage organ to accumulate photosynthates (Dwelle, 1990) and depends on the sink activity and on the sink size (Engels and Marschner, 1986). Sink filling is mediated through concentration/osmotic gradients, thus the activity of enzymes of the starch metabolism determines sink activity (Herbers and Sonnewald, 1998). Moreover, Engels and Marschner (1986) found a positive correlation between sink strength and sink size in potato. Further, Basu *et al.* (1999) could show, that in potato plants, the presence or absence of sinks (tubers) directly influences photosynthetic rate. By examining photosynthetic performance in potato plant with and without tubers (tubers excised) to fully-watered or water deficit conditions, Basu *et al.* (1999) could show, that the absence of tubers sharply limits photosynthesis by a feedback

inhibition of accumulated sucrose and hexose in leaves. As in potato plants the ability to compete for assimilates increases with increasing tuber weight (Engels and Marschner, 1986), the susceptibility of potato genotypes during tuber initiation in the present study to drought conditions in terms of HI reduction might be due to a low sink strength of few and small tubers. Tuber DW and HI reduction in T54 was highest in Gen B, a genotype that had produced only few tuber during that time, and tuber number was additionally reduced under drought stress. HI reduction was less in genotypes that already had a greater number of tubers at bulking stage.

4.3.2. Drought in T67

Drought in T67 reduced HI only in late senescencing genotypes, when plants were flowering (Gen B) and forming berries (Gen E), which probably redirected assimilates away from tubers, reflected in increased partitioning to above-ground plant parts. In contrast to early senescencing genotypes, late senescencing genotypes additionally had part of their tubers/tuber initials at tuberization stage when reduction in HI occurred, again indicating susceptibility to water shortage during that development stage. Further, the results (as well as partitioning patterns of Gen A in T54) highlight the importance of timing of drought stress, as Gen E was exposed to low SSI of 0.62 at 6 DAWI, and nevertheless, HI was reduced.

HI of early senescencing genotypes was unaffected by drought and plants of these genotypes displayed characters of senescence from 16 DAWI on. During the re-organization phase of senescence (second step after initiation phase) nutrients are remobilized in source tissue and translocated to sinks (Munné-Bosch and Alegre, 2004). Senescence characteristics of early maturing genotypes and the reduction in leaf ratio in Gen A at all three sampling occasions therefore point to a remobilization of assimilates from leaves and translocation to tubers. Early senescencing genotypes therefore were less susceptible to withholding water at 67 DAP than late senescencing genotypes, as they were able to escape adverse effects of drought by fast development (Tourneux *et al.*, 2002) and by this preventing reduction in HI. By using average data from 1960 till 1990 to simulate crop growth in potato, Havercort and Goudriaan (1994) could show that HI and tuber yield in late potato cultivars was more susceptible to drought induced late in the season than in early cultivars as they cannot escape drought.

Withholding irrigation at 67 DAP affected tuber DW only in genotypes, that were flowering and forming berries (Gen, B, D, E). Late senescencing genotypes highly depleted soil water and were exposed to very high stress severity 26 DAWI (SSI~ 10.3). The high stress severity at 26 DAWI reduced tuber DW in late senescencing genotypes to a lesser extent in Gen E. This indicates a higher drought tolerance of this genotype, probably due to a faster development of stolons and tubers compared to Gen B. In Gen D, a reduction in tuber DW was found under low and intermediate stress conditions. Since no change in partitioning patterns under drought was found, tuber DW reduction resulted from the diminishing effect on overall plant growth. This is supported by the fact that leaf expansion was reduced by 87 % compared to control (highest reduction among genotypes) and that leaf, stem and BGB dry weights were highly affected already 6 DAWI. Results indicate low tolerance of Gen D to water deficit occurring during reproductive phases (berry formation).

No reduction in tuber DW in early senescencing Gen A and C was found, as they were probably able to escape drought (Spitters and Schapendonk, 1990; Tourneux *et al.*, 2002). Non-flowering genotypes A and C were not using assimilates to form reproductive organs in canopy under drought stress. Under drought conditions that development stage was rather skipped and premature senescence was induced. As tuber DW was not affected by drought, non-flowering under water deficit conditions might be an important strategy to save energy and cope with the adverse drought situation during this development stage.

4.3.3. Drought in T80

Late drought (T80) increased partitioning to tubers and reduced leaf ratio in early senescencing Gen A and D. Half of leaves were brownish in plants of Gen A and in Gen D most leaves and stems were dead, indicating the degree of nutrient remobilization and translocation to tubers. In both genotypes, all tubers were at bulking stage. When drought occurs after tuberization has finished, partitioning to tubers is advanced (Jefferies, 1993). Further, accelerated senescence processes under drought allow plants to complete their life cycle before drought stress reaches lethal levels and by this ensures plant reproduction (Munné-Bosch and Alegre, 2004).

Late drought affected partitioning to tuber in Gen B already at low stress severity (6 DAWI) and increased partitioning to BGB. As BGB includes roots and stolons it cannot be explicitly said whether the increase in BGB % constitutes a strategy of plants to ensure water supply, but as root width was increased relative to control at 6 DAWI, result point to an increased partitioning to roots under drought. As plants of this genotype were still at tuberization stage at 6 DAWI, assimilate supply was driven away from tubers and were preferentially supplied to BGB/roots, to ensured survival/ water uptake probably as reproduction by tubers at that development stage was uncertain. Furthermore, Gen B was able to sense and respond to small changes in soil water availability (SSI= 0.2). When more than 50 % of tubers were at bulking stage, HI in Gen B was increased by 30 % compared to control and leaf and BGB ratio was reduced. Based on crop modeling approaches, Spitters and Schapendonk (1990) reported that drought during tuber bulking increases HI in potato plants. However, HI in Gen C was reduced by drought, 26 DAWI although all tubers were at bulking stage in T80.

The observations in partitioning pattern fit very well with results from tuber DW investigation. Late induced drought increased tuber DW by 40 – 117 % in comparison to control at intermediate stress severity (SSI> 1.8; 16 DAWI), whereas the increase was highest in genotypes that were exposed to lowest SSI. Withholding irrigation at 80 DAP accelerated plant development and speed up or induced senescence in potato plants. As already mentioned above, accelerated senescence can help plants to complete their life cycle and thus ensure reproduction/survival. Especially when drought occurs at a late development stage, a rapid remobilization and translocations of assimilates from foliar tissue to reproductive organs is promising to produce fertile descendants, as tubers then typically are at a high development stage. Therefore, the increase in tuber DW under drought conditions relative to control might be the result of escape mechanisms (Fischer and Maurer, 1978).

The earliest genotype A already showed strong sign of senescence (most leaves yellowish) at 6 DAWI, which probably led to the strong increase in tuber DW by 130 % compared to control even under low stress severity.

However, the strong increase in tuber DW was followed by a sharp decline as drought became more severe, except in Gen A. The decrease in tuber DW was higher in early senescencing Gen C and D than in late senescencing genotypes. The relative maintenance of LAI and light harvesting structures (chlorophyll) under drought in late senescencing genotypes probably were major determinants. Early senescencing Gen A showed a high tolerance to the late induced drought (T80), as tuber DW was not reduced by drought, even at a high stress severity level (26 DAWI). The differences in tuber DW reduction under drought conditions at 26 DAWI in early senescencing genotypes might also be due to differences in soil water usage. The higher reduction in LAI in Gen A reduced water losses by foliage and prevented the evolution of severe drought conditions.

4.4. Effect of soil moisture availability on tubers and stolons

Drought stress had different effects on tuber number and area, stolon number and length depending on the time/phenological stage in which it occurred. Tuber number and tuber area showed highest reduction under early drought (T54) and lowest under late induced drought (T80), pointing to a higher sensitivity of potato genotypes to drought stress applied at tuber initiation/early tuber bulking stage susceptibility. Across genotypes, tuber area was more affected by drought in all three treatments than tuber area, probably due to higher plasticity of the latter one. The effect of drought on stolon number and length was highly variable.

Lahlou and Ledent (2004) reported an increase of stolon number under drought stress, but a reduction in length, which reduced potential sites for tuber formation, as stolon length was positively correlated with tuber number in their study. Struik and van Voorst (1986) also reported an increase in stolon and tuber number when water availability in the solon medium was reduced during tuber initiation, and also mentioned the relationship between stolon growth and availability of potential sites for tuber formation.

Drought in T54 did not have much impact on stolon parameters. However, 26 DAWI stolon number in Gen A was highly increased and stolon length was reduced in Gen B, which is in accordance with findings of other studies (see above). The reduction in stolon length in Gen B reduced possible tuber formation sites and by this reduced tuber number. In Gen B the high stress severity at 26 DAWI had devastating effect on tuber number, area

and tuber DW. The effect of drought on these tuber parameters was highest in Gen B among all genotypes. Based on results from drought stress trial in potato MacKerron and Jefferies (1985) reported that drought applied during tuber initiation reduced tuber number during tuberization but drought had no effect on tuber number when it was applied after tuber initiation. They hypothesized that either drought eliminates potential sites for tuberization or that existing ample sites for tuberization are hierarchically supplied with assimilates (depending on sink strength) and that restricted assimilate supply under drought then limits number of tubers. 26 DAWI, early senescencing genotypes and Gen E already had a higher percentage of tubers at tuber bulking stage which might explain why tuber parameters were most affected by drought in Gen B.

The increase in stolon number observed in Gen A did not lead to a higher number of tubers, but reduced tuber area. Struik and van Voorst (1986) also found that tubers grow to a smaller size under drought, despite the increase in stolon number. The increase in stolon number creates additional sinks and therefore assimilate demand locations, and the competition between sinks, plus the reduced C-capture under drought might have led to a reduction in tuber size.

Witholding irrigation at 67 DAP, reduced tuber number in comparison to control only in early senescencing Gen C and D. A lower number of stolons in comparison to control at 16 DAWI was found in these genotypes. Havercort *et al.* (1989) stated that tuber number mainly is reduced via a reduction in number of stolons. Since tuber number reduction under drought and reduction in stolon number were not always found simultaneously, there must be other reasons than a decline in stolon number. Walworth and Carling (2002) mentioned the possibility of tuber loss via reabsorption. However, as the reduction in tuber number at 26 DAWI in Gen C and D did not result in a reduction of tuber DW, therefore tuber loss could be somehow compensated. Deblonde and Ledent (2000) also observed that the reduction in tuber number not necessarily reduces tuber DW. Contrary, 26 DAWI in T67 tuber DW in late senescencing genotypes was reduced in comparison to control, but tuber number was unaffected. At that sampling occasion, smaller tuber than under control conditions were found, indicating that tuber DW reduction was due to a lower dry weight per tuber. Therefore results show that there are many different ways by which potato genotypes adjust or respond to drought conditions.

The increase in stolon length observed in Gen A and E at 16 and 26 DWI, would have hypothetically increase the amount of potential tuber site, but no increase in tuber number under drought conditions was found. Following the hypothesis of MacKerron and Jefferies (1985), a reduced assimilate availability under drought conditions might have limited the supply of assimilates to potential tuber formation sites and thus prevented an increase in tuber number.

A reduction in tuber area was mainly found in flowering genotypes. In flowering genotypes, reproductive organs exist in the above-ground biomass and in the below-ground biomass, that both demand assimilates and compete for assimilate supply. The reduction in tuber area might be partly due to a preferential assimilate supply to above-ground reproductive organs.

Under late drought stress T80, a reduction in tuber area at 26 DAWI was found in all genotypes, except Gen A. The reduction in tuber DW at treatment end therefore was mainly due to a reduction in dry weight per tuber. Trebejo and Midmore (1989) also reported that limited water supply reduced the number of large tubers. In plants of Gen D additionally tuber number was reduced via a decrease in stolon number. 26 DAWI, a reduction in stolon number was also found in Gen A and C, whereas this reduction was accompanied by a decrease in tuber number only in Gen A . During the late drought treatment it is unlikely that the reduction in stolon number was due to an inhibited initiation under drought stress. Struik and van Voorst (1986) mentioned that the initiation of stolons proceeds during the whole period of tuber initiation. However, tuber initiation was already over in T80, so that there must be other reasons for such a late reduction in stolon number. Lahlou and Ledent (2004) suggested that the disappearance of stolons after they had been set could result from a complete remobilization of its components.

The reduction in tubers via the loss of stolons in Gen A did not result in a reduction in tuber DW in comparison to control. This was probably due to the high increase in tuber DW in T80, so that the loss of some tubers did not result in a clear reduction below values of control.

4.5. Effect of drought on final tuber dry weight

Drought stress reduced final tuber DW in all genotypes. Reduction was highest in T54, what is not surprising, as potato genotypes were exposed to longest period without irrigation in this treatment, and lowest in T80. Length of drying period (T54: 71 days, T67: 58 days, T80: 45 days) and development stage at drought induction therefore determined final tuber yield. Gen B, where tuberization had only started when water was withheld in T54, suffered the highest reduction in final tuber DW of 98 % of control. Drought at early stages of tuberization therefore eliminates tuber dry weight, probably as it inhibits tuber formation, reflected in the reduction in tuber number and tuber area by 80 % 26 DAWI in T54. The long drying period inT54 least affected final tuber DW in plants of Gen D. As plants of this genotypes showed no outstanding difference in the behavior under drought among the investigated parameters, it is not clear which plant characteristic contributed to the lower drought susceptibility. Although characterized as an early maturing genotype, Gen D constitutes somehow an intermediate between early and late senescencing genotypes. This means, that Gen D combines characteristic from early and late senescencing genotype groups, like early senescence, high reduction in LAI under drought, maintenance of LWP and a relatively large root system. However, it just can be speculated whether such combination had contributed to the lower drought susceptibility in T54. Withholding irrigation 67 and 80 DAP least affected early senescencing Gen A , and in case of late drought, also Gen C. Under control conditions, tuber dry weight (absolute terms) in Gen A and C was lower than that of Gen B, D and E, i.e. yield potential in Gen A and C is lower. The better performance of genotypes with a low yield potential could point to a crossover interaction as described by Blum (2005). He suggested that in selection programs for drought tolerance, not only a high yield potential should be taken into consideration, but also non-yield influencing dehydration avoidance characteristics, to overcome the crossover interaction. Tourneux *et al.* (2002), that evaluated drought responses in six potato cultivars came to the same conclusion, as genotypes with a high adaption potential to drought produced lowest yields.

Gen D therefore seems to be a good option, as this genotype combines a high yield potential, with an intermediate reduction under drought stress and relatively high

dehydration-avoidance potential due to its relatively large root system and maintenance of LWP under drought conditions.

4.6. Effect of soil moisture availability on potato canopies

4.6.1. Leaf area index and leaf expansion rate

The amount of intercepted solar radiation by the plant canopy and the efficiency by which the incoming radiation is converted into dry matter influences crop yield (Araus *et al.*, 2001). A reduction in LAI under drought conditions therefore limits dry matter accumulation (Dalirie *et al.*, 2010). However, the maintenance of LAI under drought stress not necessarily leads to high yield under drought conditions in potato genotypes (Tourneux *et al.*, 2002).

LAI was reduced by drought in all genotypes and treatments. Across genotypes, LAI under drought stress was most affected under late drought in T80, and least under the early induced drought in T54. Further, LAI in T80 declined more rapidly with increasing stress severity than in T67 and T54, indicating the influence of larger canopies and effects of aging/senescence. Likewise, leaf area expansion rate was most affected by late drought (T80) and least by early drought (T54).

4.6.1.1. Drought in T54

At the end of the early drought treatment (T54) no big differences in relative LAI among the five genotypes were found, as LAI was reduced by about 40 % compared to control in all genotypes.

Contrary to the effect of early drought on reduction in LAI, genotypic differences were found in the effect of drought on leaf area expansion. Drought most affected leaf expansion of genotypes that exhibited high expansion rates under fully-irrigated conditions i.e. Gen B, D, E (flowering genotypes). In early senescencing Gen A and C, leaf expansion under fully-irrigated conditions was considerably lower probably due to their earliness and drought reduced leaf expansion to a lower extent than in flowering genotypes, especially in Gen C.

Drought stress not only decreases leaf expansion (Durand *et al.*, 1995), but also reduces the formation of new leaves and accelerates shedding of leaves (Haverkort and Goudriaan,

1994; Jefferies, 1989; van Loon, 1980). The reduction in LAI by 40 % in all genotypes, 26 DAWI therefore probably had different underlying causes. Early senescencing Gen A and C maintained leaf expansion at higher relative level than Gen B, D and E, but the higher leaf expansion might have been counterbalanced by a higher shedding of leaves or higher degree of wilting, as in the end, LAI was reduced to the same extent in all genotypes. LAI reduction in late senescencing genotypes was mainly due to the high reduction in leaf area expansion by 56 and 73 % and delayed or inhibited formation of new leaf and probably less due to leaf shedding. In Gen D, LAI reduction probably can be attributed to both, reduction in LER by 43 % and shedding of leaves, supported by the fact that senescence characters were found at treatment end.

Drought in T54, least affected leaf expansion in Gen C (reduction only by 16 % relative to control). Especially in young leaves, expansion under drought stress continued, probably due to high osmotic adjustment to sustain turgor (Blum, 2005). As senescence and thus shedding first occurs in old leaves (Munné-Bosch and Alegre, 2004; Achten *et al.*, 2010), plant of Gen C could maintain leaf area expansion in the upper plant canopy and thus sustain light interception for dry matter production. This could be one contributing factor for the good performance of Gen C (low reduction in tuber DW) compared to the other genotypes under drought conditions in T54. The observation of relative maintenance of leaf expansion and low reduction in tuber DW is in accordance with findings of other authors (Jefferies and MacKerron, 1986; Spitters and Schapendonk, 1990)

4.6.1.2. Drought in T67

LAI reduction in early senescencing genotypes under drought conditions was higher (reduction by 60 % compared to control) in T67 than in T54. The high reduction might be due to increased shedding of leaves, as early senescencing genotypes already exhibited strong characters of senescence (most leaves were yellowish or brownish) from 16 DAWI on and due to the fact that early senescencing genotypes formed less new leaves than late maturing genotypes (Haverkort and Goudriaan, 1994). Shedding of leaves in T67 additionally might be advance by high temperatures during this treatment that accelerated leaf aging (Fleischer and Timlin, 2006). Furthermore leaf expansion rate was reduced to a higher extent under drought conditions in T67 than in T54. Differences in the effect of drought on LAI in T54 and T67 also originate from a higher stress severity level in T67.

Canopies of potato genotypes were larger and temperature was higher during the T67 treatment period and thus the transpirational surface and the evaporative demand.

However, LAI of early senescencing genotypes was more affected by drought stress in T67 than LAI of late senescencing genotypes and declined more rapidly with increasing stress severity. Differences probably resulted mainly from contrasting senescence patterns in early and late genotypes, as shedding of leaves due to accelerated senescence was unlikely in late senescencing genotypes and very likely in early genotypes (see above). This is supported by the fact that leaf expansion rate was reduced by 53 – 87% in all genotypes.

However, the maintenance of LAI/high transpirational surface under drought stress in late maturing genotypes resulted in higher depletion of soil water. A low reduction in LAI under drought on the one hand is advantageous to maintain light interception by foliage and thus dry matter production, but on the other hand side it creates high water loss by transpiration and rapidly depletes soil water (Spitters and Schapendonk, 1990). Yield is a function of intercepted solar radiation, light use efficiency and harvest index (Araus *et al.*, 2001; Haverkort and Goudriaan, 1994). The maintenance of LAI/light interception in late senescencing genotypes did not result in a lower relative reduction of tuber DW under drought stress, quite the contrary. The sustained light interception can only have positive effects when the incoming light is efficiently transformed into dry matter that is then allocated to tubers. In late senescencing Gen B, photosynthates were rather allocated to stems than to tubers (HI reduced), resulting in tuber DW reduction. At time of tuber DW reduction, HI in Gen E was not reduced, indicating restrictions in the conversion of light to dry matter, which could be a result of high soil water depletion (high SSI) (Spitters and Schapendonk, 1990). Similar observations were found by Tourneux *et al.* (2002): In potato genotypes that sustained light interception, tuber yield was reduced due to a strong decline in light use efficiency and HI. Therefore, the strategy of early senescencing genotypes to reduce LAI and by this the water use, was more effective as it prevented high stress severity levels.

4.6.1.3. Drought in T80

Late drought treatment also reduced LAI to a higher extent in early senescencing genotypes that in late senescencing genotypes. LAI in early senescencing genotypes was

already reduced by 47 – 59 % compared to control at low stress severity at 6 DAWI whereas LAI in late senescencing genotypes were diverged from control 16 (Gen E) and 26 DAWI (Gen B) by 40 %. Likewise, leaf expansion rate ceased completely 7 DAWI in Gen C and D, 3 DAWI in Gen A and 12 and 16 DAWI in Gen E and B. The early cease of leaf expansion in early senescencing genotypes was probably due to senescence patterns and therefore higher sensitivity to changes in soil water content. This is supported by the fact that leaf expansion reached zero levels already at 3 DAWI (SSI= 0.13) and as 6 DAWI most leaves were yellowish, it is assumed that senescence started earlier compared to Gen C and D. Leaf expansion patterns in late senescencing genotypes also fit well to observations of senescence in the field, as senescence started earlier in Gen E and also leaf expansion ceased earlier under drought conditions. As leaf expansion in early senescencing genotypes ceased already during the first days after withholding irrigation, the further reduction in LAI by 62 – 73 % that was found at 26 DAWI, can only be the result of leaf shedding.

The relative maintenance or later reduction of LAI in late senescencing genotypes seems to be advantageous when considering relative tuber DW at 26 DAWI (T80) that was reduced only by ~37 % compared to control. However, late genotype displayed differences in water extraction. Gen E extracted a high amount of soil water and at 26 DAWI was exposed to an SSI of 13.0, whereas Gen B used water less excessively and was exposed to an SSI value of 3.9. This is surprising as LAI in absolute values was nearly equal in both genotypes. Therefore plants of Gen B must have reduced their water losses somehow. However, the fact that plants of Gen E were exposed to a three-fold higher SSI than plants of Gen B and nevertheless tuber DW was reduced to the same extend, shows high drought tolerance of Gen E to late induced drought.

The high reduction in LAI relative to control that was found already 6 DAWI in early senescencing genotypes, did not result in a lower usage of soil water in Gen D and C, which resulted in high SSI values at treatment end of 7.1 (Gen D) and 6.0 (Gen C). High water losses despite a high reduction in LAI might on the one hand show the higher evaporative demand due to high temperatures but on the other hand it also shows the inability of these genotypes to regulate waters losses. The high reduction in tuber DW, 26

DAWI might result from reduced light interception due to the strong reduction in LAI, combined with the effects of high stress severity that probably reduced light use efficiency.

Gen A could prevent a reduction in tuber DW, probably by combining the effects of reduced transpiration surface and a conservative water usage. Spitters and Schapendonk (1990) stated that high water use efficiency in combination with a low transpiration rate under severe drought stress might advantageous in producing high tuber yields, as soil moisture is conserved. The relative higher reduction in chlorophyll content (higher degree of senescence) in Gen A relative to early senescencing Gen C and D under drought in T80 might also have contributed to the lower water usage, as leaf senescence s is another strategy to reduced water losses by the canopy (Munné-Bosch and Alegre, 2004). Gen A seems to be more resistant to late induced drought stress than late maturing genotypes and early senescencing Gen C and D. As Gen A also shows highest tuber DW in absolute values, it seems to be a promising candidate for situations, when in rain-fed system soil water becomes limiting and the end of the growing season.

4.6.2. Leaf expansion rate and Leaf water potential

Across genotypes leaf area expansion under drought stress decreased with decreasing LWP and completely ceased when LWP fell below -0.5 MPa in T54, -0.45 MPa in T67 and -0.40 MPa in T80. These results are in accordance with findings of Gandar and Tannar (1976) that could show that leaf elongation in potato plants ceases at leaf water potential between -0.4 to -0.5 MPa. The cessation of leaf expansion at higher LWP in mid (T67) and late induced drought (T80) in comparison to T54 might result on the one hand from plant age, indicating higher sensitivity to drought at late stages of leaf expansion. On the other hand, the higher evaporative demand in T67 and T80 in comparison to T54 probably was an additional factor influencing leaf expansion (Jefferies, 1989). By using data from studies of Boyer (1970) and Tanguilig *et al.* (1987), Yang *et al.* (2009) could confirm observation of Gandar and Tannar (1976) that leaf expansion ceased when leaf water potential reaches values lower than -0.50 to -0.4 MPa. Gandar and Tannar (1976) moreover could demonstrate that leaf elongation in the field mainly occurs at night and argued that the reduction in leaf elongation is likely due to a lower recovery of LWP overnight.

Leaf expansion rate in Gen A and C was least affected by drought in T54 and T67. Contrary, predawn leaf water potential diverged earlier from control than in the other genotypes probably as a result of smaller root system. Therefore, efficient mechanisms to sustain leaf expansion under drought conditions like increasing cell wall elasticity to maintain turgor (Rodrigues *et al.*, 1995) must exist in these two genotypes. Jefferies and MacKerron (1986) comment on the work of Gandar and Tannar (1976) that factors like turgor potential and osmotic adjustment influence leaf extension rather than leaf water potential. In a review, van Volkenburgh (1999) mentioned tugor pressure, cell wall elasticity, hydraulic conductance of cell walls, osmotic regulation, and endogenous growth regulators as influential factors for leaf expansion. Indeed, a reduction in leaf expansion/elongation prior to a reduction of LWP under drought stress has often been found (Wang and Bughrara, 2007; Durand *et al.*, 1995). The higher sensitivity of leaf expansion rate to changes in soil water was also found for the five potato genotypes.

Under all drought treatments, predawn LWP of late senescencing genotypes and Gen D was reduced in comparison to control only at high drought stress severity in or not at all. However, leaf expansion rate was highly reduced by drought stress. This high reduction in water-loosing surface area probably enables these genotypes to delay tissue dehydration and maintain LWP (Pérez-Ramos *et al.*, 2012).

4.6.3. Relative chlorophyll content

The degradation of chlorophyll/senescence was once evaluated by visual inspection at harvest and by SPAD meter reading in a seven day rhythm. Sometimes there is a discrepancy between the measured reduction of leaf relative chlorophyll content and data collected by visual inspection, especially in T67. For example, 16 DAWI in T67, senescence characters were identified in plants of early senescencing genotypes, but no decline in relative chlorophyll content was discovered via SPAD meter. The differences could be due to: (1) differences in data collection, as data was raised once at leaves from five different plant levels on the physiological plant, and in the other case data was collected from the whole plot (2) SPAD readings were carried out in a 7 day rhythm and BBCH evaluation in a 10 day rhythm, leading to a discrepancy of 2 days at the second sampling occasion and of 5 days at the third sampling occasion.

However, drought stress typically decreases relative chlorophyll content in plants (Anithakumari *et al.*, 2012; Rong-hua *et al.*, 2006; Parida *et al.*, 2006). The formation of free radicals under drought is mainly responsible for chlorophyll degradation under drought stress. Stomatal closure finally leads to a reduced availability of electron acceptor NADP+, due to a depletion of internal CO_2 by calvin cycle, and thus to an over-reduction of the electron transport chain. The surplus electrons from the ongoing light reaction are transferred to oxygen, creating free radicals (reactive oxygen species, ROS) which, if not detoxified by enzymes, damage cell membranes, inhibit enzymes, and reduce chlorophyll content. Enzymatic as well as non-enzymatic defense mechanisms exist to mitigate the effects of free radicals (Sharifi *et al.*, 2011; Liu, 2010). However, the ability or the effectiveness of such mechanisms varies between and within plant species. By subjecting wheat lines to drought by withholding irrigation at flowering, Sharifi *et al.*, 2011 could show that the activity of antioxidant enzymes like peroxidase increase under drought to a higher extent in drought tolerant than in drought sensitive lines. Peroxidase activity was linked with chlorophyll stability and yield. The ability to maintain high chlorophyll content (stay green) under drought is considered as an important trait for drought tolerance (Anithakumari *et al.*, 2012). Staying green is thought to be either due to a continued chlorophyll biosynthesis (Thomas and Ougham, 2014) or due to constraints in chlorophyll degradation (Vicentini *et al.*, 1994). Chlorophyll is degraded via the combined enzymatic action of chlorophyllase, Mg-dechelatase and pheophorbinde a oxygenase (Matile *et al.*, 1996; Vicentini *et al.*, 1994). Stay-green mutants of *Festuca pratensis* Huds. display a deficiency to carry out oxygenolysis of pheophorbinde (Vicentini *et al.*, 1994).

However, in this study, relative chlorophyll content (SPAD readings) was only reduced relative to control, when drought stress was applied during a late development stage (T80). Under early drought (T54) and partly under drought in T67, higher SPAD values were recorded compared to fully-irrigated conditions. Higher SPAD values under water limited conditions in potato were also found by Yactayo *et al.* (2013) and in *Planatago ovato* and *P. psylluim* (Rahimi *et al.*, 2011). The observation of increasing SPAD values with increasing stress severity in the present study probably was not due to an increase in chlorophyll content per se, but rather the result of an accumulation per unit leaf surface. According to Tardieu *et al.* (1999) the higher sensitivity of leaf expansion to drought stress

compared to photosynthesis, reduces specific leaf area and results in a higher amount of chlorophyll per unit leaf area (Liu and Stützel, 2003). This is supported by studies of Niagam and Aruna (2007) and Marenco *et al.* (2009) that found a negative relationship between SLA and SPAD. As SLA examination of potato genotypes in this study gave unclear and inconsistent results, it cannot be said whether the increase in SPAD values under drought is the result of reduced cell elongation at sustained growth. However, the data received from plants of Gen C confirm the hypothesis. Leaf expansion rate of Gen C was least affected by drought in T54 and T67 and relative SPAD readings exhibited a decreasing trend with increasing stress severity.

If drought stress in T54 and T67 resulted in a degradation of chlorophyll is difficult to say, as the effects of a reduction in leaf area expansion were maybe overwriting the degradation of chlorophyll. That this probably was the case (even if only at high SSI, 26 DAWI), is indicated by the higher reduction of leaf expansion under drought conditions in T67 compared to T54 and no perspective high increase in SPAD values. In early senescencing genotypes SPAD values in T67 rather decreased or remained at level of control. Additionally, the visual inspection five days after the last SPAD readings (BBCH determination at harvest) found senescence characteristics in early maturing genotypes. In late senescencing genotypes, SPAD values increased with increasing stress severity under drought in T67. The reduction in chlorophyll content in early senescencing genotypes (at treatment end), but not in late senescencing genotypes in T67, might be due to the differences in maturity class and/or sink source relationships (Thomas and Ougham, 2014). Genotypes of the early senescencing group already showed senescence characteristics (visual inspection) under well-watered conditions 83 and 86 DAP, whereas in late senescencing genotypes plants yellowing of leaves appeared 96 DAP or not at all during the experimental period in case of Gen B. This might indicate a higher susceptibility to drought in terms of chlorophyll degradation at a late development stage. 80 DAP, flowering was already over in plants of Gen D, and flowering did not occur in Gen A and C under drought conditions. Also in late senescencing genotypes early signs of senescence only were found (visual inspection) after berry formation. This indicates that efficient mechanisms exist within late senescencing genotypes, to protect chlorophyll from degradation and that they probably are susceptible to chlorophyll degradation only at a late

development stage and at high stress severity. The predisposition for chlorophyll degradation by environmental factors is therefore age dependent (Thomas and Ougham, 2014). Thomas and Ougham (2014) also suggest that source sink relationships are involved in the determining the transition point between C-capture and N-mobilization (senescence initiation). Thus, maybe also the faster development of tubers in early senescencing genotypes also might have played a role in the differences in chlorophyll degradation between early and late senescencing genotypes.

Late drought stress (T80) reduced relative chlorophyll content in early, but not in late senescencing genotypes in comparison to control. 21 DAP, relative chlorophyll content was reduced by 75 %, 37 % and 50 % compared to control in Gen A, C, D. The high reduction in Gen A is in accordance with observations in the field (visual inspection), as 6 DAWI most leafs were already yellowish whereas in Gen C and D, leaf yellowing just started. This point to a fast nutrient remobilization and translocation under drought in Gen A, supported by the fact, that tuber DW highly increased by 130% and 116% compared to control, 6 and 16 DAWI. The other genotypes displayed such an increase in tuber DW only at 16 DAWI. At treatment end (26 DAWI), tuber DW was reduced in all genotypes, except in Gen A. The reduction in tuber DW was highest in early senescencing genotypes C and D. Thomas and Ougham (2014) stated the importance of a fast and complete nutrient transfer from senescencing tissue to reproductive organs, besides a sustained C-capture. As chlorophyll degradation started later in Gen D and C compared to Gen A, nutrient transfer might have been incomplete contributing to tuber DW reduction under drought stress.

Late senescencing genotypes could maintain relative chlorophyll content under drought stress longer than early senescencing genotypes and therefore were probably able to sustain C-capture, leading to a lower reduction in tuber DW 26 DAWI in T80. Therefore either the early and fast nutrient mobilization to escape drought or the maintenance of chlorophyll for a prolonged C-assimilation contributes to tolerance to drought at late development stage.

Whether the maintenance of chlorophyll content under drought conditions in T54 and T67 contributes to drought tolerance (in terms of low tuber DW reduction under drought) depends on development stage of above-ground plants part and development of tubers. Under drought in T54, chlorophyll content showed a decreasing trend with increasing

stress severity only in Gen C and tuber DW was least affected by drought. The maintenance of chlorophyll content especially during early stage of drought stress in T54 (low stress severity) might have contributed to C-assimilation, but assimilates were preferentially partitioned into non-tuber biomass in Gen A, B and D. However, at the end of T54 (highest stress severity) senescence characters were found in all early senescencing genotypes, but that did not lead to a lower or higher reduction in tuber DW than in late senescencing genotypes that did not display senescence. The relative maintenance of chlorophyll content at the beginning of T67 in early senescencing genotypes and the observed senescence at treatment end probably contributed to C-capture under low stress severity and nutrient remobilization at high stress severity level, allowing these genotypes to maintain tuber DW under drought stress. Therefore, it cannot be said generally that chlorophyll stability under drought contributes to tuber DW maintenance per se. Also other influential factors must be taken into consideration.

4.6.4. Chlorophyll fluorescence

As chlorophyll content and chlorophyll fluorescence have been shown to be closely related (Percival *et al.*, 2008), the increasing SPAD values under drought conditions might partly explain the results from chlorophyll fluorescence analysis under drought conditions. Maximum quantum yield in the dark adapted state; Fv/m, was not affected by drought or was higher than under fully-irrigated conditions.

Fv/m refers to the maximum efficiency of PSII to use absorbed light for photochemistry, i.e. to reduce the primary quinone acceptor Q_A, and is widely used to examine performance of the photosynthetic apparatus (Baker, 2008). The maximum quantum efficiency is often reported to decrease under drought conditions (Anithakumari, 2012; Puteh, 2013; Hayato and Mukhtar, 2010) due to photoinhibition or photo oxidation in PSII complexes (Rohacek, 2002; Filipović *et al.*, 2013). However, there are also studies showing that drought not always affects quantum efficiency of PSII. Jeffries (1994) subjected potato plants from time of 50 % emergence on to drought conditions, but found no clear effect drought on Fv/m during the drying cycle. As also was observed in the present study, minimal fluorescence Fo in droughted potato plants in the experiment of Jeffries (1994) was reduced by about 9 % relative to control. However, the reduction in Fo did not affect maximum quantum efficiency of PSII. Minimal fluorescence is measured by applying a

weak PPFD (0.1 µmol m^{-2} s^{-1}) that is low enough not to drive photochemistry, to a previously dark adapted sample so that all reaction centers were in a `open state´ (Q_A maximally oxidized, capable for photochemistry) (Baker, 2008). Jefferies (1994) suggest that either a degradation of chlorophyll or a change in leaf structure were underlying causes for the reduction in Fo. When concerning the positive relationship between chlorophyll a content and Fv/m found by Filipović *et al.*, (2013) in leaves of apricot and the assumption stated previously that the measured increase in SPAD of droughted potato plants might result from a chlorophyll accumulation due to reduced leaf area expansion, the observed increase in Fv/m under drought condition probably resulted from a high density of chlorophyll per unit leaf area.

As Fv/m in potato genotypes did not decline under drought, photoinhibition probably did not occur in photosystems (Jeffries, 1994). Based on the fact that drought in his experiment had no effect on the operating efficiency of PSII (Fv'/m') under light conditions, Jefferies (1994) suggested that the excess energy resulting from CO_2 limitation due to stomatal closure was used in photorespiration and oxidized in the pentose phosphate pathway and by this dissipated from the system. Such mechanisms would allow the proceeding of photochemical processes and thus adaption to drought stress conditions (Jefferies, 1994; Kingston-Smith, 1997).

In potato genotypes Fv/m under drought conditions was increased relative to control in case of Gen B, D and E or remained at level of control in Gen A and C in all drought treatments. The increase Fv/m in late senescencing genotypes and Gen D in contrast to early senescencing Gen A and C might be due to a higher accumulation of chlorophyll per unit leaf area resulting from a higher reduction of leaf expansion rate.

The fact that maximum quantum efficiency in dark-adapted state was not reduced under drought conditions implies that the potato genotypes were able to adapt to drought stress conditions and protect photosynthetic complexes from damage. The degradation of chlorophyll that was observed by visual inspection or by SPAD meter reading did not impact Fv/m. Munné-Bosch and Alegre (2004) and Liu *et al.*, 2010 reported that the loss of chlorophyll under adverse conditions constitutes a photoprotective mechanism. By subjecting six woody plant species to drought, Liu *et al* 2010 could show that drought

stress increases the chlorophyll a/chlorophyll b ratio, i.e. reduced the amount of light harvesting pigments in relation to light processing pigments. Furthermore, under drought the woody plants species were increasing their photoprotective and antioxidant capacity by increasing the ratio of carotenoids/chlorophyll a+b.

In contrast to early senescencing genotypes, degradation of chlorophyll under drought stress could only be detected at high stress severity in T80. As maximum photochemical efficiency under drought was not reduced in comparison to control, highly efficient dissipation mechanisms to protect photochemical processes might exist within these genotypes.

4.7. Effect of soil moisture availability on root architecture

The efficiency by which plants can extract soil water depends on distributions patterns within the soil profile, root length characteristics, hydraulic conductivity and the ability to penetrate even compacted soil layers, factors that all have been shown to be affected by drought stress (North and Nobel, 1991; Jeffries, 1992, Rodrigues *et al.*, 1995; Bengough, 2010). In lupins, the increased portion of fine roots and an enhanced penetration of deeper soil layer under drought stress improved the efficiency of water uptake (Rodrigues *et al.*, 1995). Further, the balance between water losing and water obtaining organs, i.e. root/shoot ratio under drought is important to adapt to water limited conditions (Liu and Stützel, 2003). However, shoot/root decreased under drought stress due to due a higher reduction in leaf dry weight than root dry weight and not due to an increase in root dry weight (Blum, 2005).In potato, the relative high susceptibility to drought stress is ascribed to its shallow root system, its low capacity to extract soil water (van Loon, 1980). Further, potato plants are reported to be unable to penetrate compacted soil layers (Parker *et al.*, 1988).

4.7.1. Drought in T54

Early drought reduced root length in all genotypes. Late senescencing genotypes showed a higher susceptibility to even mild drought stress, as ARL and MRL were already reduced in comparison to control 6 or 16 DAWI. In early senescencing genotypes, both parameters were affected at higher stress severity. No effect of increasing drought stress on MRL was found in Gen C. Therefore, plants of this genotype could maintain maximum root length

and efficiently deplete soil water, which is reflected in the high stress severity (SSI) at treatment end and in early reduction in LWP compared to control. LWP in the other genotypes was reduced only at highest stress severity. Rodrigues *et al.* (1995) also found that a reduction of available soil water by 60 % had no effect on predawn leaf water potential of lupine plants, which points to a better relation of predawn water potential with soil moisture content from deeper soil layer compared to total available soil water. Moreover, the physical properties of sandy soils allow a high extraction of soil water (Rodrigues *et al.*, 1995).

4.7.2. Drought in T67

Increasing drought in T67 affected root length in early genotypes. 26 DAWI ARL and MRL were reduced in comparison to control, however, in plants of Gen D only a reduction in MRL under drought was found. Although ARL was reduced by drought to the same extent in early maturing genotypes, LWP diverged from control 16 DAWI in Gen A and C and not at all in Gen D. The higher MRL (absolute length) and the maintenance of ARL under drought might have enabled plants of Gen D, to extract water from deep soil layers and thus to retain LWP. This is supporting the statement of Rodrigues *et al.* (1995) that predawn LWP is better related to soil water content from deep soil layers. Moreover, as plant canopy (LAI) in Gen D was reduced by 60 % compared to control, as in the other early senescencing genotypes, but the advantage of a large root system was mostly maintained under drought, Gen D could create a better balance between water gaining and water loosing plant parts (see above). Although plants of Gen D had a higher potential to extract soil water due to its larger root system in comparison to Gen A and C, soil water depletion was not clearly higher, indicating a more conservative water use and lower transpiration (Liu and Stützel, 2002). In late senescencing genotypes, increasing drought stress did not lead to reduction in root length. Plants of late senescencing genotypes were equipped with the largest and widest root systems among genotypes and thus were able to deplete a large soil volume, as reflected in high SSI inT67. The high water usage was probably driven by the high demand of the canopy, as late senescencing genotypes maintained LAI under drought in T67. LWP in late senescencing genotypes and in Gen D was maintained longer than in early senescencing Gen A and C and likewise leaf area expansion was reduced to a higher extent, which might be indicative (as previously stated)

of a lower SLA. Pérez-Ramos *et al.* (2012) found a negative relationship between SLA and LWP in four perennial herbaceous species under drought conditions and stated that an alteration in leaf structure and the maintenance of root length contributes to leaf dehydration avoidance.

However, the root system of Gen A was smallest among genotypes in terms of RW, ARL and MRL. Despite the small root system, plants of this genotype under drought in T67 were able to extract a huge amount of soil water, resulting in an SSI in T67 that was not much lower than in late senescencing genotypes. The ability of potato plants to extract considerable amounts of soil water even from below their rooting depth under drought conditions was shown by Parker *et al.,* (1988). Therefore, Gen A seems to be able to efficiently extract soil water under drought conditions.

4.7.3. Late drought in T80

Late drought (T80) did not lead to smaller root length (ARL, MRL) in Gen B. Predawn LWP was maintained during the whole drying cycle, but soil water depletion was low in this genotype. The low usage did however not lead to a strong decrease in tuber DW, indicating that water usage was highly efficient in Gen B (Wang and Bughrara, 2007). Contrary, plants of Gen E used a high amount of soil water. MRL and predawn LWP were only found to be reduced by drought in comparison to control 26 DAWI. The high usage of water points to a lower efficiency to use the extracted soil water. The reduction in average and maximum root length at treatment end in early senescencing genotypes probably had a higher effect on Gen C and D than on Gen A, as they used a high amount of soil water during T80 due to the lower reduction in LAI. A shortage of roots at treatment end additionally lowered the already small amount of potentially available soil water, having negative consequences for plant performance.

Often, drought had a higher effect on average root length than on maximum root length. Therefore, potato cultivars under droughts seem to put more emphasis on the maintenance of excess to water from deeper soil layers. In a review of Wasson *et al.* (2012), deep rooting and a redistribution towards higher branching in lowers soil layers were considered as crucial determinants for water access and drought tolerance.

Under drought conditions, often an increase in root system width was observed, mainly in T80 and T67. This was observed mostly under low or intermediate stress severity conditions. Unfortunately, not much information is available about the effect of drought on width of root systems. However, it could be speculated, that with a wider root system, plants could access a larger soil compartment and thus improve access to water.

4.8. Problems and suggestions

The inconsistent data received from the SLA examination raises the question whether it was due to (1) inappropriate sampling design, (2) data confusion at leaf weight and area determination or (3) due to physiological and morphological behavior of potato genotypes under drought conditions that does not alter SLA.

Under drought conditions, SLA is expected to decrease due to a higher impact of drought on leaf expansion than on photosynthesis (Tardieu *et al.*, 1999). As data from leaf expansion and relative chlorophyll content determination point to a clearly reduced leaf area and since photosynthetic apparatus was probably not severely inhibited by drought (based on chlorophyll fluorescence observations) SLA was likely to decline under drought stress. Therefore, there is evidence, that the source of error could be confounded date at leaf weight or area determination. As sample size was huge, and three samples from every plant were taken, this could have been possible. However, as the whole data set was affected and not just single sampling occasions or genotypes, such source of error would not completely explain the inconsistent SLA results. The most probable influential factor was the inappropriate sampling design. Sampling of leaves started in the early morning before sun rise and proceeded throughout the day. By examining the influence of sampling method on SLA of three contrasting wild species (annual forb, perennial legume and sklerophyllous tree) Garnier *et al.* (2001) stated, that varying source sink relationships throughout the day and the hydration status of leaves could influence specific leaf area of crops. However, a further attempt of the present study was to examine the combined effect of leaf age and drought on the SLA of the five potato genotypes. Unfortunately, the sampling design did not have to potential to allow such examinations, as SLA was determined at every sampling occasion on the third, sixth and ninth fully-expanded leaf. It

would have been better, to label developed leaves on potato plants and by this knowing their age, and then following them through their development.

Knowing the time of leaf emergence also would have been advantageous for leaf expansion rate determination. This would have allowed distinguishing exactly between an age-related decrease in leaf expansion and the effects of drought. Further, one would have been able to determine the leaf age, at which potato leaves are fully-expanded.

The evaluation of plants phenological sage throughout the treatment period was appropriate to display the development of potato plants. However, to increase data quality and accuracy BBCH evaluation should also be done on the perspective harvest plant and not only on the whole plot.

Also a higher data quality on tuber area would have been obtained by measurement of not only tuber length and tuber width, but also tuber height.

At the different sampling occasions, stolon and root dry weight was not analyses separately. This should have definitely been done, as from an increase or decrease in below-ground biomass DW (roots + stolon) no clear conclusions can be drawn. The change in below-ground biomass DW could either result from weight changes in stolons or roots.

The stress severity index developed in this study gives insight into the water usage patterns of the contrasting potato genotypes. However, as the index was based on an exponential function, it probably overestimated the impact of a small change in soil water content. A small reduction in soil water content does not necessarily constitute a drought stress situation for plants and at very low soil moisture content a further reduction in water content does not substantially increase the high drought stress for plants. Therefore, the use of a sigmoid function could improve the stress severity calculation. However, an exponential function had the advantage of just one parameter

5. Conclusion

The effect of drought on potato plants was highly variable, depending on the time/ development stage in which it occurs. All potato genotypes were shown to be highly susceptible to water shortage during tuber initiation and early tuber bulking. HI was markedly reduced under early drought as partitioning was driven away from tuber, in favor of non-tuber biomass. As chlorophyll content and Fv/m were largely maintained under drought, and LAI was reduced by about 40 %, reduction in intercepted radiation (besides HI reduction) mainly contributed tuber DW reduction under early drought. The relative maintenance of leaf expansion and deep roots under drought conditions in Gen C probably was advantageous to sustain light capture and access to water, leading to a low reduction in tuber DW in terms of early drought. In potato production, a water shortage during tuberization and early tuber bulking should be prevented, as otherwise, tuber yield is at risk.

When a drought situation occurs after flowering and when all tubers are at bulking stage (early senescencing genotypes, T67), drought does not affect HI or tuber DW as genotypes can escape the adverse effects of drought. When potato genotypes are flowering or forming berries and have some tubers still at tuberization stage (late senescencing genotypes in T67), then water deficit highly affects tuber DW, probably as flowering/berry formation creates a competition for resources. Non-flowering under drought therefore seems advantageous to cope with the drought situation. The maintenance of LAI under drought conditions as seen in late senescencing genotypes when plants are flowering doesn't seem to have the potential to positively impact tuber DW. Light interception is maintained, but assimilates are rather partitioned into non-tuber biomass (HI reduction), and the maintenance of a large transpirational surface rapidly creates severe drought situations that could hamper light use efficiency. The maintenance of average as well a maximum root length allowed these genotypes to highly deplete soil water. The reduction of LAI in early senescencing genotypes under drought reduces water losses, resulting in less severe drought conditions that probably decrease light use efficiency to a lesser extent. The reduction in chlorophyll content at the end of T67 seems to contribute to tuber DW maintenance under drought stress due to nutrient remobilization/translocation and the

photoprotective potential of such chlorophyll degradation. The reduction in chlorophyll content therefore can help to sustain photochemical efficiency in potato plants under drought stress. As chlorophyll degradation did not occur in late senescencing genotypes and nonetheless Fv/m was maintained, highly efficient photoprotective mechanism must exist within these genotypes. Irrigation water can therefore be saved in early maturing genotypes after flowering, as this will not largely impact tuber DW.

For the situation of late drought there seems to exist two possible strategies to deal with the water shortage. Potato plants can either maintain LAI and chlorophyll content to sustain C-capture as the high share of tubers being at tuber bulking and the completion of flowering/berry formation seem to prevent a reduction in HI, and thus assimilates are partitioned to tubers. However as root length under drought conditions was maintained, the late senescencing genotypes seem to differ in their efficiency to use soil water. The other possibility is an early reduction in LAI and a fast degradation of chlorophyll, to avoid high water losses/a severe drought situation and efficiently translocate nutrients to tubers. The reduction in root length in early senescencing genotypes under high stress severity at treatment end did not negatively affect Gen A, probably as water loosing organs were highly reduced and thus water demand.

In summary, assimilate partitioning patterns in potato genotypes under drought conditions constitutes an important factor determining the effect of water shortage on tuber DW. Moreover, the phenological development stage in which potatoes are exposed to water limiting conditions is a major influential factor and largely determines the performance under drought stress. Further, the contribution of physiological and morphological adaption patterns to drought tolerance highly depend depends on the respective phenological development stage.

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