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Growth responses of a *Tritordeum* hybrid and its ancestors to drought

Master Thesis

by

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Acknowledgments

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Statement of Originality

I hereby confirm that I have written the accompanying thesis by myself, without contributions from any sources other than those cited in the text, references and acknowledgements. This applies also to all graphics, drawings, maps and images included in the thesis.

Stuttgart, 13.11.2013

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Ivan Katsarov

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List of Abbreviations

BBCH	Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie
DAS	Days after Sowing
DM	Dry Matter
ET water	Evapotranspired water
EWR	Ear Weight Ratio
FH	Final Harvest
GDU	Growing Degree Unit
HI	Harvest Index
IH	Intermediate Harvest
IPCC	Intergovernmental Panel on Climate Change
LAR	Leaf Area Ratio
LDMC	Leaf Dry Matter Content
LWR	Leaf Weight Ratio
MLA	Mean Leaf Area
RDW	Root Dry Weight
RGR	Relative Growth Rate
RWR	Root Weight Ratio
SLA	Specific Leaf Area
SLF	Senescent Leaf Fraction
SRES	Special Report on Emission Scenarios
SRR	Shoot/Root Ratio
SWR	Stem Weight Ratio
TDW	Total Dry Weight
WUE	Water Use Efficiency

Chapter I: Introduction

1.1 Global change and agriculture: Impacts, adaptation, vulnerabilities

Despite the numerous uncertainties connected with the largely-disputed on-going climate change, at present most leading experts dealing with its assessment are unanimous in their decision to point out some of its predicted effects. Some scientists believe that it is linked to the outcomes of anthropologic activities paved by the globalization and expansion of the world's population (FAO, 2009). Others claim that it is due to the fact that it is a naturally-coded cyclical process (Satterley, 1996). But regardless of the reason for warming up of the Earth's atmosphere it is getting hotter and that could have a role to play in development of certain regions of the world. For some a few degrees temperature increase would perhaps mean good news, with associated benefits ranging from improved touristic potentials to a major boost to agricultural production, whereas for others the same increase could lead to partial or complete devastation (Pollock, 2005).

According to the latest IPCC (Intergovernmental Panel on Climate Change) assessment reports (both in Assessment Report 4 and in the brand new Assessment Report 5) and the different scenarios various regions of the world would have to face conditions, which differ from the current ones so severely that certain adaptation measures would be required. The scenarios deal with the potential spread and magnitude of climatic alterations, depending on socio-economic, political and environmental among other developmental factors. The foreseen steady increase in the world's population by a staggering 34% by year 2050 will skyrocket the pressure in food security. This will possibly lead to the risk of being unable to cope with the demand for food. That would undoubtedly put more pressure on agriculture and its output levels.

Although a significant overall increase in crop production is projected in central and northern Europe, certain regions, such as the Mediterranean basin will have to face a reduction of absolute precipitation amounts and increased plant evapotranspiration levels, a fate which is more or less predicted by all scenarios (Alcamo et al., 2007). That will, in turn, lead to a modification of their current land-use practices, mainly due to the imminent amplification of

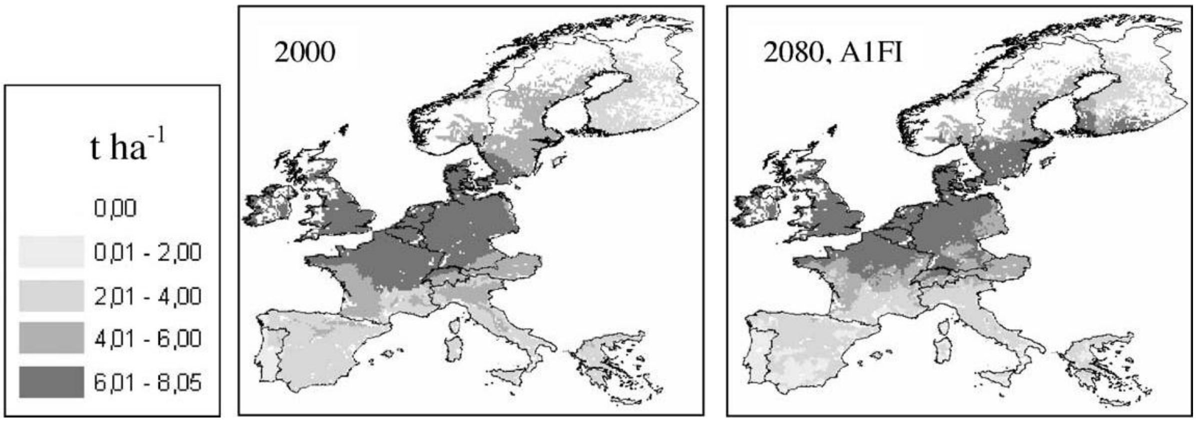

Figure 1: Estimated changes in wheat yields in Europe following SRES A1FI between years 2000 – 2080 (IPCC, 2007)

the current drought stress conditions (Villegas et al., 2009). In the end, those regions of the world could face serious problems in producing enough food to cover the demand.

A general northwards shift of some land-use practices could be expected (Fig.1), especially where adaptation measures in negatively affected regions fail. Climate-infused boost to crop yields could mainly be expected in northern Europe with the leading example of the most important crop in Europe – wheat. The respective increases discussed for northern Europe in time are as follows: +2 to +9% increase by year 2020, +8 to +25% by year 2050, +10 to +30% by year 2080 (Villegas et al., 2009) However, the favourable modification in yearly precipitation and CO_2 levels, allowing for such an increase in production in the north, comes in contrast with the promotion of stress conditions for areas, which are considered as sufficiently productive in present terms (such as the Mediterranean and the south Balkans).

But this shift is not only confined to the example of wheat. Other valuable species are believed to follow the same path. Crop plants, predominantly grown in southern Europe (e.g. maize, soybeans, sunflower and sugar beet) nowadays will become ever more feasible for mass growing in northern areas or at higher altitudes in the south. The projected increase in grain maize supporting cropland in northern Europe will rise by 50% in 2050 (Alcamo et al., 2007).

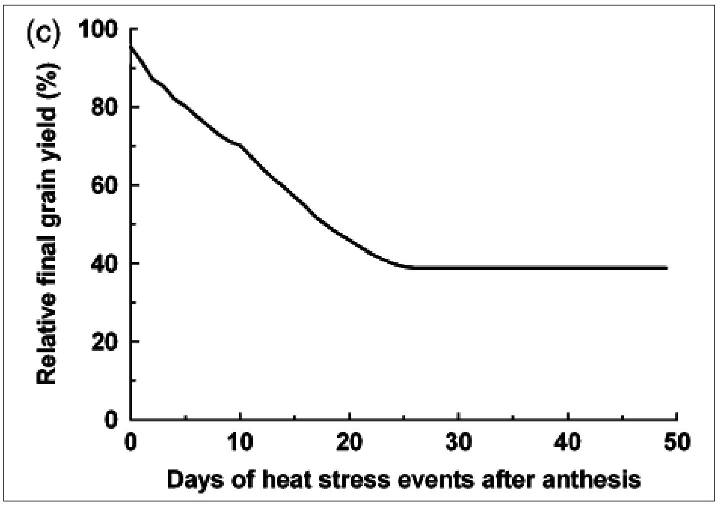

Figure 2: Expected relative final yield decrease with increasing number of days with temperature >34C^0 after anthesis. Source: Asseng et al., 2011.

Same or similar projections are made for oilseed crops (e.g. rapeseed and sunflower), starch crops (e.g. potatoes), cereals and solid bio-fuel crops. Furthermore, an increase in weather extremes may lead to increased yield variability and a reduction in average yields in affected lands (Alcamo et al., 2007). The increase in frequency and severity of heat spells and flood occurrences after excessive precipitation events will add a further line to the vulnerability list of agriculture in southern Europe. For instance, the grain yield of wheat could drop significantly with the amount of hot days during the reproductive phase of growth (as illustrated by Fig. 2) (Asseng et al., 2011).

Those increasingly negative expectations, whether justified or not, will undoubtedly serve as a driving force to certain producers in the sphere of agriculture to start discussing possible impact mitigation or adaptation strategies to their enterprises in order to avoid potential market risks in future. Being adaptive and able to reduce fluctuations in production or quality of output in a world driven by economics and markets is likely to be a lucrative goal for anybody who would want to stay competitive or even excel on those markets.

1.2 Objectives and scope of the study

The following study is exclusively focussed on providing a description of the growth behaviour of three different plant species when put under three predetermined water supply levels. It is restricted to the environmental settings described in chapter II only.

Additionally it strives to outline and test a simple experimental approach that could be used as a phenotypic platform for studies related to drought stress on plants. It does not represent an attempt at providing any ultimate guideline on how those plants are likely to respond to drought stress under any other conditions, e.g. increasing levels of ambient CO_2 concentrations, which might alter the sensitivity of crops to drought.

Although it was intended to simulate the conditions of Central Europe, the conditions realized in year 2013 may differ from expectations based on long-term observations. Also, the prevention and analysis of pathogenic effects on growth were not assessed by the trial.

1.3 Plant material

1.3.1 *Tritordeum*

Tritordeum is an amphiploid hybrid species obtained upon the inter-generic cross-breeding of wild perennial barley (*Hordeum chilense*) and wheat (in this case *Triticum durum*) parent species. It exhibits agronomic, chemical, physico-chemical and rheological properties comparable to bread wheat (Martín et al., 1998). In addition, due to the contribution of its barley genes it possesses better resistance to pathogens such as *Fusarium culmorum*, *Septoria nodorum* and powdery mildew (Rubiales et al. 1992; Rubiales et al. 1993; Rubiales et al. 1996). A scheme on the inter-specific breeding is shown in Fig. 3.

This hybrid species was first generated by the group of Dr. Antonio Martín at the Sustainable Agriculture Institute of CSIC Córdoba, where the researchers have developed a number of advanced lines with agronomic traits that compete with conventional grain (AgraSys, 2013; Martinez de la Concha Doncel, 2010).

Tritordeum is regarded as a possible alternative to bread wheat in the future where environmental conditions might render the cropping of wheat economically unfeasible. Although its bread-making quality is inferior to that of wheat (Gallardo & Fereres, 1993; Martinek et al., 2003), the extremely high protein content in its grains hints at a certain potential for large-scale introduction of *Tritordeum* as a source of human nutrition.

Certain amount of the elements found in *Tritordeum* deliver outstanding nutritional and health benefits (AgraSYS, 2013). Some examples of the potential marketing options for this cereal are in food products aiming at improving digestion or tackling obesity and diabetes. It is also touted for its beneficial effects in sinking bowel cancer risks and in strengthening cardio-vascular health. Remarkably rich in Lutein, a carotenoid antioxidant efficient in prevention of macular degradation, *Tritordeum* is stoutly recommended food for the safeguarding of eye health. Its levels of Lutein surpass by up to ten-fold the amount observed in common bread wheat (AgraSYS, 2013).

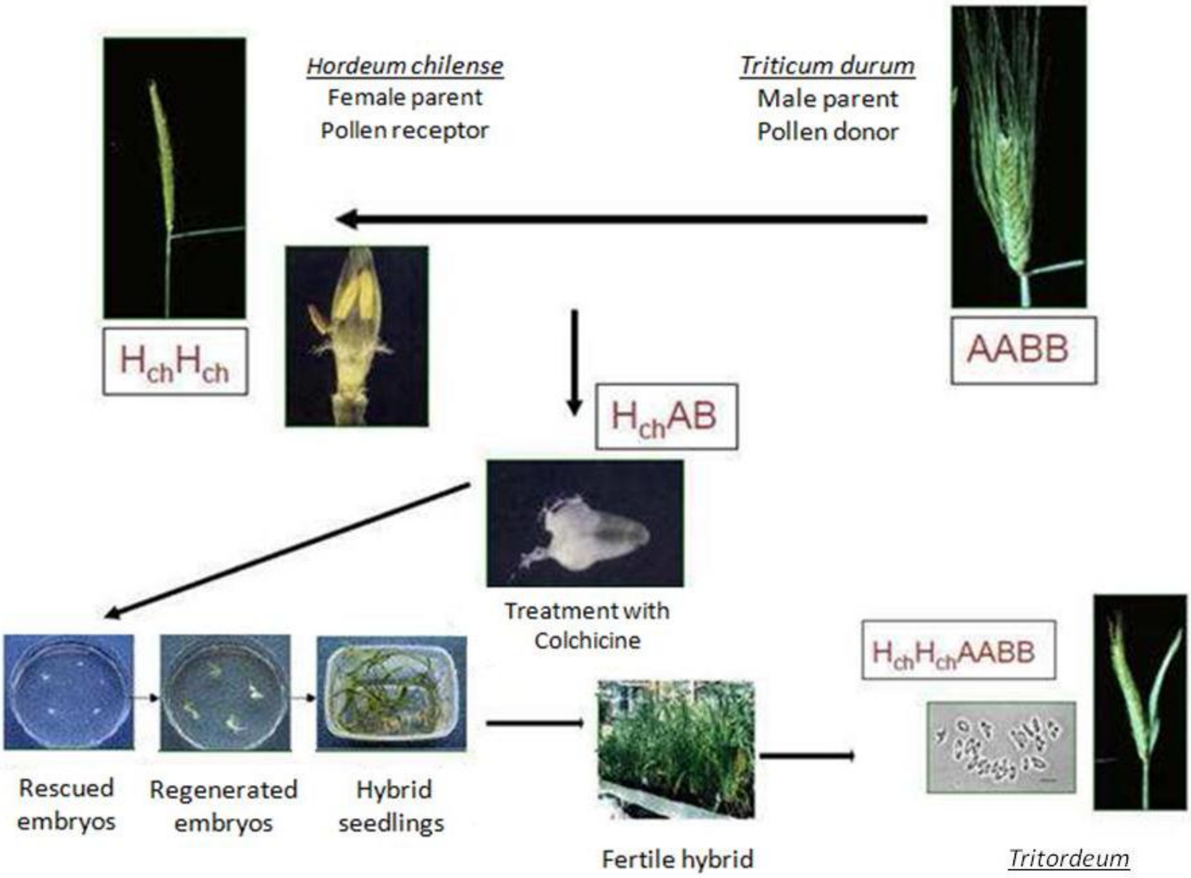

Figure 3: Simplified scheme of the method to obtain a *Tritordeum* hybrid. Abbreviation AABB stands for the genome of tetraploid durum, $H_{ch}H_{ch}$ for the genome of a diploid *H. chilense*, $H_{ch}AB$ for the genome of the infertile hybrid offspring and $H_{ch}H_{ch}AABB$ for the genome of the fertile hexaploid hybrid species. Source: Martinez de la Concha Doncel et al., 2010

Tritordeum exhibits specific qualities and traits unlike any other cereal, providing an opportunity for introducing brand-new cereal-based substantial foods to the market. Nowadays in development are lines with and cultivars highly rich in soluble fibre, phenolic antioxidants and microelements. Besides, advanced lines are being selected for enrichment in functional elements, such as starch composition, tocols, vitamins or sugars among others (AgraSYS, 2013)

1.3.2 *Hordeum chilense*

Hordeum chilense is a diploid wild perennial barley type, common for South America (Chile and Argentina). It was already described in the book of botanical descriptions Systema Vegetabilium, written jointly by J.A. Schultes and J.J. Roemer as early as in year 1817.

Nowadays it is mainly to be found in Chile and the western regions of the Argentine provinces Rio Negro and Neuquén. Unlike the eastern foothills of the Andes in Argentine side, where large parts between the coastline and the mountains remained ice-free, the Chilean side of the Andes was almost completely glaciated to the coast during the glacial periods and that led to the severe decrease of the species population (Jacob, 2005). Nowadays, it is well adapted to the climatic conditions in mountainous Chile, where the geography forms no uniform climatic pattern, but a huge variety of microclimates and transition zones (Schwedtfeger, 1976), which probably account for the adaptive properties of *H. chilense*.

The species genome is regarded as a source of valuable traits for potential wheat breeding, such as induced hereditary resistances to both biotic and abiotic stresses. Furthermore it is also seen by scientists as a possible contributor to the expansion of the genetic basis for bread-making quality of traditional wheat species (Martín et al., 1998).

1.3.3 *Triticum durum*

Triticum durum is a member of the wheat family long known to humankind. It can be dated back as far as 4000 years BC to certain areas in today’s Georgia and Pakistan. The species is also known as pasta wheat, for it is closely linked with the history of pasta production due to the specifics of its dough. This characteristic makes it one of the most prominent cereals worldwide with a high economic value. Germany, where the durum croplands amount to around 20000 ha, is currently only able to cover around one third of the country’s domestic demand for this good. As a result, the durum-processing companies are readily providing an incentive for land-owners to produce more high-quality durum grain by pricing it higher than bread wheat (Miedaner & Longin, 2012).

Nowadays around 30 million tonnes of *T. durum* grains per year are produced around the world, with leading producers being Canada, USA, Italy, France, Spain and Greece. Yield of durum is highly variable every year, mainly because of the climate variations or unsuitability of the land chosen in the areas it is grown at (Miedaner & Longin, 2012).

Fig. 4 demonstrates how the productivity of *T. durum* croplands differs across Europe and the general disadvantage of countries with a Mediterranean climate in comparison to countries like Germany and Austria.

If climate is concerned, several totally diverse sowing practices were established in order to alleviate the negative effects of climate on crops.

In Mediterranean regions the sowing begins in late autumn and the grain is harvested in June or July. This stems from the fact that durum is extremely sensible to drought during grain filling (Miedaner & Longin, 2012) and, as mentioned in the previous sub-chapter, to hot weather spells during anthesis. The winters in those areas are mild and moist, which are suitable conditions for the development of the species. On the other side of the coin, the weather in spring may often rapidly get too hot and too dry for durum to thrive.

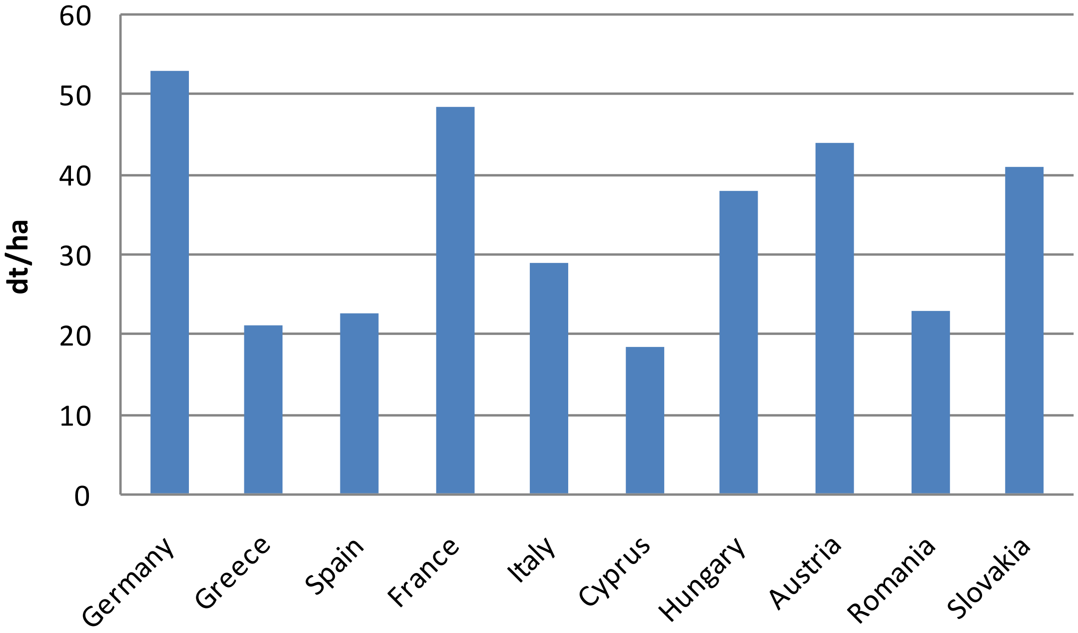

Figure 4: Mean yield in *T. durum* in various European countries per hectare cropland from 2004 to 2011. Source: Miedaner & Longin, 2012.

This is not the case in croplands with a more temperate climate such as Canada, USA and Germany. There, the environmental conditions allow sowing in late spring and harvest in July or August with a relatively short vegetation period as compared to the Mediterranean areas. In terms of pathogenic vulnerability *T. durum* is exactly as susceptible to diseases as bread wheat is. The most notorious infestations observed are by brown rust, powdery mildew, *Fusarium culmorum* and *Septoria nodorum.* Treatment of croplands with a fungicide might increase the yield with up to 5 dt/ha (Miedaner & Longin, 2012).

1.4 Methodology and organization of the thesis

This thesis is predominantly based upon the outcomes of a plant growth experiment, carried out with the species described within the preceding sub-section. In addition to a literature review, the main part of it involved the setting up and conducting of the practical experiment. A subsequent statistical analysis of its findings has served as the basis of a discussion that would allow to test against the central hypothesis of the study, which revolves around the expectations that the hybrid *Tritordeum* is likely to exhibit traits that suggest an increased drought adaptive capacity. A side hypothesis could also be checked to see if *Tritordeum* would in reality exhibit a higher drought tolerance than its wheat parent *T. durum*.

Chapter II: Materials and methods

2.1 Seeds

All plant material (shown in Fig. 5) was received in the form of viable seeds from the supplier **Agrasys SL**. The company is seated in Spain and since 2006 possesses the exclusive rights to operate with the *Tritordeum* brand and to introduce its first commercial varieties to the market.

The grains provided could be easily distinguished by the naked eye, each with its unique characteristic. The 100 seeds weights of the different grain types were measured prior to the initiation of the experimental part and resulted in 6.2 g per 100 seeds in *T. durum* of the cultivar Simeto*,* 3.8 g in *Tritordeum* of the cultivar AUCAN and only 0.4 g in *H. chilense.* This already gives an early hint about the phenological differences that were to be expected from the three species (see parts results and discussion).

Figure 5: *Triticum durum* (left), *Hordeum chilense* (middle) and *Tritordeum* seeds received by the distributing company

2.2 Experimental set-up

The beginning of the experiment was on 15.04.2013 with sowing of the seeds in shallow trays, meant for temporary storage. Those contained enough fertile soil and were carefully watered to ensure proper germination. Sixty seeds were sown for each species studied in the trial. After 9 days almost all of them germinated successfully.

The trial included three different species, which were subjected to three different water supply regimes and two harvesting periods. Four replications of each combination were used. The experiment required a total of 72 individual pots, in which the seedlings were subsequently transplanted 14 days after the start of the trial.

Each pot had the following dimensions – 40 cm height, 10.3 cm inner diameter, 83.3 cm^2 area, 680 g own weight and a volume of 3.3 litres. Two plants per pot resulted in a density of 240 individual plants per m^2, which is close to the density under field conditions. Each pot was initially filled up to a weight of 4.3 kg, which, upon subtracting the pots own weights, resulted in 3.62 kg of soil substrate.

The soil substrate used was a pre-mixed 1:1 combination of sand and a commercially distributed soil – LD80 Fruhstorfer Erde® produced by Hawita GmbH (Vechta, Germany). This brand is characterized by a mixture of 50% peat, 15% bark humus, volcanic clay material and a slow release fertilizer. The overall organic matter content in this soil type amounts to 35%. The soil density is 434 g/L, its pH ($CaCl_2$) is 5.9 and salt content is 1 g/L KCl. In terms of macronutrient availability, the slow release fertilizer provides 150 mg/L Nitrogen, 150 mg/L P_2O_5 and 250 mg/L K_2O. When calculated for the volume of the pots used, a 1:1 mixture of LD80 and sand contains in total 0.25 g per pot of Nitrogen. That corresponds to a nitrogen supply of almost 300 kg/ha, which is more than enough to exclude nutrient availability as a limiting growth factor for this experiment.

The prepared pots were placed in a greenhouse. It was under the same conditions where the seeds were sown and allowed to germinate. Upon the transfer of the seedlings to the pots, initial uniform water supply of 400 ml was applied over the next 10 days. That allowed the seedlings to survive and grow in a healthy fashion, without experiencing any stresses.

On 09.05.2013 or 24 days after sowing (DAS), the differentiated water supply was initialized. It comprised of three substantially varying levels. The medium water amount per day to be used was based on long-term observation data (1991-2005) collected at the Stuttgart airport by DWD (Deutscher Wetterdienst). It showed an average 21 ml per day per pot area rainfall over this 14-year period. For the experiment that amount was rounded to a 20 ml per day per pot and considered as a medium water treatment level.

The other two treatment levels were chosen as percentages of the medium water supply. Conditions of drought were simulated by watering the pots under a treatment with 50% less the amount of the medium water supply or 10 ml per day per pot. On the other hand, the moist conditions were chosen to be characterized by a 50% higher water supply than the medium one or 30 ml per pot per day.

Watering took place every three days with the cumulative amount due for each water treatment, i.e. 90 ml for moist, 60 ml for medium and 30 ml for dry treatment. In cases of prolonged spells of cool or cloudy daylight conditions, watering was partially or fully skipped over the three days watering interval to avoid water leaking from the pots. Water drainage out of the pots was avoided at all costs in order to minimize the error connected with the calculation of evapotranspired water (ET water) later on.

Figure 6: Trial pots at their initial location at the greenhouse (left) and in the outdoor shelter (right)

Following a 37 days of growth in the greenhouse, all pots were transferred to a roof-protected shelter outdoors (Fig. 6) that provided temperature conditions more comparable to in-filed ones. In addition to the modified temperatures, a metallic ring stabilizer was added to each pot during the stem elongation phase to avoid lodging.

The date of the intermediate harvest (25.06.2013) was carefully selected to represent the moment at the turnover from the vegetative to the reproductive growth stage. The onset of flowering was picked as demonstrative for this switch. At that time *T. durum* was slightly past this occasion, *Tritordeum* was almost reaching it and *H. chilense* did not yet show any sign of moving on to reproductive growth. The phenology of the three species differed, but growth accumulated biomass was intended to be compared at exactly the same time for all species, thus ensuring a better evaluation at the end. Additionally, the harvest was chosen to coincide with the day of maximum length.

The final harvest was performed on 31.07.2013, i.e. 107 DAS. That was at a point in time, when durum had already matured, with filled grains ready to be harvested. *Tritordeum*, apart from its ongoing tillering was mostly senescent and *H. chilense* had still not changed to reproductive growth and was still tillering vigorously (see results and discussion).

2.3 Studied parameters

2.3.1 Non-invasive

The ambient **temperatures** were measured by a Tinytag Ultra 2 logger that recorded both temperature and relative humidity every half an hour for the complete duration of the experiment. The same device was used both in the greenhouse, where the pots were initially situated, as well as in the cage after having transported all the plants. Growing degree units (GDU) were calculated as the sum of all the remainders of averaged daily temperatures, obtained after the subtraction of a temperature base of 5. Negative values were excluded from this count (Miller et al., 2001).

The **phenological development** of the plants was followed throughout the course of their growth in order to synchronize and compare species in terms of growth development at a certain point in time. The extended BBCH-scale (Hack et al., 1992) made use of a standardized key of phenologically analogous growth stages for all mono- and dicotyledonous plant species in order to assist the distinction between growth stages (Hack et al., 1992). Stage identifications were performed with a variable frequency over time, ranging from once per week in the initial stages of growth to three times per week during later stages (e.g. after 60 DAS).

Measurements of the **greenness of the plants leaves** were conducted utilizing a Konica Minolta SPAD-502Plus. The device is used to measure the absorbance of the chlorophyll in two wavelengths bands – red and near infrared fraction of light. The relationship between the stronger absorbance of the red fraction of light and the very low to zero absorbance in the near-infrared range is employed in order to give an estimation of the absolute chlorophyll content in the leaf. More information on relative chlorophyll content evaluation and product details are to be found on http://www.konicaminolta.eu/en/measuring-instruments/products/colour-measurement/chlorophyll-meter/spad-502plus/.

Measurements were taken from the appearance of a fully unrolled flag leaf (58 DAS) with a constant frequency of once per every three days until full maturing of plants (~100 DAS). The final readings were obtained by the averaging of four different values taken from the leaf tip of the same flag leaf on the different plants (i.e. eight observations per pot, where flag leaves were fully unrolled).

Height measurements were done manually with a meter on a weekly basis over the course of the entire trial – from the moment of first leaf appearance (18 DAS) up until the final harvest.

Pot weights were measured continuously, at first fortnightly, until the 51st DAS and then weekly until the end of the trial. The measurement of the weight of each pot was done to follow the exact amount of water lost to evapotranspiration, which was subsequently used to calculate water-use efficiency.

2.3.2 Invasive

Harvests were performed twice over the duration of the trial. The Intermediate Harvest (IH) was executed on 26.06. 2013 or 72 DAS. The Final Harvest (FH) took place on 31.07.2013 or 107 days after the date of sowing.

Total biomass was calculated as the accumulative sum of both the underground and above ground portion of the plants. More precisely, it is the sum of the roots, stems, leaves and ears. Those fractions of total biomass were individually detached from the plant and then, wherever necessary, weighted upon finally being separately dried in paper bags in a drying oven at 80^{o} C for two days.

Green leaf number was expressed as number of green leaves per pot

The **mean green leaf area (MLA)** was calculated in this study as the area of green leaves divided by the number of green leaves in each pot. Therefore the resulting unit was cm^2/leaf.

The calculation of the **senescent leaves fraction** was done by relating the weight of senescent leaves to the total leaf dry weight either at IH or at FH and was expressed in percentage (%). Leaves were regarded as senescent if at least 50% of their area had turned yellow.

Specific leaf area (SLA) represents the “leafiness of the leaf” (Hunt, 2003) or a measure of the relative thickness of the leaves. It can be computed as the relationship between the leaf area and the associated leaf dry weight. Its dimensions are given as area per mass (cm^2/g).

Leaf area ratio (LAR) represents the leafiness of the plant. The calculation method made use of the relation between an individual plant’s green leaf area to the plant’s total dry weight and the dimensions associated with it are again as in SLA - area per mass [cm^2/g].

Shoot root ratio (SRR) relates the total dried shoot mass to the total dried root mass of a plant. Shoot mass in this case was the comprising mass of all the stems, leaves and ears that were produced. Mathematically this ratio was calculated as follows:

$$SRR = \frac{Total\ biomass - RDW}{RDW}$$

Leaf weight ratio (LWR) describes the leafiness of the plant on a dry weight basis (Hunt, 2003). It relates total leaf dry weight to the total dry biomass or the dried mass fraction of a plant's leaves. The corresponding dimension is mass per mass, which is rightfully also considered as dimensionless.

Stem weight ratio (SWR) is used to express the fraction of total dry weight of the plants occupied by their stems. Unit in use is mass per mass, or dimensionless.

Root weight ratio (RWR) acts as an instrument of plants that modulate their growth traits in changing environments (Reynolds & D'Antonio, 1996). Furthermore, efficient command of a plant's RWR would then boost its chances of maximising the relative growth rate (RGR), e.g. by acquiring access to water and nutrients. RWR represents the fraction of dry roots to total dry matter.

Ear weight ratio (EWR) is the corresponding portion of plants developed ears to the total dry weight of the plants.

In order to examine better the biomass allocation of the three plants the total dry weight of the plants will be decomposed to its constituents and tested for performance under different treatments:

$$LWR + SWR + EWR + RWR = 1$$

The total weight of the roots after a drying period of three days at 80 ^{0}C resulted in the **root dry weight (RDW).** Prior to drying, all harvested roots were carefully washed with a set of utility tools, including an assortment of sieves, buckets and a water sprinkler system. Clay attached particles were carefully disentangled from root protrusions by hand. A total of 15 minutes washing time per root was kept in order to even out any variation in impurity infused error in the results.

Leaf dry matter content (LDMC) represents the fraction of the leaf dry weights in relation to the fresh leaf weights. It is a dimensionless variable, but for convenience reasons it will be used in this analysis as a percentage (%) that is the resulting fraction value being multiplied by 100.

Water use efficiency assesses the output of productivity of a plant per litre of ET water (Steduto & Albrizio, 2005). The choice of using ET water for this calculation is based on the fact that evaporation and transpiration occur simultaneously and are hard to be precisely separated by means of simple measurements. An approximation is possible by the use of blank (non-vegetated) pots to measure only the amount of water evaporation. However, such control pots were not conceived by the initial experimental set-up. Nevertheless, in agronomical terms it would be correct to use ET water, since under field conditions evaporation from bare ground is rarely determined. The resulting unit is grams/litre [g/L].

$$Water\ Use\ Efficiency\ = \frac{Total\ Dry\ Weight}{ET\ water}$$

Evapotranspired water amounts were calculated as the sum of the differences in pot weights observed by weekly-taken pot weight measurements. The assumption behind this method of ET estimation is that no water leaked out of the system by the force of gravity.

$$ET\ = \sum_{k=0}^{n} Wk + Watk - W(k+1)$$

Where, Wk = initial weight

Watk = water supplied for the interval between weighing sessions

W (k+1) = weight of pot at next weighing

Relative growth rate (RGR) is also referred to as “efficiency index” (Hunt, 2003). It conveys the growth as the rate of increase in size per unit of size. Therefore, it is of a certain interest to look at it in order to gain a bit more impartial way of comparing growth rates of plants, which find themselves in dissimilar stages of growth. It is vital to note that in some cases the plants are exhibiting a negative RGR. This stems from the fact that RGR quantification is based on the assumption that all of a given plant’s current biomass will be able to produce in future terms more mass of the same proportion. However, at some point in growth of most plants, especially after flowering, the fraction of their biomass, which is mostly supporting material, expands (Hunt, 2003).

The equation behind the results of the time interval between just after sowing until IH was described by Hunt, 2003 and was th*e* following*:*

$$Relative\ Growth\ Rate\ = \frac{Ln(Total\ Dry\ Weight\ at\ IH) - \ Ln(0{,}001)}{72}$$

Initial start weight of 0.001 g in the formulae above was presumed in order to be able to estimate the mean RGR for the interval discussed, approximating the magnitude of growth very close to the day of seeding. Factor 72 represents the length of the interval in days between sowing and IH. The calculation of the mean RGR for the interval between IH and FH (35 days) was done accordingly with a denominating factor of 35:

$$Relative\ Growth\ Rate\ = \frac{Ln(TDW\ from\ IH\ to\ FH) - \ Ln(TDW\ from\ sowing\ to\ IH)}{35}$$

Harvest Index (HI) represents the portion of the seeds produced as a part of the total shoot weight.

Yield is the estimated amount of absolute grain yield, derived from the dried weight of the seeds in tonnes per hectare [t/ha], having in mind the dimensions of the pots, using the following equation:

$$Yield = \frac{Seed\ dry\ weight * 120 * 10^4}{10^6}$$

It must be noted here, however, that the yield estimated by the pot experiment cannot be extrapolated to the field due to the large discrepancy of growth conditions, e.g. root growth restriction in pots or due to the different microclimates that are formed by artificial and field canopies. Therefore, the values will also be mentioned in grams per plant (see results).

2.4 Statistics

The statistical analysis of data was performed utilising an SPSS® Statistics 19 software package from IBM for the more complex statistical analysis and Microsoft® Office Excel® 2007 for creating all the supporting graphs and summary tables.

For calculating the levels of significance of the differences between species and treatments, standard two-way ANOVA multiple comparison tests were performed, featuring a Least Significant Difference Method (LSD) post-hoc test. As independent variables "species" and "treatment" were picked to ensure the representative analysis of the effect of those two factors with regard to the rest of the variables. All the tests included a table of descriptive statistics, supplemented by tables of the overall effects of the treatments, species and the interaction between the two factors.

Three specific cases (for each of the species groups, e.g. species = *H. chilense*) were formed in the analysis. Hence, the effect of the factor water treatment within each species was inspected more closely. Differences among the three species were also examined for each water treatment, but in contrast to the within species comparison there were no specific cases formed. For detailed ANOVA results for each parameter see tables in Appendix III.

Chapter III: Results

3.1 Weather conditions

Since the plants were grown in a greenhouse in the early stages of their growth (0-37 DAS), the observed temperatures they were subject to largely varied from outdoor conditions. Fig. 7 gives an overview of the measured temperature over the whole growing period. The difference is easily observed. While under the protection of the greenhouse, the pots were exposed to a mean temperature of 18.93° C with considerably reduced daily amplitudes, especially at night. In comparison to outdoor conditions, where for the same interval mean temperature was 12.6 ° C (LTZ, 2013). While being situated in the greenhouse, the plants accumulated 529 growing degree units (GDU).

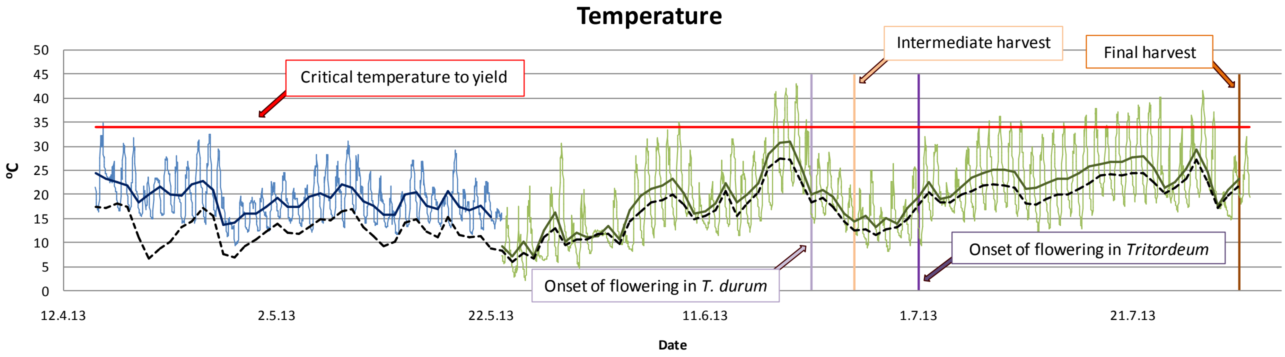

Figure 7: Temperature data featuring highlighted occurrences in time. Temperatures in the greenhouse are denoted by a continuous blue line, with a darker blue line for mean daily temperatures. Data from outdoor shelter are in green, with mean daily ones denoted by a darker green line. The dotted line represents the official average daily air temperatures measured by LTZ.

Following their transfer to the roof-covered shelter outdoors, the climatic pattern was also modified to a large extent. The observed mean temperature increased to 19.96° C, but in addition to it, also daily amplitudes were far more pronounced as compared to the greenhouse conditions. While under the outdoors shelter another 1047 GDU were realized.

It is important to note at this point that trial realised temperatures were not representative of a typical Central European summer with gradually increasing temperatures from spring to summer. To illustrate that, the mean ambient temperature outside of the shelter was 17.8 ° C or more than 2 degrees lower (LTZ, 2013). The total GDU in trial conditions of 1576 largely contrasted to the 1186 GDU over the same period of 107 days in the field. This may have altered plant growth to some extent (see part discussion).

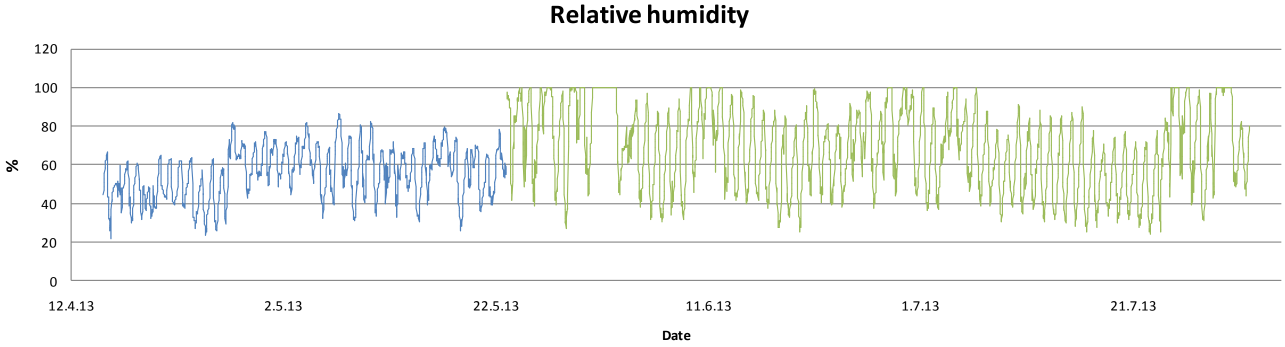

Figure 8: Relative humidity for the growth period. Relative humidity in the greenhouse is indicated by a blue line and relative humidity in outdoor conditions is indicated in green.

The modification of the pattern in relative air humidity the plants were subject to, after the pots had been transferred outdoors, is also discernible (Fig. 8). As with temperature, both the mean value and the amplitude of relative humidity increased. The air dampness meter showed a relative humidity of 55.65% on average for the first weeks in the greenhouse and 68.97% on average for the shelter outside.

Some of the characteristic differences in growth were also observable to the eye (Appendix I). Species were easily discernible from one another (e.g. due to differences in height). In addition, there were certain perceivable differences between various treatments (i.e. leaf greenness). Nevertheless, in order to acquire a better understanding of the more complex aspects of plant growth and to describe responses in different treatments in the three species, a more thorough analysis of a selection of parameters for quantification of growth responses (both invasive and non-invasive) is to be made in the following sections.

3.2 Non-invasive parameters

3.2.1 BBCH development

H. chilense featured a different plant development when compared to the other two species (illustrated by Fig. 9). During the trial it never switched from vegetative to reproductive growth and actually never gave an indication of reaching the stem elongation phase (Principal growth stage 30 according to BBCH-Scale).

In contrast, the species focussed on expanding laterally instead of vertically and kept on producing new tillers throughout the whole experiment (see discussion and the evaluation of biomass allocation in Fig. 27). No striking differences in treatments were observed in the timing and duration of the different growth stages in Chilean barley.

Given species-specific phenology, probably a more scrutinized comparison of only the growth stages in *T. durum* and *Tritordeum* would be viable. In terms of development of leaves (BBCH-Scale, principal growth stage 10), durum wheat dedicated a somewhat shorter time to its vegetative phase, ceasing to develop new leaves around 60 DAS, whereas *Tritordeum* spent 74 days to develop new leaves. In this case drought affected the duration of the phase in the hybrid species and resulted in its shortening by 12 days.

With respect to tiller formation (BBCH-Scale stage 20), the two crop species showed a dissimilar conduct. The tillering in moist *T. durum* began very early on the 24th DAS and lasted for 37 days, while the dry treatment shifted the development of tillers in time. The phase commenced three weeks later and then the absolute length of that phase was shortened by 8 days. *Tritordeum'*s development of tillers in the medium water supply began 38 DAS and lasted for 36 days, while dry conditions delayed the appearance of the first tiller with a week and reduced the length of the period to 16 days. Something that is important to note here is that the hybrid managed to produce on average 4.6 tillers at medium water supply and only 2.6 under drought stress until IH, while *T. durum* at that point in time had 1.9 tillers in the medium treatment and 1.6 under dry conditions.

Another intriguing fact to point out is that the hybrid species resumed its tiller production after two weeks of no tillering. *Tritordeum* plants under moist treatment recommenced their tillering after 85 DAS, while under medium and dry conditions, the plants did the same, only after a further two weeks time (hence after four weeks of no tiller production). The reintroduced tiller growth lasted until the end of the experiment 107 DAS and was a feature observable only in *Tritordeum* and *H. chilense* (see discussion).

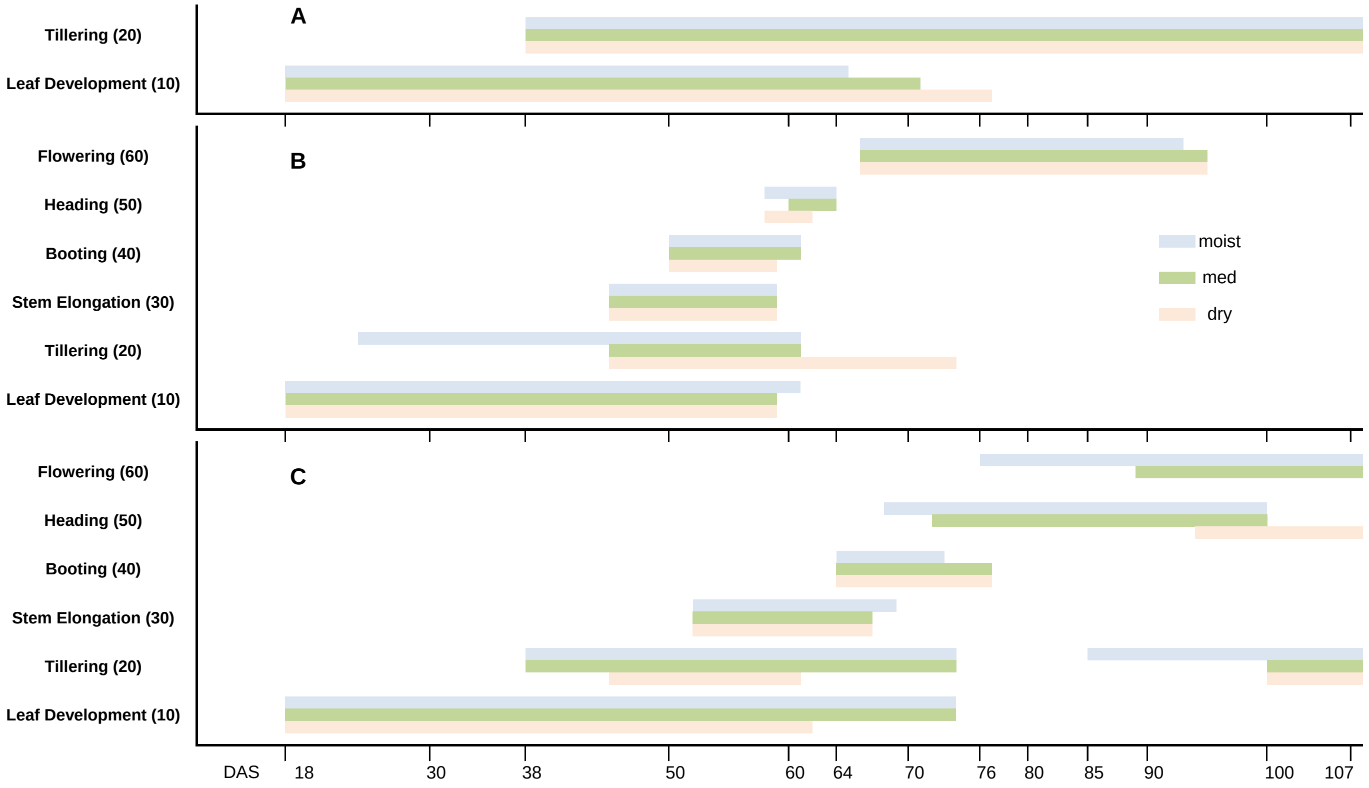

Figure 9: Development of *H. chilense* (A), *T. durum* (B) and *Tritordeum* (C) with time, according to the BBCH-Scale. In stage flowering (60) the lines represent the duration of anthers still being visible on the inflorescence, which does not necessarily correspond to the exact flowering period.

The stem elongation phase proceeded with more or less similar behaviour in the two species, with the only major difference being the fact that *T. durum* began its vertical elongation seven days before the hybrid species. Pots under all treatments performed correspondingly, ending with all flag leaves fully unrolled after 14 and 15 days after initiation of the phase in durum and the hybrid species respectively.

Booting (BBCH-Scale stage 40) followed the same trend as the previous growth stage, with a similar extent of length, but with a delayed commencement in the case of *Tritordeum.* This time the difference between the two species was more pronounced and *T. durum* started with extending its flag leaf sheaths (early booting stage) 14 days prior to those of

Tritordeum. However, the duration of the whole phase of booting was comparable – 11 days for durum and 13 days for the hybrid, with no major differences between treatments.

The following step in plant development is the emergence of the inflorescence or heading (BBCH-Scale stage 50). Its initial step is the visibility of the tip of inflorescence and the appearance of first ear spikelet. The divergence in the two crop species at this stage was once again by far distinguishable. *T. durum'*s inflorescences began emerging at 58 DAS and were all out of the flag leaf sheath in only six days. *Tritordeum*, however, exhibited a different strategy and initiated the 50 BBCH stage at 68 DAS with a major inconsistency of behaviour for the plants put under drought. Plants under dry conditions struggled in general and only attempted emerging their ears after 94 DAS. Until the trial's end only one pot of this species managed to fully complete an inflorescence emergence.

In terms of flowering (BBCH-Scale stage 60), a considerable mismatch between species was also observed in the onset of this stage. While *T. durum* started with its anthesis two days after the completion of the heading phase (i.e. at 66 DAS), *Tritordeum'*s beginning of anthesis overlapped with the stage of ear emergence (i.e. anthers became visible even before the ear completely emerged from its sheath). This occurrence happened at 76 DAS for the moist treatment and at 89 DAS for the medium, whereas dry plants seemed to fail to flower properly, since there were no anthers to be observed on their spikelets.

3.2.2 SPAD measurements

Having a glance back at Fig. 19 and noticing the difference in time between the end of BBCH stage 30 in durum and *Tritordeum,* which, as explained in the previous sub-chapter, accounts for the appearance of a fully unrolled flag leaf, first SPAD measurements could only be taken at different times for the two species (Fig. 10).

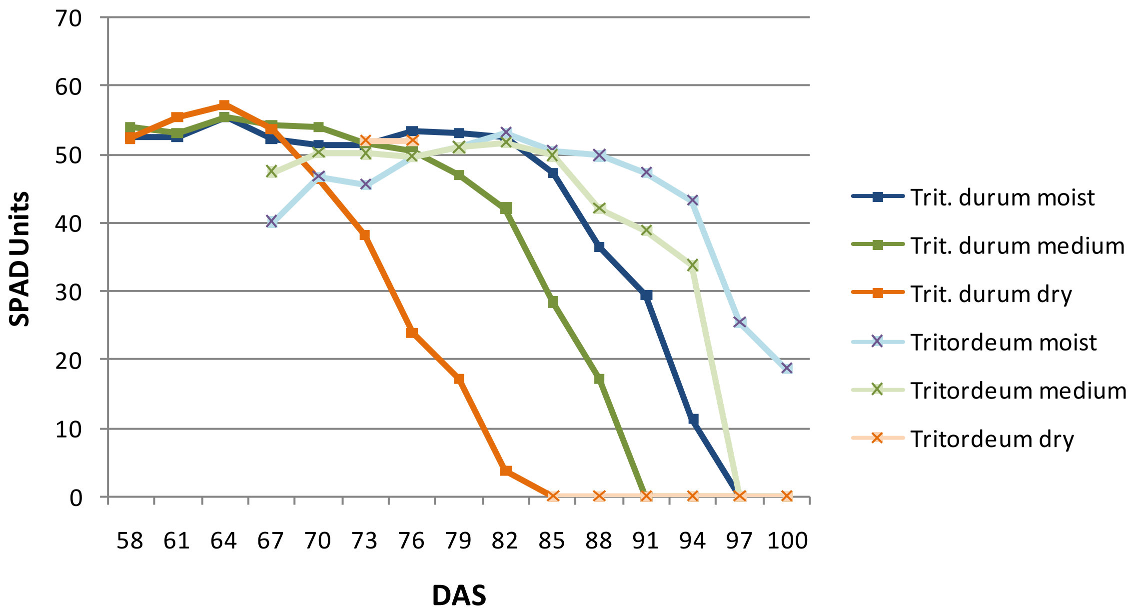

Figure 10: SPAD readings on flag leaves over time

Another feature, worth pointing out is the distinct disparity in treatment effects on the SPAD values. In general, for both species that produced flag leaves (*T. durum* and *Tritordeum*), drought enforced a faster loss of photosynthetic pigments of the flag leaves, whereas greater availability of soil moisture postponed senescence of those leaves in time.

3.2.3 Height

Height measurements showed that *T. durum* managed to expand vertically more than the other species with average final height of 62.25 cm (Fig. 11). It was followed by *Tritordeum* with 47.33 cm and *H. chilense* with its modest 12.41 cm mean height. For a visual depiction of growth over time see Appendix I.

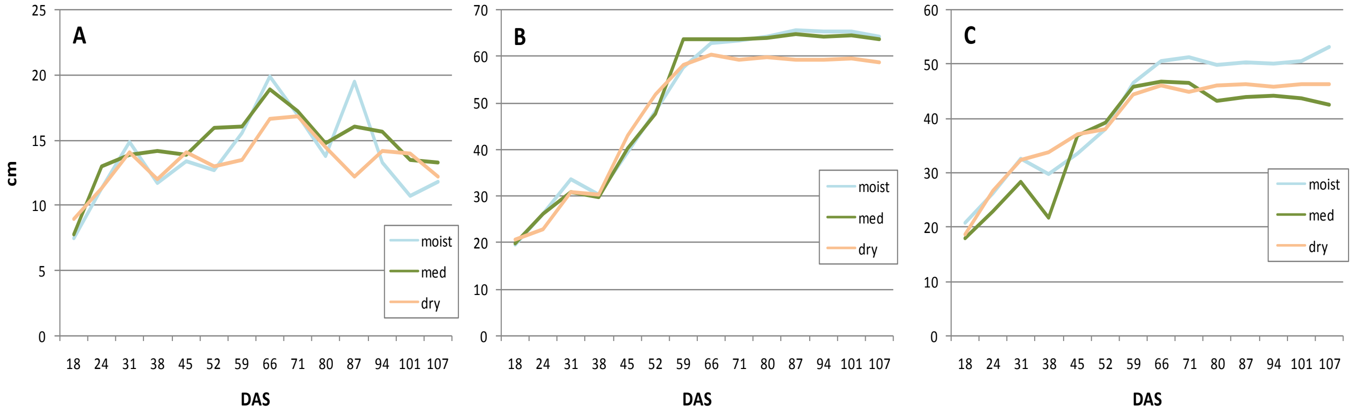

Figure 11: Height progression in time in *H. chilense* (A), *T. durum* (B) and *Tritordeum* (C)

3.3 Invasive parameters

3.3.1 Intermediate harvest

An overview of all investigated variables and their respective differences between different treatments within a species group is to be found in Table 1. Results of most investigated variables indicated that already at the intermediate harvest there were significant differences between treatments and species in relation to the medium water level, which was chosen to represent Central European precipitation levels.

Having a glance at the assortment of parameters included in the analysis, it would make sense to begin with the simpler and yield relevant variables, representing an absolute rate of change. The first to be mentioned is the most prominent one when discussing plant sizes, namely, the total dry weight of plants, or total biomass (Fig. 12).

T. durum grown under dry conditions showed a reduction in its total dry biomass production by 22%, when compared to the medium water level. The reduction of such magnitude was characterised by the statistical analysis as highly significant, with a p-value lower than 0.001. *Tritordeum* showed an even higher susceptibility to drought and this was indicated by the shrinkage in dry biomass by a staggering 27%, which attained the same level of significance in comparison to what the species showed at the medium water treatment case.

Table 1: Summary table of all parameters investigated at the intermediate harvest. Percentage difference was computed to describe the differences between treatments within a species. Resulting means of the dry and moist conditions are compared with respect to those of the reference medium treatment. Statistical significance is denoted by an asterisk symbol, where significance was found, and by "n.s." where none was observed. Levels of significance are rated as follows: *(p-value <0.05), ** (p-value <0.01) and * (p-value <0.001).**

		Hordeum chilense							*Titicum durum*							*Tritordeum*							Overall effects		
Variables		Moist	Med	Dry	Dry/Med %	sign.	Moist/Med %	sign.	Moist	Med	Dry	Dry/Med %	sign.	Moist/Med %	sign.	Moist	Med	Dry	Dry/Med %	sign.	Moist/Med %	sign.	SPEC	TREAT	SPEC*TREAT
Total biomass	means	1.26	0.9675	0.94	-2.8	n.s.	30.2	n.s.	5.9525	5.575	4.335	-22	***	6.77	n.s.	5.8325	5.91	4.31	-27	***	-1.3	n.s.	***	***	**
[g/pot]	*sd*	*0.7341*	*0.187*	*0.3647*					*0.4172*	*0.2615*	*0.2252*					*0.325*	*0.3827*	*0.3293*							
Mean Leaf Area	means	4.815	4.9143	4.3281	-12	n.s.	-2.0	n.s.	23.826	32.688	25.538	-22	n.s.	-27	*	18.507	16.55	15.4	-6.9	n.s.	11.8	n.s.	***	n.s.	*
[cm^2/leaf]	*sd*	*0.4774*	*0.4038*	*0.6222*					*6.9456*	*5.6758*	*2.075*					*3.202*	*0.9589*	*1.419*							
Specific Leaf Area	means	501.77	471.06	397.99	-16	n.s.	6.5	n.s.	219.22	188.98	199.86	5.75	n.s.	16	*	211.87	188.05	180.11	-4.2	n.s.	12.7	*	***	***	*
[cm^2/g]	*sd*	*43.698*	*19.965*	*64.174*					*15.478*	*18.318*	*19.082*					*10.789*	*12.345*	*13.677*							
Leaf Area Ratio	means	218.24	201.2	174.83	-13	n.s.	8.5	n.s.	36.09	24.062	23.583	-2	n.s.	50	*	57.233	46.647	47.105	0.98	n.s.	22.7	n.s.	***	*	n.s.
[cm^2/g]	*sd*	*49.432*	*18.491*	*24.231*					*8.8231*	*3.2952*	*5.1122*					*15.844*	*9.7023*	*8.6489*							
Shoot/Root Ratio	means	1.0983	1.0458	1.1613	11.1	n.s.	5.0	n.s.	6.3976	5.0422	6.1519	22	n.s.	26.9	n.s.	3.0396	3.5715	3.3296	-6.8	n.s.	-15	n.s.	***	n.s.	n.s.
[g/g]	*sd*	*0.2078*	*0.1806*	*0.201*					*1.0261*	*0.5241*	*1.6532*					*0.438*	*1.3403*	*0.5406*							
Leaf Weight Ratio	means	0.4418	0.4387	0.4578	1.92	n.s.	0.3	n.s.	0.2609	0.2311	0.1969	-3.4	**	2.97	*	0.399	0.3896	0.3894	-0.01	n.s.	0.94	n.s.	***	n.s.	n.s.
[g/g]	*sd*	*0.0692*	*0.0467*	*0.0146*					*0.0122*	*0.0135*	*0.0155*					*0.0262*	*0.0356*	*0.0225*							
Stem Weight Ratio	means	0.078	0.0698	0.0765	0.68	n.s.	0.8	n.s.	0.4318	0.3973	0.4075	1.03	n.s.	3	*	0.3023	0.317	0.316	-0.1	n.s.	-1	n.s.	***	n.s.	n.s.
[g/g]	*sd*	*0.0275*	*0.0189*	*0.0426*					*0.0111*	*0.0074*	*0.0204*					*0.02*	*0.0257*	*0.016*							
Ear Weight Ratio	means								0.1703	0.2055	0.2505	4.5	**	-4	*	0.0488	0.06	0.0608	0.08	n.s.	-1	n.s.	***	*	*
[g/g]	*sd*								*0.0283*	*0.0137*	*0.0104*					*0.0314*	*0.0206*	*0.0477*							
Root Weight Ratio	means	0.48	0.4916	0.4657	-2.6	n.s.	-1.2	n.s.	0.1371	0.1664	0.1449	-2.2	n.s.	-2.9	n.s.	0.2498	0.2334	0.2337	0.03	n.s.	1.64	n.s.	***	n.s.	n.s.
[g/g]	*sd*	*0.0469*	*0.0425*	*0.0431*					*0.0186*	*0.0136*	*0.0294*					*0.0275*	*0.067*	*0.0292*							
Root Dry Weight	means	0.63	0.475	0.4275	-10	n.s.	32.6	n.s.	0.8175	0.925	0.63	-32	**	-12	n.s.	1.4625	1.395	1.0125	-27	n.s.	4.84	n.s.	***	*	n.s.
[g]	*sd*	*0.4155*	*0.0985*	*0.1452*					*0.1384*	*0.037*	*0.1435*					*0.2321*	*0.4733*	*0.1873*							
Sen. Leaf Fraction	means	2.2558	2.44	3.7333	1.29	n.s.	-0.2	n.s.	37.222	44.427	40.181	-4.2	n.s.	-7	n.s.	32.72	36.926	32.929	-4	n.s.	-4	n.s.	***	n.s.	n.s.
[%]	*sd*	*1.012*	*0.4809*	*1.2618*					*12.66*	*9.695*	*9.9937*					*14.431*	*6.2947*	*9.9521*							
LDM Content	means	19.037	20.402	24.491	4.09	*	-1.4	n.s.	25.548	31.165	33.419	2.25	n.s.	-5.6	*	23.834	29.635	31.743	2.11	n.s.	-5.8	***	***	***	n.s.
[%]	*sd*	*1.6961*	*0.4197*	*2.6573*					*1.0398*	*1.9583*	*5.396*					*1.3499*	*1.3453*	*2.0661*							
Water Use Efficiency	means	0.886	0.824	1.055	28	n.s.	7.5	n.s.	3.616	3.8578	3.859	0.03	n.s.	-6.3	n.s.	3.476	3.9543	3.741	-5.4	n.s.	-12	*	***	n.s.	n.s.
[g/L]	*sd*	*0.3998*	*0.145*	*0.4278*					*0.3151*	*0.171*	*0.1301*					*0.2082*	*0.2888*	*0.1185*							
Relative Growth Rate	means	0.0973	0.095	0.094	-1	n.s.	2	n.s.	0.1207	0.1198	0.1163	-2.9	***	0.73	n.s.	0.1204	0.1206	0.1162	-3.6	***	-0.2	n.s.	***	*	n.s.
[g/g*day]	*sd*	*0.0086*	*0.0029*	*0.007*					*0.001*	*0.001*	*0.001*					*0.001*	*0.001*	*0.001*							

Table 2: Summary table of all parameters investigated at the final harvest. Percentage difference was computed to describe the differences between treatments within a species. Resulting means of the dry and moist conditions are compared with respect to those of the reference medium treatment. Statistical significance is denoted by an asterisk symbol, where significance was found, and by "n.s." where none was observed. Levels of significance are rated as follows: *(p-value <0.05), ** (p-value <0.01) and * (p-value <0.001).**

		Hordeum chilense							*Titicum durum*							*Tritordeum*							Overall effects		
		Moist	Med	Dry	Dry/Med		Moist/Med		Moist	Med	Dry	Dry/Med		Moist/Med		Moist	Med	Dry	Dry/Med		Moist/Med		SPEC	TREAT	SPEC*TREAT
Variables					%	sign.	%	sign.				%	sign.	%	sign.				%	sign.	%	sign.			
Total biomass	means	5.3125	4.0275	2.5575	-36	***	31.9	***	7.435	5.77	4.1925	-27	***	28.9	***	6.835	5.5875	4.0075	-28	***	22.3	***	***	***	n.s.
[g/pot]	*sd*	*0.3312*	*0.2172*	*0.2849*					*0.1936*	*0.3647*	*0.2193*					*0.4407*	*0.1044*	*0.1775*							
Shoot/Root Ratio	means	0.6245	0.6997	0.6854	-2	n.s.	-10.7	n.s.	10.011	9.7171	6.3822	-34	**	3.0	n.s.	2.5063	2.485	3.1796	28	n.s.	0.9	n.s.	***	*	***
[g/g]	*sd*	*0.0742*	*0.0726*	*0.0868*					0.8749	1.6706	1.2805					0.496	0.4825	0.3263							
Leaf Weight Ratio	means	0.3124	0.3278	0.3225	-0.5	n.s.	-1.5	n.s.	0.1822	0.1591	0.1806	2.15	**	2.3	**	0.3248	0.3552	0.4008	4.56	*	-3.0	n.s.	***	**	**
[g/g]	*sd*	*0.0268*	*0.0245*	*0.0175*					0.0085	0.011	0.0057					0.0206	0.0262	0.0193							
Stem Weight Ratio	means	0.0713	0.0828	0.083	0.03	n.s.	-1.2	n.s.	0.275	0.2948	0.3468	5.2	**	-2	n.s.	0.3303	0.2895	0.3183	2.88	n.s.	4	n.s.	***	n.s.	n.s.
[g/g]	*sd*	*0.0048*	*0.0132*	*0.0153*					*0.0116*	*0.0182*	*0.0159*					*0.0425*	*0.0281*	*0.0122*							
Ear Weight Ratio	means								0.4515	0.451	0.334	-12	***	0.1	n.s.	0.0553	0.064	0.0405	-2.4	n.s.	-1	n.s.	***	***	***
[g/g]	*sd*								*0.015*	*0.0345*	*0.0452*					*0.0266*	*0.0391*	*0.024*							
Root Weight Ratio	means	0.6165	0.5891	0.5945	0.54	n.s.	2.7	n.s.	0.0913	0.095	0.1387	4.37	**	-0.4	n.s.	0.2896	0.2912	0.2404	-5.1	n.s.	-0.2	n.s.	***	n.s.	**
[g/g]	*sd*	*0.0285*	*0.0249*	*0.0314*					0.0073	0.0148	0.0254					0.0418	0.041	0.0199							
Root Dry Weight	means	3.2775	2.375	1.515	-36	***	38.0	***	0.6775	0.545	0.5825	6.88	n.s.	24.3	*	1.97	1.625	0.965	-66	***	21.2	*	***	***	***
[g]	*sd*	*0.2829*	*0.2042*	*0.1091*					*0.0386*	*0.0592*	*0.1187*					*0.2214*	*0.2105*	*0.1091*							
Seed Dry Weight	means								2.58	1.885	0.665	-65	***	36.9	***										
[g]	*sd*								0.1659	0.2201	0.1453														
Harvest Index	means								0.3817	0.3608	0.1834	-49	***	5.8	n.s.										
[g/g]	*sd*								0.0179	0.032	0.033														
Yield	means								3.096	2.262	0.798	-65	***	36.9	***										
[t/ha]	*sd*								0.1991	0.2641	0.1743														
Water Use Efficiency	means	1.9793	1.9625	1.9253	-1.9	n.s.	0.9	n.s.	2.89	2.7623	2.9418	6.5	*	4.6	n.s.	2.5655	2.5755	2.7973	8.61	n.s.	-0.4	n.s.	***	n.s.	ns
[g/L]	*sd*	*0.1138*	*0.2785*	*0.1219*					0.0616	0.0654	0.1435					0.0495	0.1446	0.2816							
Relative Growth Rate	means	0.0411	0.0407	0.0285	-30	***	0.9	n.s.	0.0063	0.0009	-0.001	-205	n.s.	584	***	0.0045	-0.002	-0.002	-29	n.s.	375	***	***	***	***
[g/g*day]	*sd*	*0.0017*	*0.0015*	*0.0031*					*0.001*	*0.0018*	*0.0015*					*0.0019*	*0.001*	*0.0013*							

On the other hand, the analysis of mean values for the *H. chilense* plants failed to show any significant difference in biomass production, resulting in a decrease of only 3% under water stressed conditions.

H. chilense was the best performer at moist conditions, increasing its biomass by 30% (n.s.), whereas the other two species showed far lower numbers, ranging from a 6.8% increase in *T. durum* to a 1.3% decrease in *Tritordeum*. Nevertheless, none of those changes indicated a significant response relative to the plants grown at normal water supply.

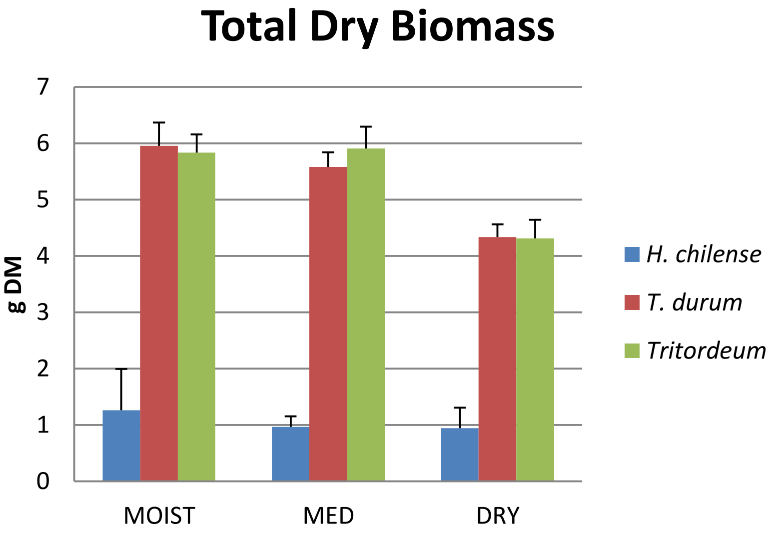

Figure 12: Total biomass (dry mass) of the plants at intermediate harvest. For significant differences refer to Table 1.

Additionally, the post-hoc multiple comparison test showed a significant effect of both independent variables in the context of dry matter. Both main effects on the species as well as the treatment levels were found to be highly significant, while also an interaction between the factors was observed.

Another simple parameter presented is the mean size of the leaves and its variation with the water supply (Fig. 13). Durum had the largest leaves in this experiment with a MLA under medium conditions of over 32 cm^2. Although only half the mean size as durum the second broadest leaves on average were *Tritordeum's* – 16.5 cm^2. *H. chilense* came third in terms of MLA with a score of only 4.9 cm^2.

Although such distinguishable differences have been observed between the species, only in one case the statistical analysis came up with a significant difference of the treatments within respective plant groups. It happened to show the adverse effect of luxurious water supply in regard to size of leaves in *T. durum*, which MLA dropped by 27%.

A drop in MLA under dry conditions was observed in all species, with reductions of 7% (n.s.) and 12% (n.s.) in *Tritordeum* and *H. chilense* respectively, to a 22% (n.s.) decrease in mean leaf size in *T. durum*.

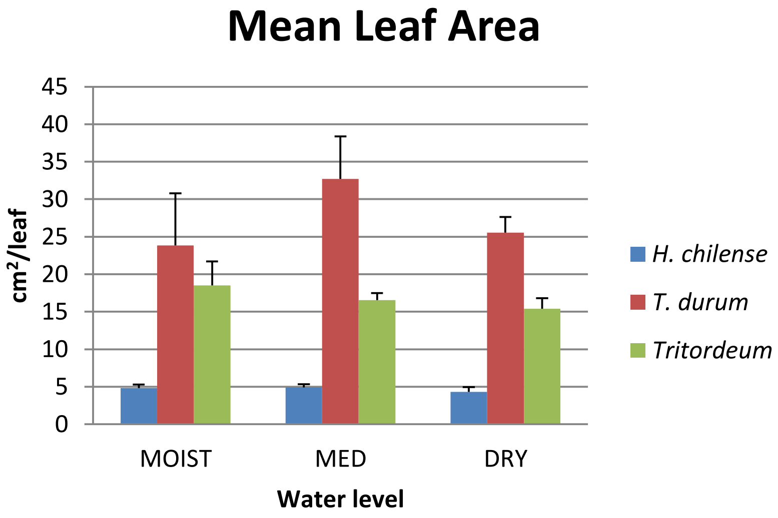

Figure 13: Mean leaf area and effects of treatments within a species at the intermediate harvest. For significant differences refer to Table 1.

According to the multiple comparison tests the factor species yielded a highly significant effect on the mean leaf area of the plants, while the different water treatments failed to show any significant differences. The interaction between the species and treatment variables gave evidence for a significant effect.

Further on with the indicators of drought stress, the performance of the plants with respect to the senescence of their leaves is to be mentioned. At IH *H. chilense* battled by far most efficiently against an increased senescent leaf fraction (SLF) and under medium conditions on average only 2.4% of the weight of its leaves was affected by senescence. *T. durum* was not that capable in avoiding loss of photosynthetically active leaves and had a mean 44% SLF. In between those two ranked *Tritordeum* with an SLF of 37%.

Induced drought affected negatively *H. chilense* and increased the share of its senescent leaves to 3.7%, while the crop species marked a decrease in their mean SLF to 40% in durum and to 33% in *Tritordeum.* However, those changes failed to show significance.

Moist conditions turned out to be more beneficial in *H. chilense* and *T. durum,* which were able to cut the proportion of their senescent leaves to 2.2% and 37% respectively. For *Tritordeum* the additional water did not provide any extra advantage and it exhibited the same behaviour as under drought – resulting in a 32.5% SLF. Again, the ANOVA did not find any statistical significance in those differences.

The factor “species” played a highly significant role in the result formation, whereas the factor “treatment” did not provide any significant effect. The same holds for the interaction between those two factors, which was also found to be insignificant.

Another parameter that needs to be assessed at this point is the specific leaf area (SLA). The differences at this point between the two crop species and the wild barley are easily observable (Fig. 14). *H. chilense* exhibited the highest SLA in plants grown under a medium water supply with its 471 cm^2/g. The differences between *Tritordeum* and *T. durum* were negligible, both achieving a mean value in the medium water treatment in the range of 190 cm^2/g.

For the variation between the treatments within each species it would be worthy to mention that, when subjected to drought, none of the plants managed to show any significant difference in this parameter. Both wild barley (16%) and *Tritordeum* (4%) exhibited a decrease in SLA at dry conditions, but that drop was never shown to be significant. Alternatively, durum wheat even went on to increase its SLA by almost 6% at the dry levels.

Significant effects on SLA were only observed with respect to the effect of excessive moisture conditions, with durum and *Tritordeum* both boosting their record with an increase of 16% and 13% respectively. Tests for significance returned an extreme overall effect of the different species, as well as that of the different water treatments. In this case, also the interaction between those two independent variables was found to be significant at the 0.05 confidence level.

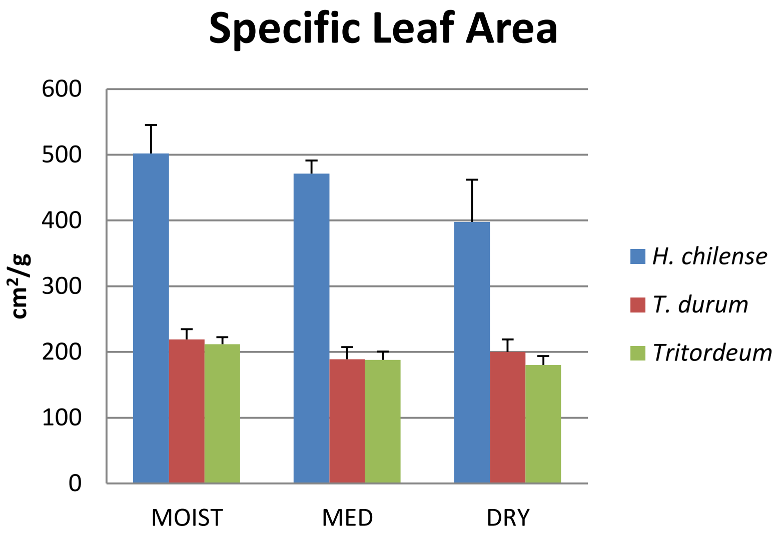

Figure 14: Specific leaf area at the intermediate harvest. For significant differences refer to Table 1.

Having had a glimpse at the outcome for SLA, it makes sense to also check the leaf dry matter content. While *Tritordeum* and *T. durum* showed a similar behaviour on average under normal watering with a LDMC of around 30%, H. *chilense* took a step aside from the other species in this category and produced leaves with a lower dry matter - 20% LDMC.

In this trial, all of the plants showed a higher dry matter content in their leaves under dry conditions underlined by a significant 4% increase in barley and followed by a 2% (n.s.) increase in the other two species. Understandably, moist conditions proved to decrease the LDMC in all species with *Tritordeum* leading the chart with a highly significant 6% decrease, followed by *T. durum* with a significant 5.5%. *H. chilense* also reduced the dry matter fraction in its leaves by 1% (n.s.).

The next parameter to be presented is the Leaf Area Ratio (LAR). Here the results diverged strongly between the species. Even though *Tritordeum* exhibited a nearly twice-fold higher

LAR than *T. durum* (46 cm^2/g and 24 cm^2/g respectively), none of them reached the very high values recorded in *H. chilense* – 201 cm^2/g.

Resembling the results of the previous parameter tested (SLA), LAR failed to show any evidence of a significant difference in the performance of plants under dry conditions. With Chilean barley and durum still showing a drop in LAR by 13% and 2% respectively, *Tritordeum* actually displayed an increase of its LAR by 1%. Comparably, all three species readily increased their leaf area per total dry weight, when grown under moist conditions. Only in durum statistically significant difference due to the higher water amount received was indicated. That was the case for the 50% higher LAR under moist conditions than that of the settings provided at medium water treatment. *Tritordeum's* performance under moist conditions failed to show any significant difference to the medium treatment, although reaching 23% higher levels.

The overall effects of the species to the variation in LAR were found to be highly significant, while treatment effects proved to be only significant at the 0.05 confidence level. The interaction of those factors failed to show significant effect on LAR.

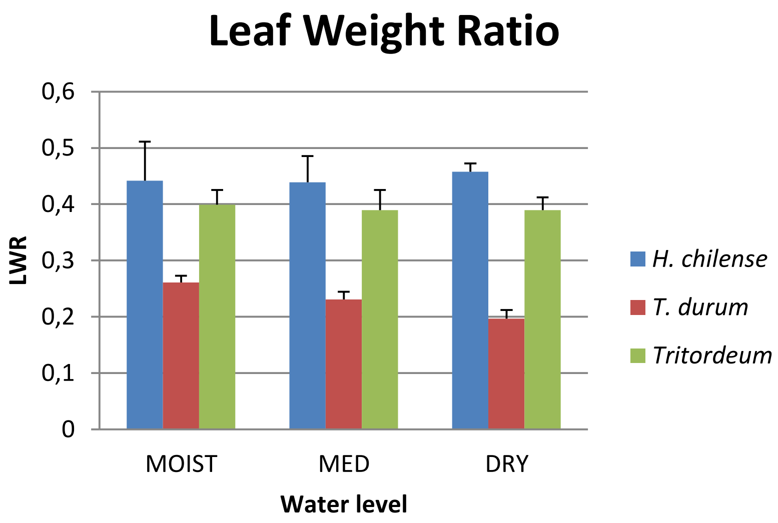

Figure 15: Leaf weight ratio (leaf dry weight/total dry weight) at intermediate harvest. For significant effects refer to Table 1.

Next of the leaf-related parameters is the Leaf Weight Ratio (LWR) of the species (Fig. 15). *T. durum* had the lowest LWR of the three – only 0.23 or 23% of the total biomass. Both *Tritordeum* and barley were more "leafy" and this was evidenced by their LWR – 0.38 and 0.43 respectively.

Tritordeum and its ancestor species *H. chilense* behaved in a similar fashion according to the LWR and its dependence on water availability. As Fig. 15 shows drought did not force *Tritordeum* to decrease its leaf fraction significantly. On the other hand, durum's mean leaf fraction dropped with a 3.5% (p-value = 0.0066) as a result of the drought stress. The top performer in the between-species comparison was *H. chilense*, which did not only keep a comparable LWR, but even showed an almost 2% increase despite the dry conditions.

All plants succeeded in increasing their leaf fractions at moist conditions, utilizing the extra water available to produce higher LWR ranging from 0.3% (n.s.) in *H. chilense* to up to 3% (p-value = 0.0138) in durum. *Tritordeum* also produced relatively more leaf mass, but the difference of 1% did not show any significant change.

The overall effect of the different species was again highly significant, while differences in treatment did not exhibit any significant responses. This time the interaction between species and treatment was also of insignificant magnitude.

The fraction of the plants total dry weight occupied by their stems (SWR) is to be considered next. *H. chilense* did not invest a large amount of its mass into stems under medium conditions at IH – only 7% on average, while the crop species were a lot more likely to distribute their energy to build-up of stems. Durum had a stem fraction of 40% at this point and *Tritordeum* showed 32% SWR.

Drought increased the percentage of stems in *H. chilense* and *T. durum,* resulting in a 0.7% (n.s.) and 1% (n.s.) higher stem fractions, respectively. The hybrid did not exhibit the same response and maintained a SWR of the same level as in medium water supply. Drought did not bring any significant differences to this parameter at IH.

Moist conditions, alternatively, induced a significant difference in SWR, at least in *T. durum,* which increased its stem fraction by 3%. Chilean barley reacted the same way and added 0.8% (n.s.) to its SWR, while *Tritordeum*s stems did not seem to favour moist conditions and their fraction decreased by an average 1% (n.s.)

Overall effects were again highly significant for the factor “species” and non-significant for both “treatment” and the interaction between those two factors.

Onward with the fractional parameters, the plants ear weight ratio (EWR) in durum and *Tritordeum* is to be shown. At intermediate harvest only those species had developed any ears. *T. durum* invested more in its ears at medium conditions until that time with on average 20% of its total dry matter being allocated there. *Tritordeum* was far behind at that point with only 0.06 EWR.

Dry conditions made durum increase its ear fraction by the significant 4.5%, while the hybrid, although similar in reaction, reached only a non-significant 0.08% increase. Increased moisture, on the other hand, decreased ear fraction in both species – significantly with 4% in durum and non-significantly by 1% in *Tritordeum*. The overall effect for factors “treatment” and “treatment x species” were significant, whereas the factor “species” showed a high significance.

The root-related parameters are the subsequent area of interest, beginning with a variable of an absolute magnitude – the dry weight of the roots (RDW) (Fig. 16). At this point in time, *Tritordeum* had the heaviest root system and under medium conditions was the only species which was able to exceed 1 g RDW. It was followed by durum with its 0.92 g root weight, while *H. chilense* only invested 0.47 g on average into its roots.

In all three species assessed, drought led to a reduction of the dry root mass. *T. durum* showed the highest impairment to belowground growth and decreased its root weight significantly by 32% in relation to the medium water supply amount, while the 27% drop of this value in *Tritordeum* under dry conditions was not found to be statistically significant. On the other hand, *H. chilense* managed to limit its reduced root growth to only 10%.

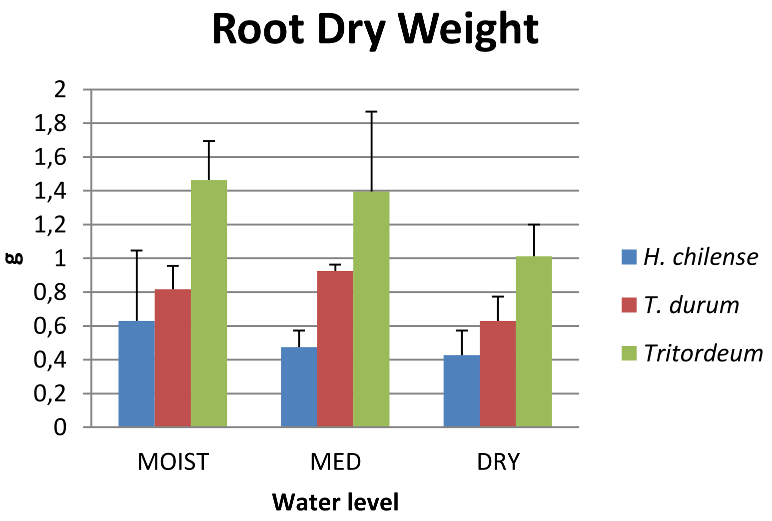

Figure 16: Root dry weight at intermediate harvest. For indication of significant differences refer to Table 1

Under moist conditions the plants demonstrated behaviour of a dissimilar nature. More water certainly did not mean more roots in durum, which, in accordance to its performance under dry conditions, manifested another drop in its root mass of 12%. The other two species managed and increased their root mass as a reaction to the excess water supplied by 5% and 32% in *Tritordeum* and *H. chilense* respectively. However, none of those changes proved to be statistically significant.

RDW was significantly affected by the factor “species”, as well as the variable “treatment”, but no interaction was observed between those two.

Mass fraction of the total dry weight, dedicated specifically to root formation is the next feature of the result description. With regard to this growth parameter, the three species showed contradicting behaviour.

The Chilean barley appeared to be very vigorous in root formation under medium water supply, resulting in a root fraction unmatched in this trial – almost 50% on average of its total biomass went to roots under medium conditions. In contrast, *T. durum* only dedicated 17% of its mass to roots. At this point in time the hybrid species had on average a RWR of 0.23 or 23%.

Albeit the difference in absolute values (Fig. 17), both *H. chilense* and durum wheat behaved similarly under modified conditions and marked a descent in their RWR – a 2.6% and a 2.2% drop respectively when exposed to drought and a 1.2% and a 2.9% fall to their root fractions respectively under higher water supply. *Tritordeum* showed a different pattern, one with no decrease of its root fraction, i.e. 0.03% increase under drought stress a 1.6% increase under moist conditions. None of the observed differences in RWR among the various treatments, however, proved to be significant.

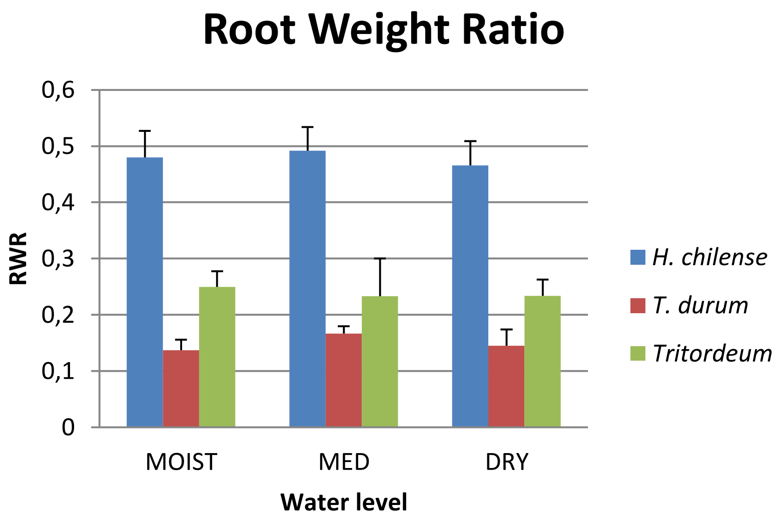

Figure 17: Root weight ratio at intermediate harvest. For significant differences refer to Table 1.

The statistical analysis failed to identify significant effects of different water treatments. However, differences between species were considerable since the main factor "species" turned out to be highly significant.

Next variable dealing with the allocation patterns, the shoot/root ratio (SRR), represents a mechanism for the adaptation of plants to changing environmental conditions, including drought stress. Again, as the outcome in RWR at the IH, *Tritordeum* and *T. durum* showed similar behaviour, while *H. chilense* exhibited quite the opposite response, choosing a different growth strategy than its ancestor species. This is indicated by both the five times larger shoot mass than root mass in durum as well as the 3.5-fold larger shoot weight of *Tritordeum* at medium water supply. Chilean barley had a more balanced SRR of 1.04.

Drought resulted in favour of shoot investment in *H. chilense*, which increased its shoot share by 11%, while *T. durum* managed to go even further to 20%. The hybrid invested more in underground development, decreasing the SRR by 7%.

Moist conditions yielded results alike for the species. *H. chilense* and durum went up with their SRRs by 5% and 27% respectively, whereas *Tritordeum* still showed a decline – this time by 15%. Statistical analysis was relentless, however, in pointing out that for SRR all those above mentioned differences were actually statistically insignificant. The same holds true for the overall effect of the factor "treatment" and "treatment-species" interactions, while the only significant difference could be detected between species.

Arguably one of the crucial factors to take under consideration when discussing plants responses to drought and a valuable indication of their actual adaptive responses to those pressure, be it favourable or not, is the plants' water use efficiency (WUE).

At IH it became clear that *T. durum* and *Tritordeum* were superior to Chilean barley in terms of WUE (Fig. 18). The hybrid manifested the largest water use efficiency on average – 3.95 g dry matter/L at the medium conditions, with durum following closely with 3.85 g DM/L. *H.chilense* was left behind as it only managed to generate 0.82 g DM/L.

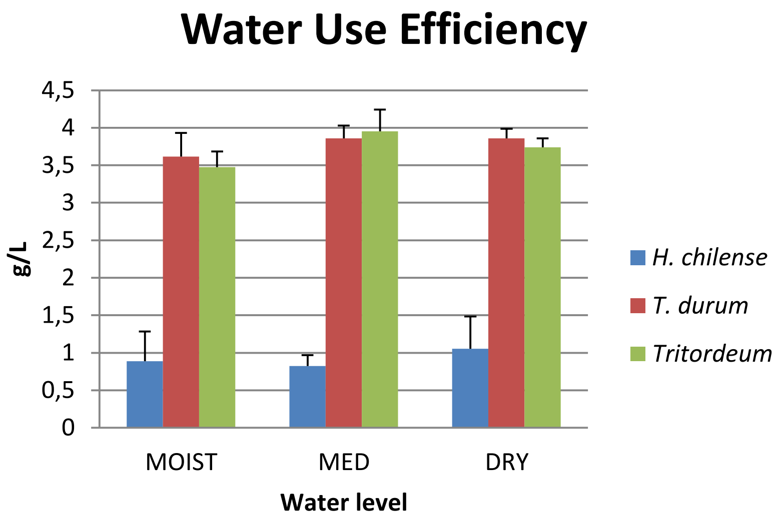

Figure 18: Water use efficiency (g dm/L) of the plants for the period between sowing and intermediate harvest. For significant differences refer to Table 1.

Nevertheless, in relative terms, *H. chilense* demonstrated actually the highest resilience against drought by not only avoiding a severe drop in its productivity, but in turn showing an enlarged WUE by 28% (n.s.). Durum also combated the pressure of water deficiency and maintained a level of output at parity with the medium. *Tritordeum*'s drop at this point with 5.4% was found insignificant using ANOVA.

As it turns, excess water might have proved to be a more considerable obstacle to optimizing the WUE, rather than drought. In the moist treatment, *T. durum* displayed a drop of WUE of 6%, whereas *Tritordeum's* output slumped with 12% (p-value = 0.0123). The overall differences among species were highly significant in comparison to the non-significant differences between the treatments (n.s.). The interrelation between the two factors was also found to be non-significant.

Relative growth rate is the last of the complex variables to be described in the results section for the intermediate harvest. Fig. 19 illustrates the mean RGR of the different plants for the interval between sowing until the day of IH. This interval includes the period of exponential growth and we can observe quite high values for relative daily growth. Both crop species were quite expansive at this stage, portrayed by their average RGRs of approximately 0.12 $gg^{-1}d^{-1}$ at medium water supply. On the other hand, *H. chilense* had a mean value as low as 0.095 $gg^{-1}d^{-1}$ in the same treatment.

Drought distinctly affected plant growth at this stage and proved to be a significant factor in *T. durum* and *Tritordeum* alike, both registering a slump from their medium treatment growth rates. It meant a 2.9% (p-value = 0.00013) decrease in RGR in durum and an even higher 3.6% (p-value = 0.00010) decrease in RGR in *Tritordeum*. *H. chilense* was the most resilient species of the three with only a 1% (n.s.) drop in its RGR.

The moist treatment proved beneficial for *H. chilense* and *T. durum*, for they marked an augmentation in their RGRs – with 2% (n.s.) for the first and 0.7% (n.s.) for the latter species. *Tritordeum* did not handle the extra water supplied so swiftly and it brought about a minor decrease of 0.2% (n.s.) in this case.

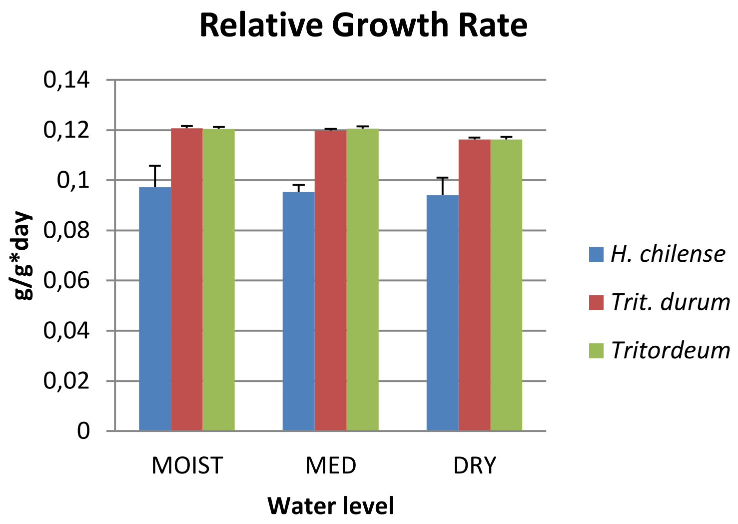

Figure 19: Relative growth rate for the interval from sowing to intermediate harvest (72 days). For significant differences refer to Table 1.

The overall effect of the factor "species" was highly significant. Similarly, but to a lesser extent, diverse water conditions affected the outcome of RGR. The overall effect of the interaction of the above-mentioned factors was found insignificant by the statistical analysis.

3.3.2 Final harvest

Having discussed the performance of the plants at the IH, the results of the final harvest should also be presented (Table 2). It is bound to deliver an overview of whether and how exactly did the three species modify their behaviour after flowering and show us if the observed differences in the discussed variables grew larger or the effect of treatment pointed rather to the opposite direction.

To begin with, it is advisable to show the absolute measurements of productivity. Following, whenever possible, the same order of variables to be gone into as in IH, the opening spot is reserved for the end biomass (Fig. 20). At this point wild barley proved to be the species that relatively advanced the most between the two harvests and applied a four-fold expansion to its dry weight, reaching averagely 4 g in the medium water treatment. The crop species maintained their productivity levels, with durum slightly increasing its dry biomass for that period, ending the experiment with an average of 5.8 g per pot. *Tritordeum* slightly decreased its total dry biomass with an end mean output of 5.6 g under medium conditions.

Drought in the latter stages of growth brought up a serious cutback in the biomass of all three species and in contrast with the results at the previous harvest, this time the biggest loser in biomass was *H. chilense* with a 36% (p-value = 0.00004) drop in mass as compared to the medium water level. *T. durum* and *Tritordeum* shared the fate of *H. chilense*, but managed to curb the losses to 27% (p-value = 0.00002) and 28% (p-value = 0.00002) respectively.

In the moist treatment level, all three species thrived well and marked their ranks with a higher biomass productivity ranging from 22% (p-value = 0.00014) in the hybrid to 32% (p-value = 0.00012) in *H. chilense*. The moist conditions proved extremely beneficial for *Tritordeum* at the post-flowering growth stages, as it managed to completely overturn its performance from the early growth stages.

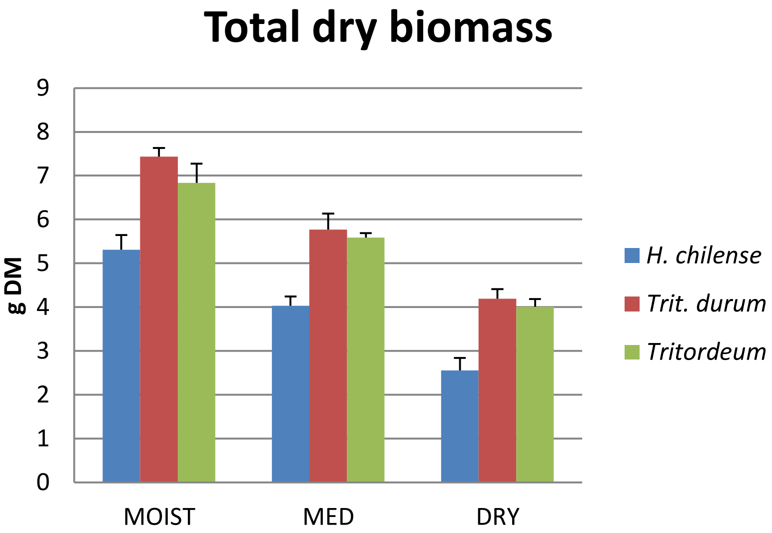

Figure 20: Total dry biomass at the final harvest. For significant differences refer to Table 2.

The overall effect of the two independent factors (species and treatment) was found to be highly significant. The interaction between those did not exhibit any statistical significance whatsoever.

Casting a glance once again at the LWR, we can observe a strong modification in post-anthesis behaviour since IH in *H. chilense* and *T. durum*. Both species reallocated their biomass investment into other growth segments rather than leaf development and decreased their LWR substantially. *H. chilense*'s leaf fraction of almost 44% on average for medium treatment at intermediate harvesting dropped to 32% for the same water level at the final harvest (FH). The shift in durum was also prominent – from 23% at IH to 16% at the FH for medium conditions.

LWR under dry conditions was higher with 2.15% (p-value = 0.0067) for durum and 4.56% (p-value = 0.0176) for the hybrid. Unlike their analogous behaviour under drought, excess water supplied led to divergent reactions in the performance of those two species. *T. durum* utilized the surplus of water to bolster its leaf fraction with a significant 2.3%, while *Tritordeum*'s LWR dropped with 3% (n.s.). Differential water treatment did not provide any statistically significant differences of LWR in *H. chilense.*

The overall effects of the independent factors were of a significant magnitude. That of "species" was again found to be highly significant, whereas the effect of "treatment" and the interaction between the two showed significant changes at the 0.01 confidence interval only.

Since at the final stages of their development most of the plants did not have any green leaves left, the analysis at this point is focused mainly at variables linked with other compartments of the plant.

Stem fractions also exhibited certain modifications in between harvests. It was in a positive direction in the case of *H. chilense*, which showed an average 0.082 SWR under medium water supply at FH. *T. durum* and *Tritordeum* behaved alike at this point with regard to their stem fractions and both finished the experiment with SWR of 0.29 or 29% of their total dry biomass.

Dry conditions resulted in an increase in stem fractions in all the species at this point starting with *H. chilense* with a 0.03% (n.s.) rise, followed by *Tritordeum* with a 2.9% (n.s.) increase and ending with a significant 5.2% (p-value = 0.0011) growth in durum.

When put under increased water supply, SWR dropped in *H. chilense* and *T. durum* alike, by 1.2% and 2% respectively, whereas the hybrid species marked a 4% increase to its stem fraction. None of those differences, however, were found significant in ANOVA.

At FH, same as in IH, only two of the species will be assessed in terms of their biomass fraction dedicated to ears. *T. durum* definitely did not remain idle and the successful filling of its grains led to almost a doubling of its ears fraction at medium water supply. At the final harvest 45% on average of durum dry weight was shared out to ears. By contrast, the ears fraction in *Tritordeum* did not exhibit any major increase between harvests and by the end of the trial the species had allotted only 6.5% to ears, as compared to 6% at IH.

Drought negatively affected the EWR in both of the species. In the case of durum it resulted in a highly significant 12% drop of its ear fraction, while the 2.5% decrease in EWR in Tritordeum was not found to be significant in the analysis.

More moisture applied did not provide any statistically significant differences in both species. *T. durum* demonstrated only a minor modification – 0.1% (n.s.) increase and *Tritordeum* decreased its ear fraction by 1%, which did not show significance either. The overall effects of the all main factors was highly significant at this point with all p-values for factors "species", "treatment" and "species x treatment" were lower than 0.001.

H. chilense exhibited an amazing expansion with respect to its RDW in the time span between the two harvests (Fig. 21). It recorded an astonishing almost five fold increase of root weight on average. *Tritordeum* also favoured root growth and at FH its mean RDW was 1.6 g per pot, as compared to 1.4 g at IH. *T. durum* was the only species that exhibited a drop in its root mass, in fact almost a double decrease in this case, finishing the experiment with the lowest mean RDW of all species – 0.55 g per pot in medium water conditions.

Here the lack of water proved to be an adverse circumstance for *Tritordeum*, which suffered a noticeable 41% (p-value = 0.00075) decrease of its root mass with respect to the medium conditions. *H. chilense*'s RDW also experienced a severe impediment and when put under drought stress came out with a hefty 36% (p-value = 0.00027) decrease. Durum did not show much of a vulnerability to drought at this point and actually succeeded in increasing its absolute root mass with 7% (n.s.) on average.

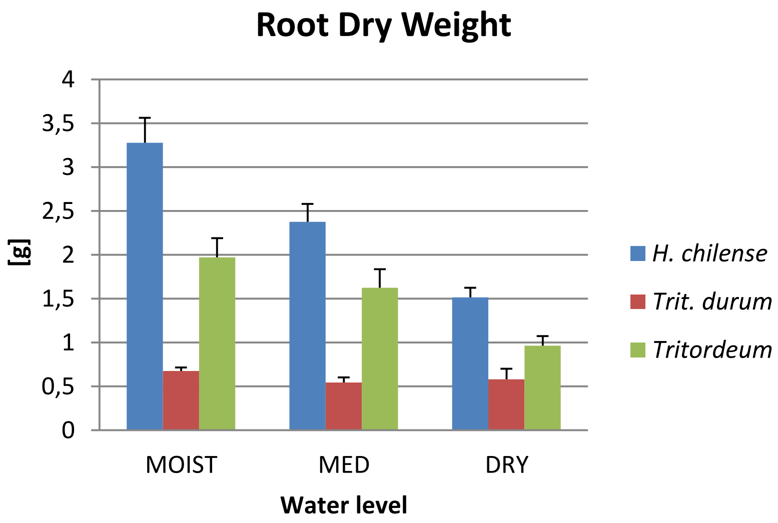

Figure 21: Root dry weight accumulated over the whole growth period from sowing to final harvest. For significant differences refer to Table 2.

Moist conditions, on the other hand, proved to be beneficial to all three species, all utilizing the abundance of water to invest in significant root extensions. *H. chilense* profited the most and put on an additional average 38% (p-value = 0.00019) to its root mass. Second best performer in this case was durum with a significant 24% raise, closely followed by *Tritordeum* and its 21% (p-value = 0.0284) expansion in terms of mean RDW.

Accordingly, all of the overall effects of the independent factors (species, treatment and the interaction between those) turned out to be of extreme significance, at least with regard to this component of growth analysis.

As a subsequent step of the growth assessment, after having observed the dry mass of the roots, it would make sense to also describe their mass fraction of the total final dry matter of plants. That would enable the comparison between the outcomes of the two harvests in relation to the plants' root fractions and hopefully give out a hint about growth investment into roots.

At the end of the growth period, subject to this study, *H. chilense* invested the highest amounts of resources into the build-up of its root system. Under medium conditions, almost 60% of its end mass was allocated to below-ground structures. In accordance, *Tritodeum* also increased its root fraction at medium conditions since IH from 23% to 29%, thus implying a higher potential in combating drought. Durum, on the other hand went under a further decrease of its anyways comparatively lower RWR, finishing the experiment with a root fraction of a bit less than 10% of its total DM.

Differential watering levels turned out to create statistically insignificant differences in the RWR of the species with the remarkable exception of *T. durum*, which showed a prominent 4.3% (p-value = 0.0064) enlargement of its root fraction in the dry water level. Drought also decreased the biomass allocated in its roots by 5.1%, but this relatively stronger drop failed to show significance (p-value = 0.075). The overall effect of the interaction between "species" and "treatment" was found significant, as was the effect of the factor "species", while "treatment" failed to provide any significant effect on the results.

Another necessary step in the understanding the behaviour of the plants under stress as well as in general terms, after addressing the magnitude and the shared size of their roots, is to have a look at the ratio between the total end shoot dry weight and their total RDW (Fig. 22).

The considerable underground expansion of *H. chilense* in the period between the two harvests accounted for the resulting drop of its SRR in medium conditions by almost a third at the time of the FH. *Tritordeum* followed the same routine and shrank its IH SRR by approximately a third. *T. durum*, quite the opposite, exhibited a raise in its shoot fraction under medium water levels, resulting in an almost doubling of its SRR.

Water shortage in the pots brought up a heavy decrease in durum wheat's SRR in magnitude of 34% (p-value = 0.0059), mainly due to its reduction in final dry shoot weight. *H. chilense* did not re-allocate resources so vigorously and maintained only a 2% (n.s.) drop in SRR. This time, the hybrid species exhibited a divergent response from that of its ancestors and expanded its SRR with 28% (n.s.) which was elucidated mainly by the reduction of root weight, rather than shoot expansion.

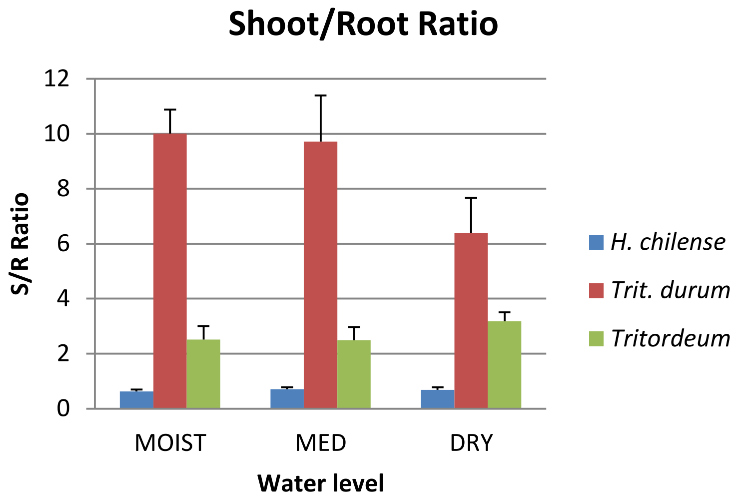

Figure 22: Shoot to root ratio at final harvest. For significance of those differences refer to Table 2.

Additional water supply failed to evoke statistically significant differences in this ratio and the only value perhaps worthy of attention is the drop of SRR in *H.chilense* by 10% (n.s.). In this case all of the overall effects of the independent factors analyzed statistically was significant – highly significant for "species" as well as for the interaction of "species x treatment", whereas the significance level of the effect of differential water treatment was significant at the 0.05 level.

Moving on with the presentation of the results it is imperative to show how the growth efficiency of the plants altered between IH and FH with the water regimes they were put under. Best performer in absolute terms this round was *H. chilense*, which increased its overall WUE by a factor of almost 2.5 – from 0.8 g/L at IH to 1.9 g/L at FH. The huge increase could be attributed to the fact that by the end of the study the Chilean barley had not shown any signs of switching from vegetative to reproductive growth (more to that in the discussion section). *T. durum* and *Tritordeum* both marked a drop their efficiency in absolute terms by approximately one third on average at medium water regime, but that descent could be somewhat expected given the stage of the development of the two species.

Drought promoted an increase in WUE in durum and the hybrid species, which was highlighted by a raised efficiency with 6.5% (p-value = 0.0289) and 8.6% (n.s.) respectively. *H. chilense* struggled at dry conditions and decreased its WUE with 1% (n.s.). Increasing the amount of water supplied did not provide any statistically significant differences with respect to this parameter, at least for the comparisons within each species. The overall effect of the different factors turned out to be highly significant for "species", non-significant for "treatment" and significant for the interaction between those two.

One of the last variables to be assessed in the result description is the mean relative growth rate of the plants over the period between IH and FH (Fig. 23). Under medium water provision mean RGR values in *H. chilense* were the highest – 0.04 grams per grams of total DM per day. Durum almost dropped its mean RGR down to 0, whereas *Tritordeum* actually had negative mean values for that period. The underlying reason behind the negative values is mentioned briefly in the materials and methods section.

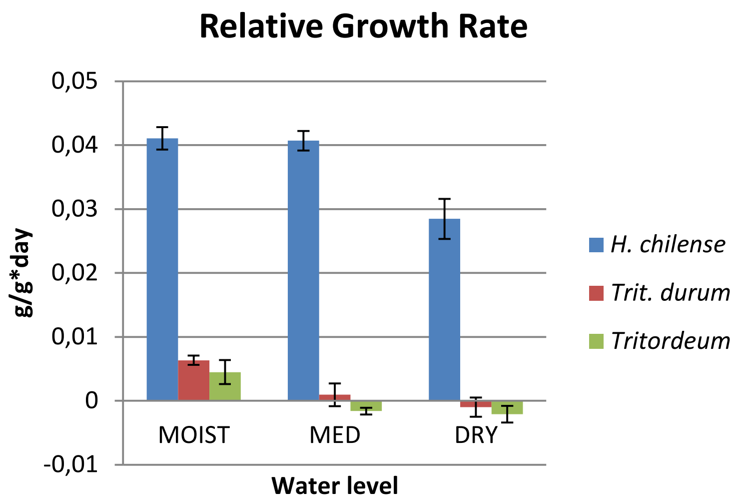

Figure 23: Relative growth rate for the period between the two harvests (35 days). For significance of those differences refer to Table 2.

Low levels of water supplied negatively influenced the RGR of all three species. *H. chilense* experienced a drop of 30% (p-value = 0.0003) and *Tritordeum* registered one of 29% (n.s.). Moist conditions, on the other hand, allowed for a prolonged growth period (indicated by the time until the switch from positive to negative RGR values) for all species, with massive discrepancies in comparison to the medium treatment. For instance *T. durum* showed on average 584% (p-value = 0.00043) higher RGR and *Tritordeum* also saw a hefty 375% (p-value = 0.00013) enhancement in this parameter at that time.

Here all the independent factors had an extremely significant effect on the development of plants all marked with p-values lower than 0.001, which point towards high significance of those differences.

Last, but not least, this study revises the grain yield performance of the plants. And since the only plant of the three that produced any seeds was *T. durum*, a scrutinized comparison of the significant differences of various treatments will be shown only with respect to this species.

First of all, the absolute grain mass per pot varied significantly between the treatments. In order to generally compare the results to crop yields under field conditions seed mass per pot was converted to tonnes per hectare taking into account the planting density (as explained in part materials and methods) However, it must be noted that actual extrapolation from results of pot experiment to agronomical yield might be problematic.

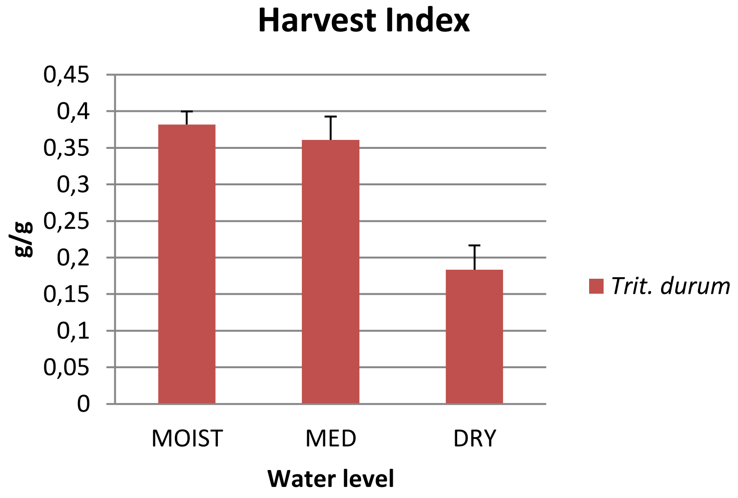

Figure 24: Harvest Index of *T. durum* at the final harvest. For the significance of those differences refer to Table 2

Drought tolerance of durum with respect to grain formation failed and the final yield plummeted down to only a mean 0.78 t/ha or 0.33 grams DM per plant – a massive 65% (p-value = 0.000005) drop in comparison to the medium watering conditions. The yield under medium water supply was 2.26 t/ha or 0.94 g DM/plant on average. On the other side of the coin, a higher water supply brought a 37% (p-value = 0.0004) higher yield – 3.1 t/ha or 1.29 g DM/plant.

Harvest index (HI) of *T. durum* is the last parameter in this analysis. Fig. 24 shows that drought decreased the HI from 0.36 grams of seeds per gram of shoot dry weight to 0.18 g/g or by a highly significant 49% on average. Moist conditions induced a slight increase in HI amounting to 6% (n.s.) on average.

Chapter IV: Discussion

4.1 Weather conditions

The transfer of the pots to the outdoor shelter was deemed necessary, since the increased amplitude in temperatures under free air conditions plays an important role in stem growth and stem hardening of light-grown plants (Lecharny et al., 1985). That holds especially for night time, where the conditions inside the greenhouse were a lot warmer than the ones outside. Cooler temperatures also work in favour of tillering in cereals.

Although being pre-devised to create climatic conditions close to the ones typical to Central Europe, the experimental set-up provided a climate that turned out hotter than the initially envisaged one. And while that was in consistency with the plan for the initial stages of growth in the greenhouse, the average temperature during the outdoor shelter phase was perhaps too hot for a regular wheat growing season. The 2.15 degrees Celsius disparity in mean shelter and air daily temperatures is perhaps what could be expected according to one of the different IPCC scenarios in the year 2100 (Alcamo et al., 2007), but the temperature conditions realised at present were perhaps more characteristic for a different climatic zone (e.g. Mediterranean basin).

Throughout the 107 days of growth, the 1576 GDU accumulated came close to what would be described as favourable conditions for wheat in general (Miller et al., 2001) and were sufficient to provide a favourable reproductive environment for *T. durum*. Contrastingly, the generally delayed initialization of phenological growth stages in *Tritordeum* and their coincidence in time with hotter days could have had a strong effect on seed set.

If *Tritordeum* were successfully grown at large scales under Mediterranean conditions, it would mean the species is well-suited for temperatures higher than the average Central Europe ones. Alternatively, it could be argued that 1576 GDU over 107 days were simply not enough for the species to successfully reproduce. That could possibly accredit the strong tillering activity up until the end of the trial as a sign of a stand-in strategy of fulfilling its reproductive requirements.

However, the available information provided by the seed supplying company suggested that the species might perform better if being sown as a winter crop. Sown normally in October-November, although not having strict vernalisation requirements, for good flowering and fertility, it would supposedly benefit from a cool period during the early vegetative growth. The winter night temperatures in South of Spain, where it is sown at larger scales, normally fall down to around 2^{o} C during winter time and frost is only rarely observed. The company admitted that spring sowings might render the plants relatively weak and reduce fertility. Therefore the suggestion that the accumulated GDU were not sufficient could be opposed. Unfortunately, this key piece of information was shared long after the trial was concluded.

4.2 General growth responses

Studies concerning the biomass allocation of plants under different water regimes are long discussed and available in the literature (e.g. Brenchley, 1916; Maximov 1929; Shirley 1929), but it was almost half a century later when Brouwer (1962) put together his theory of the so-called “functional equilibrium” of plants (Poorter & Nagel, 2000). It stipulates that plants are likely to shift their biomass allocation to that compartment of growth where acquisition of resources is hindered in order to be able to minimize growth-limiting circumstances.

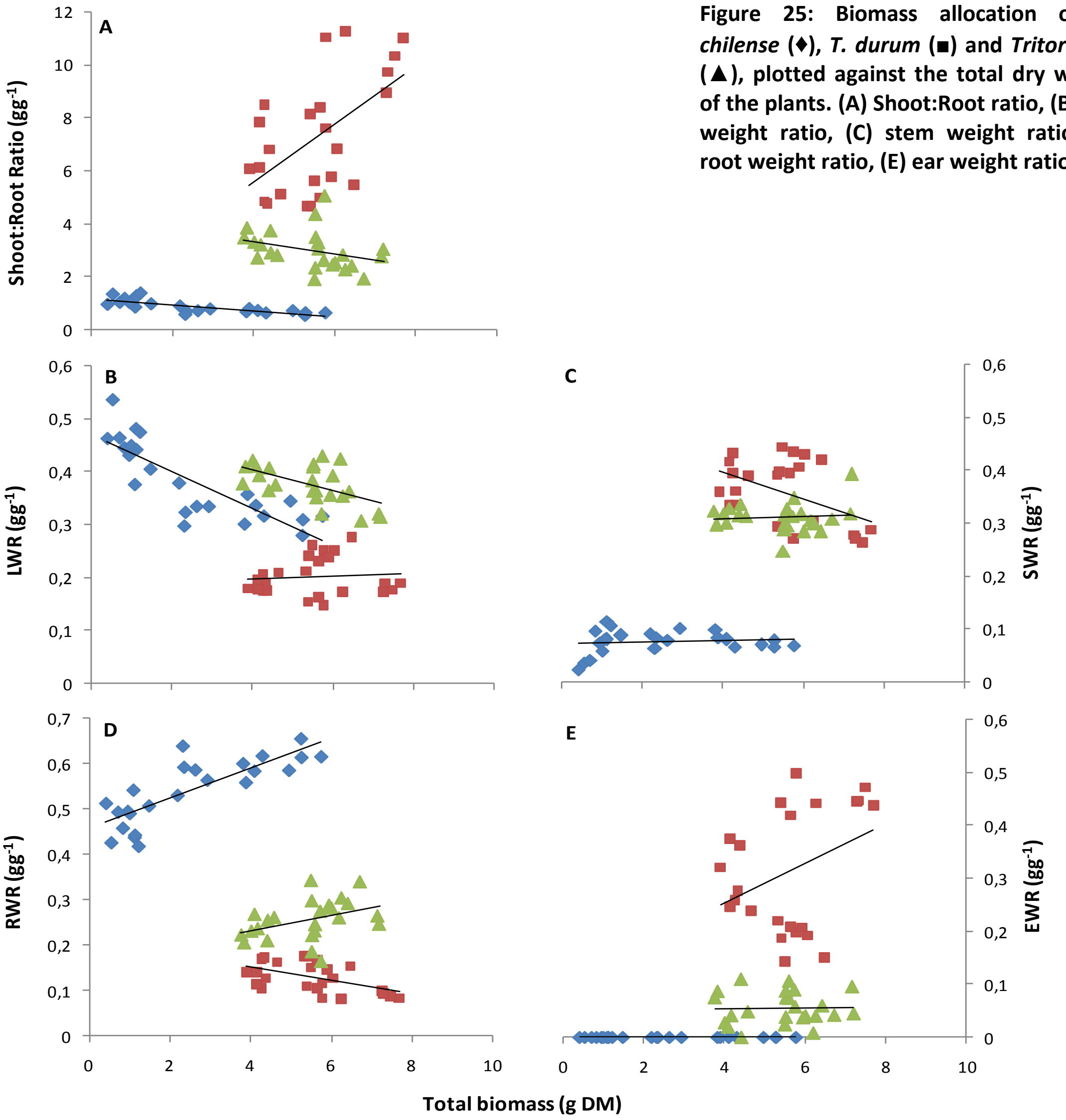

Figure 25: Biomass allocation of *H. chilense* (♦), *T. durum* (■) and *Tritordeum* (▲), plotted against the total dry weight of the plants. (A) Shoot:Root ratio, (B) leaf weight ratio, (C) stem weight ratio, (D) root weight ratio, (E) ear weight ratio

Therefore, a plant is likely to increase its allocation to its shoot, if photosynthesis efficiency is held back by a lack of above-ground resources (e.g. CO_2 concentration or light intensity). Likewise, an increased allocation towards roots would be the anticipated result in an environment, where underground factors such as water or nutrient availability are causing impediments to growth. Such behaviour is then considered adaptive to the environmental settings at hand (Poorter & Nagel, 2000).

In Fig. 25 it is shown how the different plants in the trial altered their SRR with progression of their biomass increase over the time between the two harvests. Additionally, it is possible to observe which compartment was responsible for that modification and draw basic conclusions on plant growth strategies. The graphs represent only a general comparison of the different behaviour of the species for it does not include the reactions induced by the different water treatments.

It might be interesting to note that the decrease of SRR in *H. chilense* was caused mainly by the increased root fraction and decreased leaf fraction, while its stems did not have any major part to play. Given the species perennial nature, it is reasonable to believe that it invested a major part of its biomass into root development in order to prepare better for flowering in the following season. That was not the case in *T. durum,* where the observed strong increase in SRR was brought about mainly due to the successful grain-filling, marked by a high EWR and the decrease of its root fraction. In this case there was no pronounced ontogenetic shift of biomass towards leaves between the harvests. *Tritordeum'*s behaviour compares most to the wild barley, at least in terms of biomass allocation patterns and not in absolute terms. Its SRR decreased mainly due to the drop of its leaf fraction and the raised root fraction. This performance could be attributed to the grain-filling failure in the hybrid. However, the fact that the hybrid displayed biomass allocation to different compartments comparable to the ones of durum (higher LWR and higher RWR and similar SWR) has to be considered. This matched well to the observation that *Tritordeum* had similar values of total dry biomass, specific leaf area, more tillers and actually a bigger root system at both harvests, ultimately indicating that it is better adapted than durum in environments where WUE and drought resistance are likely to be key factors for survival.

Its potential, however, was not reached in this experiment because of the inability of the hybrid to fill its grains. The reasons behind this rather unexpected result could be accredited to several occurrences. Stresses during grain-filling and their negative effects on yield have been assessed by various authors (e.g. Farooq et al., 2011; Fokar et al., 1998; Royo et al., 2006). However, the fact that the species, although later than durum, successfully reached flowering in medium and moist conditions, and anthers were visible on as many as 50% of its spikelets, suggests that the growth requirements up to that point were met and that other factors, e.g. photoperiod could be excluded. Hence it could be argued that the failure of grain filling initializationin those cases is mainly due to inefficient pollination (Asseng et al., 2011; Dolferus et al., 2011; Farooq et al., 2011; Hedhly, 2011; Harsant et al., 2013).

The most likely reason behind that could be the warm weather experienced during the post-anthesis days in *Tritordeum.* Higher temperatures tend to disrupt photosynthesis activity and that in turn lessens the availability of new photosynthates or carbohydrates being utilized for filling the species grains. That part is crucial since the far larger portion of carbohydrates required for proper grain-filling is synthesized after flowering (Brown et al., 2005). Indeed, temperatures observed were on average higher than the ones experienced by *T. durum* at the time of occurrence of its flowering and grain-filling phases (Figs. 7 and 9).

Additionally, as suggested by Rerkasem & Jamjod (1996) a deficiency in a certain chemical compound in the soil, in the case of their study boron, could lead to a partial or complete failure of grain set in wheat varieties by inducing pollen sterility. Unfortunately, detailed information on boron concentrations of the soil substrate was not provided.

Last but not least, the hybrid might have been subjected to fungal infestations which may have interfered with reproduction. However, since neither prevention against nor detailed investigation of involved diseases was performed (see objectives and scope of the study), the idea that this grain-filling phenomenon could be accredited to fungal or other infections could not be stated. Actually, *T. durum* was the species exhibiting a higher vulnerability to fungal attacks. By the time of senescence of flag-leaves almost all of the durum plants exhibited such symptoms (see Appendix II). Same infestations were also observed in the hybrid, but to a far lower extent.

Other highly negative factors to grain filling, such as frost damage (Cromley et al., 1998) or water availability (Ahmadi & Baker, 2001; Royo et al., 2006; Villegas et al, 2009) cannot be recognized as likely to have caused the grain filling failure. The reason behind this statement is based on the fact that there were no temperatures low enough recorded during the sensitive post-anthesis phase, or in fact throughout the whole trial. Additionally, grain filling failed in all water treatments regardless of the water amounts made available to the plants.

The observed failure of *Tritordeum* to initiate flowering under drought in the first place is a subject of another consideration. Adaptive potential by plants under drought stress is often linked with a number of physiological responses. Photosynthesis is one of the first crucial plant processes to be affected by water scarcity (Chaves & Oliveira, 2004). The expected closure of stomata leads to decreased amounts of CO_2 available for respiration and that subsequently will result in an impairment of the photosynthetic apparatus (Lawlor and Cornic, 2002; Chaves et al., 2003). Under more intense drought stresses also obstruction to metabolic processes (Medrano et al., 2002) and membrane damages (Inzé and Van Montagu, 1995) are to be expected. Stomata closure is strongly related with a modification in leaf area either by prevention of new leaf development or by earlier leaf senescence (Waseem et al. 2011). The canopy reduction in turn results in a drop in radiation intercepting area, which eventually decreases absolute biomass productivity (Pereira and Chaves, 1993). The water scarcity and the warmer weather at later stages of growth in *Tritordeum* under dry treatment are likely to have formed a stress level too severe for the hybrid to overcome.

It is impossible, however, to exclude the possibility that, given a hypothetical extended growth period, longer than the 107 days of trial duration, none of the newly-grown tillers in the three treatments would have managed to flower or develop well-filled grains. This, provided it had happened, would have been an adaptation to prolonged drought spells and therefore a trait of certain interest to plant breeders.

4.3 Effect of treatments

The growth responses in ***H. chilense*** under the three different treatments (Fig. 26) match the ones associated with Brouwer's "functional equilibrium" theory. A shift of shoot to root ratio with a moderately decreased leaf fraction in favour of an augmented rooting is exactly the reaction one could expect under drought (Poorter & Nagel, 2000). As a matter of fact, during the interval between the two harvests, this kind of behaviour in *H. chilense* was observed under all three treatments.

The main difference was that under limited water supply, this shift was more pronounced with regard to total dry biomass the plants built up in the different treatments. What could be the explanation of this behaviour even under medium and moist water levels is, as mentioned above, the perennial nature of this species of barley.

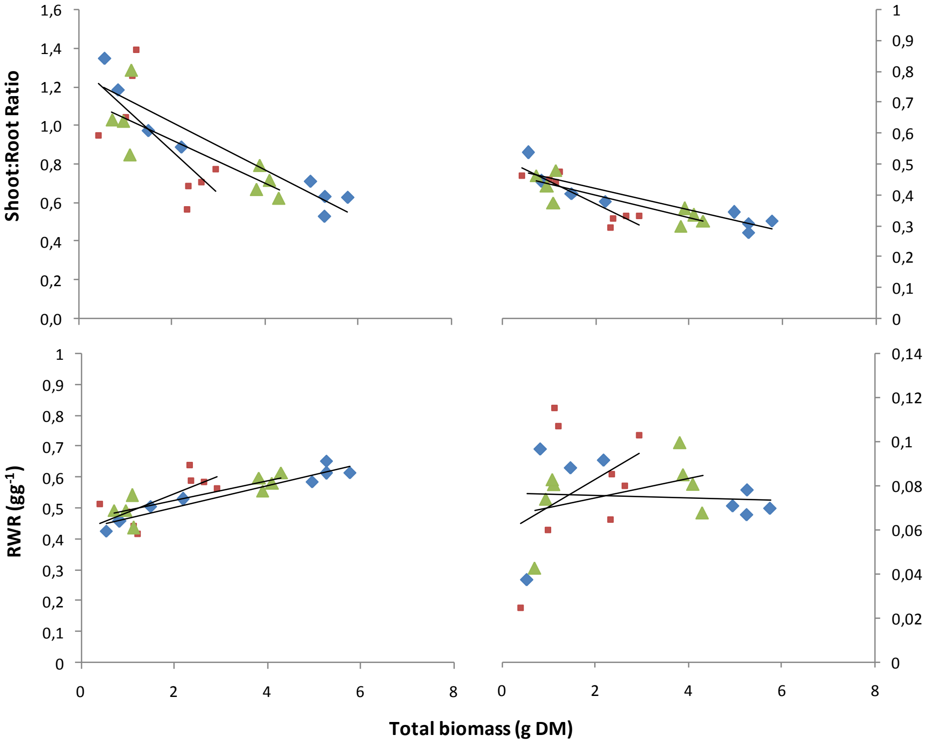

Figure 26: Biomass allocation in *H. chilense* under dry (■), medium (▲) and moist (♦) water supplies plotted against the total dry weight of the plants.

In ***T. durum,*** unlike in the case of the perennial *H. chilense,* different water treatments triggered different growth responses (Fig. 27). In an attempt to adapt itself to the induced drought and be able to complete its full life cycle in time, the species increased its root fraction. Under the assumption that a reduced water availability is likely to reduce the water that is taken up by plants and in addition also will negatively affect the nutrient uptake in the resulting less moist soil (Marschner, 1995), the plants would be expected to allocate more mass in their rooting zone. However, with lower water uptake, also the photosynthesis of the leaves is normally impaired.

Therefore, plants in dry environments might choose also to try and avoid a decrease in their leaf fraction as much as possible. Thus, the shift in the biomass equilibrium towards roots is not likely going to be as pronounced as when the acquisition of nutrients was the limiting growth factor (Poorter & Nagel, 2000).

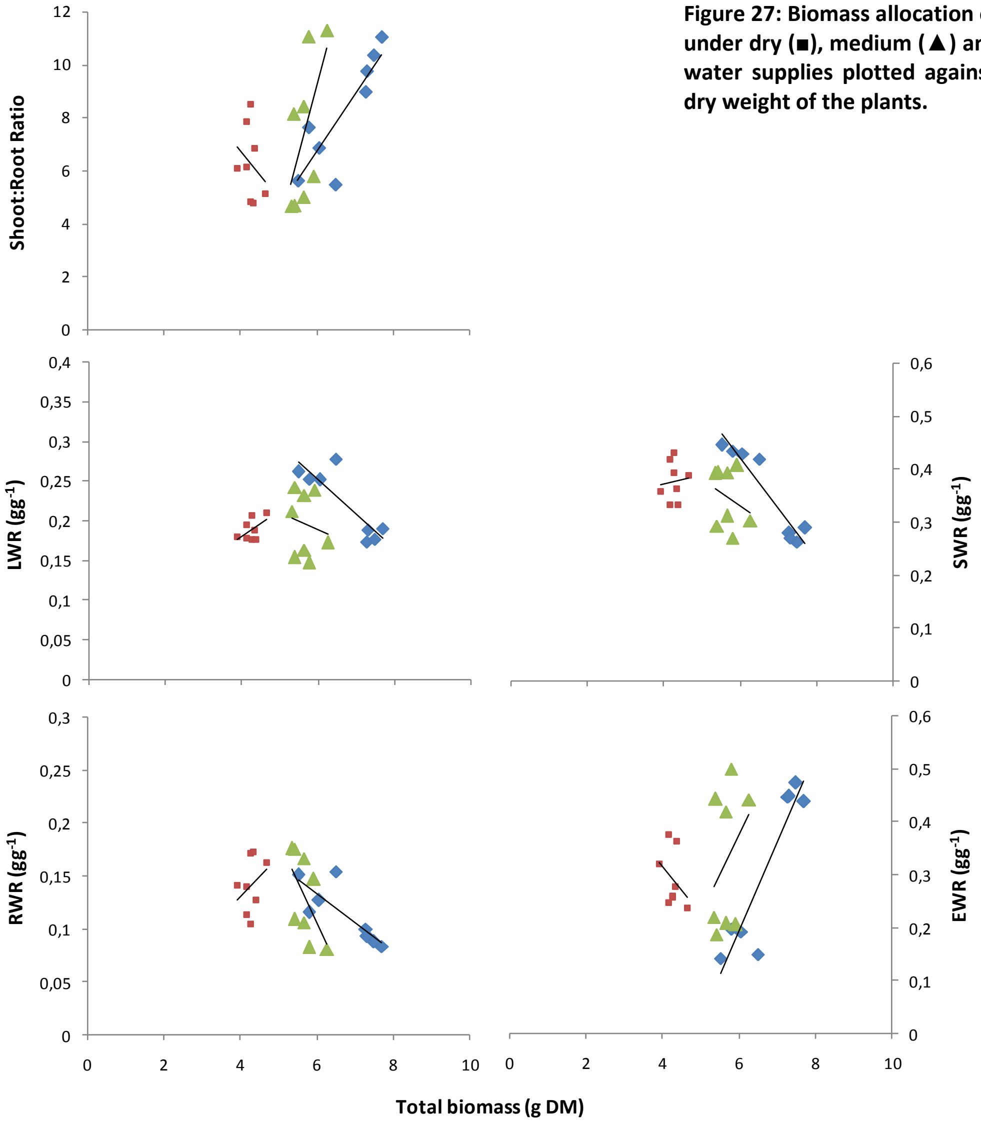

Figure 27: Biomass allocation of *T. durum* under dry (■), medium (▲) and moist (♦) water supplies plotted against the total dry weight of the plants.

T. durum was a good example of the afore-mentioned consideration and in reality, in addition to its RWR increase, did also try to avoid the shrinkage of its LWR. This, combined with the fact that proper grain filling depends mainly on photosynthetic activity and nutrient accumulation after anthesis (Sinclair & Jamieson, 2006), C-acquisition occurred at lower intensity under drought, which was underlined by the reduction of the final weight of the ears in drought-subjected plants. Lower seed filling under dry conditions subsequently led to the significantly lower yield observed in durum.

In contrast to the mentioned growth strategy, i.e. in medium and moist treatments, the species was able to focus solely on its reproductive development. Under those conditions, with increases in biomass, durum focussed on increasing its ear fraction to ensure the proper filling of its grains. That shift occurred at the expense of all other growth compartments.

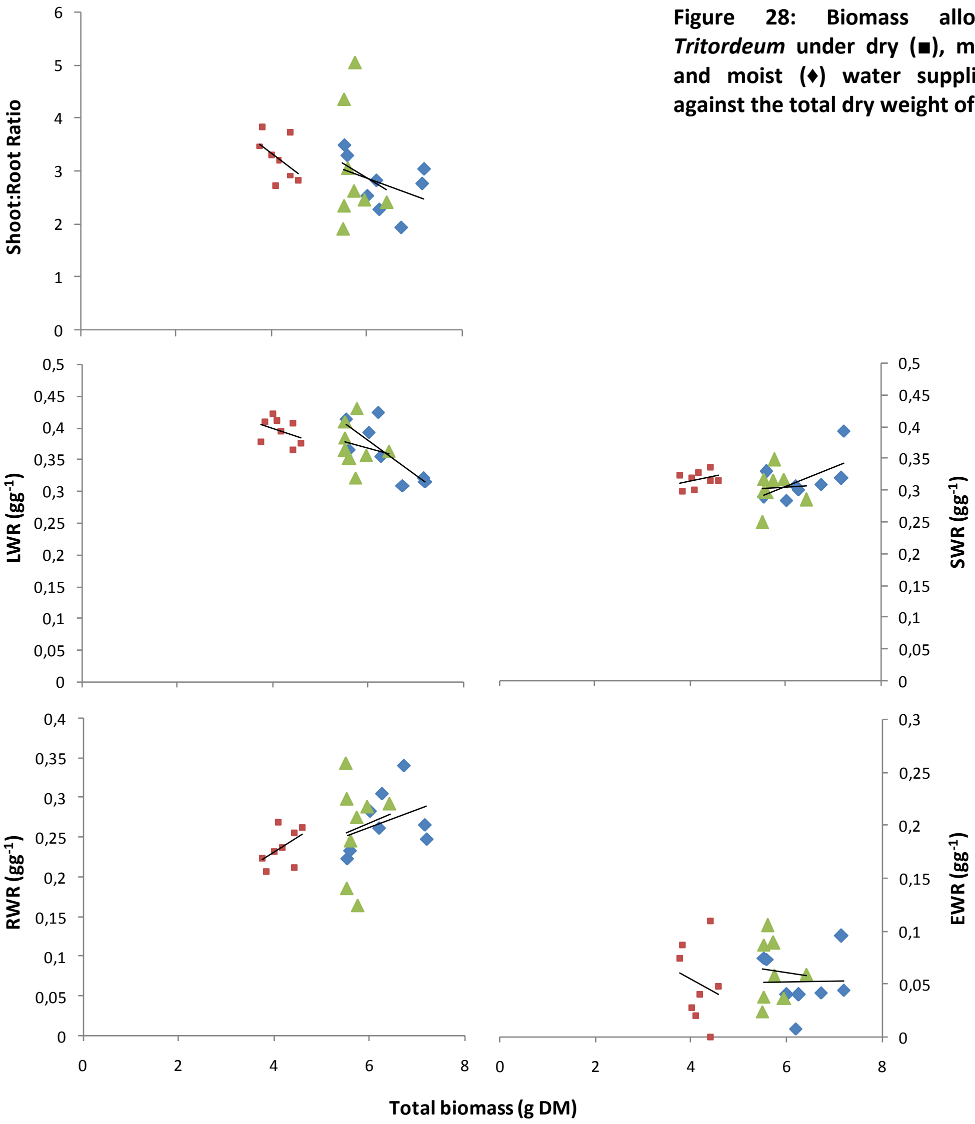

Figure 28: Biomass allocation of *Tritordeum* under dry (■), medium (▲) and moist (♦) water supplies plotted against the total dry weight of the plants.

Tritordeum showed a similar behaviour to *T. durum* under drought, with the one exception that it did not try to enlarge the LWR (Fig. 28). Under sufficient water availability the plant showed growth patterns more comparable to Chilean barley. The decrease in its SRR with increased biomass could again be explained by the breakdown in grain-filling, i.e. the lower transport of assimilates to the sinks.

4.4 Water use efficiency

Root dry weight, specific leaf area, mean leaf area and leaf dry matter content at IH were used in a linear regression model to predict water use efficiency. SLA and RDW are considered good predictors for WUE by Songsri et al. (2008). The reason behind choosing LDMC as a part in the model is that together with SLA, it forms a convincing indication for a plant's leaf thickness (Vile et al., 2005), which is a morphological parameter worth considering when analyzing plant developmental strategies. Although the study of the association between SLA, RDW and WUE by Songsri et al. (2008) was performed on different genotypes of the same species, it might be interesting to test the predictive capacity of those parameters also for *H. chilense*, *T. durum* and *Tritordeum*.

The correlations between the variables observed under **dry conditions** are shown in Table 3. All correlations with the exception of the ones between RDW and LDMC, and RDW and MLA were statistically significant (p-value < 0.05). Interestingly, even though LDMC showed a better correlation with WUE than RDW, it was the dry weight of the roots that was a better predictor in this model and LDMC was left out of the final model by the stepwise regression.

Table 3: Correlations between model predictors under dry conditions (N=12)

Variable	2	3	4	5
1. WUE	-0,922	0,88	0,681	0,763
2. SLA	-	-0,799	-0,661	-0,839
3. MLA		-	0,37	0,681
4. RDW			-	0,353
5. LDMC				-

Note. All correlations except that between RDW and LDMC and between RDW and MLA are statistically significant (p < 0.05)

Table 4: Stepwise multiple regression results under dry conditions

Model	b	*SE-b*	Beta	Pearson *r*	sr^2
Constant	2,087	1,038			
SLA	-0,005	0,002	-0,360	-0,922	0,030
MLA	0,076	0,020	0,505	0,880	0,091
RDW	1,206	0,521	0,256	0,681	0,033

Note. The dependent variable was WUE. R^2 = 0,95 R^2 adj. = 0,931.
sr^2 is the squared semi-partial correlation.

The prediction model contained three of those four initial variables and was reached in three steps with no predictor being removed. The constructed model was statistically significant F (3, 12) = 50 835, p < 0.001 and was accountable for 93% (R^2=0.95, Adjusted R^2=0.931) of the variance in WUE. The modelled WUE of plants was primarily predicted by higher MLA and RDW and a lower SLA with decreasing prediction importance respectively. That information, together with the raw and standardized regression coefficients and their correlations with the predicted variable and their squared semi-partial correlations is shown in Tab. 4. The biggest weight in the model was that of MLA, followed by RDW and SLA. With the considerable correlations between the predictors, the unique variance explained by each predictor, manifested by the squared semi-partial correlations, was rather low: MLA, RDW and SLA explained 9%, 3.3% and 3% of the variance of WUE.

Table 5 gives an overview of the correlations between predictors under **medium water supply**. Again as with dry conditions only the correlations of RDW with LDMC and MLA failed to show any statistical significance.

The constructed model was statistically significant F (3, 12) = 140 400, $p < 0.001$ and was descriptive for 98% (R^2=0.981, Adjusted R^2=0.974) of the variance in WUE (see Tab. 6).

However, unlike in dry conditions, here RDW had the highest predictive importance with around 8.5% unique explanation of the variance in WUE. Second best predictor was SLA with 1.4%, followed by MLA with less than 0.5%.

Table 5: Correlations between model predictors under medium conditions (N = 12)

Variable	2	3	4	5
1. WUE	-0,984	0,772	0,771	0,938
2. SLA	-	-0,778	-0,716	-0,958
3. MLA		-	0,328	0,803
4. RDW			-	0,656
5. LDMC				-

Note. All correlations except those between RDW and LDMC and between RDW and MLA are statistically significant ($p < 0.05$)

Table 6: Regression results under medium treatment

Model	b	*SE-b*	Beta	Pearson *r*	sr^2
Constant	4,255	0,756			
SLA	-0,008	0,001	-0,738	-0,984	0,014
MLA	0,017	0,011	0,133	0,772	0,005
RDW	0,650	0,266	0,198	0,771	0,085

Note. The dependent variable was WUE. R^2 = 0,981 R^2 adj. = 0,974.
sr^2 is the squared semi-partial correlation.

Considering the outcome of the regression analysis and the performance of the species in the trial with respect to the variables included in the model, it is worth noticing that albeit being statistically non-significant, under dry conditions all the species showed deterioration in the mean size of their leaves. Since MLA was the most important modelled WUE predictor under drought, it could be argued that Chilean barley and the hybrid exhibited a more WUE-favourable response to that of durum. Dry conditions drove a 22% drop of MLA in durum, while *H. chilense* and *Tritordeum* both marked lower reductions – only 12% and 7% respectively.

It would be appropriate also to underline the fact that under dry conditions, *T. durum* experienced the highest RDW reduction. Drought significantly reduced the species roots mass by 32%, while the other two showed a drop of only 10% (n.s.) in the case of *H. chilense* and 27% (n.s.) in that of *Tritordeum.* That could be regarded as a positive response by the latter two species in an attempt to increase their respective WUE.

With regard to the third element of the regression – SLA, it might be interesting to point out that *H. chilense* and *Tritordeum* decreased their SLA values with 16% (n.s.) and 4% (n.s.). Since SLA is negatively correlated to WUE, however, *T. durum's* 6% (n.s.) increase in SLA at the time meant again the most negative response relative to WUE optimization.

As suggested by Blum (2005), however, maximizing water-use efficiency, although rendering a plant more likely to survive in dry environments, often comes with traits and responses to growth that in the end negatively affect its yield potential. And in that regard *T. durum* was the best performing species, since it was the only one that actually managed to materialize any yield.

Chapter V: Conclusion

To conclude, the side hypothesis of the study, stating that the hybrid would be more drought tolerant than *T. durum,* can easily be rejected, at least under the specific trial conditions. Leaving aside the grain-filling phenomenon, under drought *Tritordeum* struggled with its growth and failed to initialize flowering. Therefore it is not possible to generally state that the hybrid outperformed its wheat parent species in this trial. On the other hand, the main hypothesis that the hybrid would actually exhibit drought adaptive traits, having in mind the discussed results of the trial, cannot be rejected.

Altogether, the experiment was well-devised to give a broad overview of the performance of the three species under differential watering conditions. Additional research on ecophysiological characteristics of *Tritordeum* has to be performed in order to find out what are the exact environmental requirements for its successful grain production. In similar future trials, a better evaluation of biomass allocation adjustments could be achieved by incorporating several additional harvesting dates along the course of the trial. Two harvests were not sufficient to investigate the effects of morphological and physiological factors that determine a plant's carbon balance.

In the context of climate change, the development of perennial cereals in future may be a good strategy in unsuitable environments/areas, although such plants will have a lower yield potential. Such species are associated with a number of supplementary benefits to their superior drought resistance. The bigger root systems they use to develop are likely to prevent the loss of top soil in arid climates by preventing erosion. Strong root growth also favours carbon sequestration and implies reduced requirements for water or fertilizers.

As an outlook it can be argued that similar experiments in future should be performed under controlled climatic conditions that truly resemble the situation in those areas where the crops are normally grown or are to be introduced.

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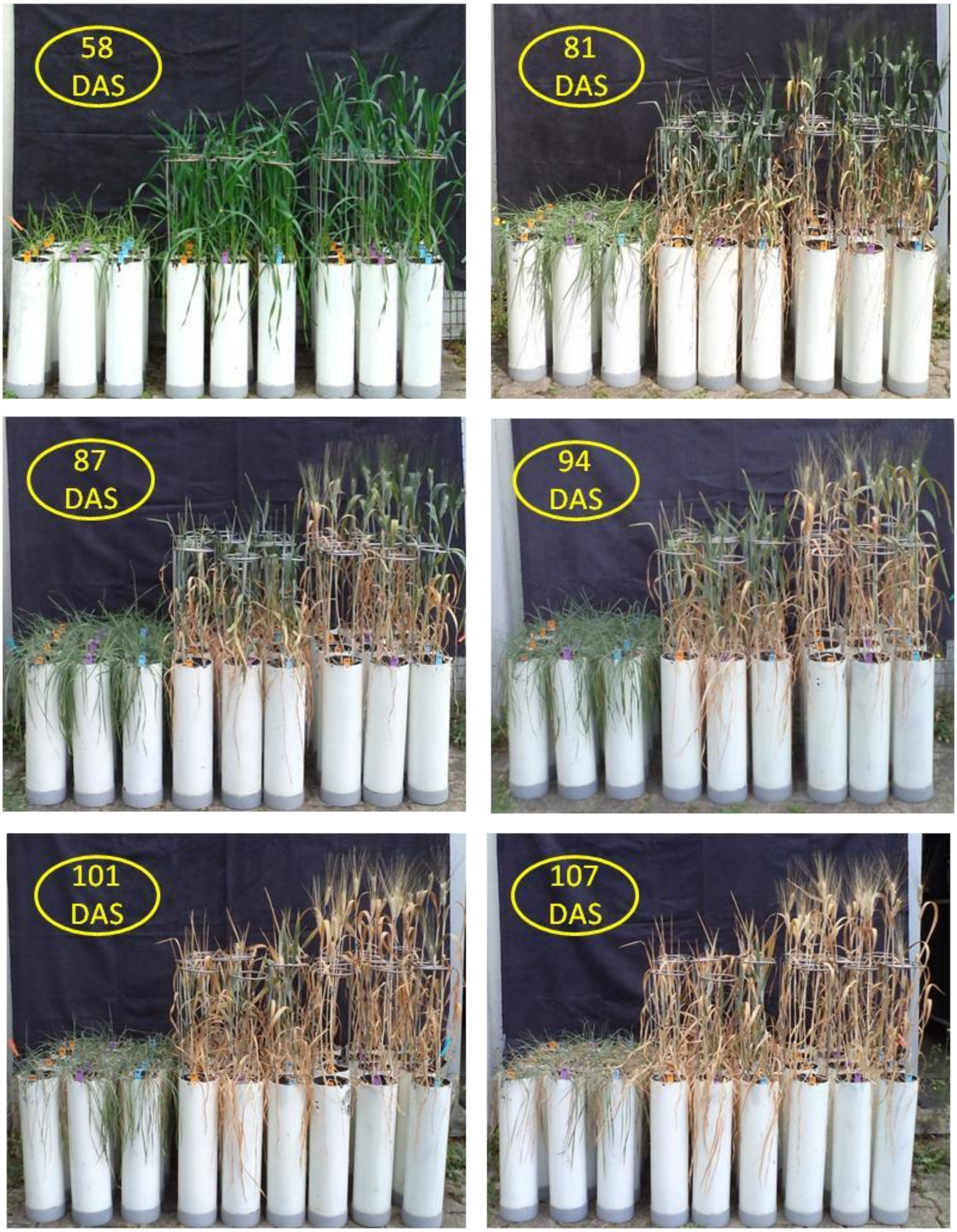
Appendix I

Comparison of the growth progression over time, colour codes: orange labels stand for dry, purple for medium and blue for moist water treatments.



Appendix II

Picture 1: *T. durum* flag leaf (pot under medium water treatment) subject to fungal infection

Picture 2: Comparison between ears of *T. durum* (under medium treatment left) and *Tritordeum* (under moist treatment, right*)*

Appendix III

In this supplementary section feature all the summary tables for the different parameters investigated in the analysis with more statistical detail.

Part Intermediate Harvest

R^2 = 0,967	Total Biomass Summary			p-value
	Species			0,00000
	Treatment			0,00000
	SPEC*TREAT			0,00213
			difference (%)	
Effect of treatment	H. chilense	moist vs med	30,2	n.s.
		moist vs dry	34,0	n.s.
		med vs dry	2,9	n.s.
	Trit. durum	moist vs med	6,8	n.s.
		moist vs dry	37,3	0,00004
		med vs dry	28,6	0,00033
	Tritordeum	moist vs med	-1,3	n.s.
		moist vs dry	35,3	0,00016
		med vs dry	37,1	0,00011
Effect of species	moist	Tritordeum vs H. chilense	362,9	0,00000
		Tritordeum vs Trit. durum	-2,0	n.s.
		Trit. durum vs H. chilense	372,4	0,00000
	med	Tritordeum vs H. chilense	510,9	0,00000
		Tritordeum vs Trit. durum	6,0	n.s.
		Trit. durum vs H. chilense	476,2	0,00000
	dry	Tritordeum vs H. chilense	358,5	0,00000
		Tritordeum vs Trit. durum	-0,6	n.s.
		Trit. durum vs H. chilense	361,2	0,00000

R^2 = 0,893	Mean Leaf Area Summary			p-value
	Species			0,00000
	Treatment			0,08786
	SPEC*TREAT			0,02959
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-2,0	n.s.
		moist vs dry	11,2	n.s.
		med vs dry	13,5	n.s.
	Trit. durum	moist vs med	-27,1	0,04277
		moist vs dry	-6,7	n.s.
		med vs dry	28,0	n.s.
	Tritordeum	moist vs med	11,8	n.s.
		moist vs dry	20,2	n.s.
		med vs dry	7,5	n.s.
Effect of species	moist	Tritordeum vs H. chilense	284,4	0,00000
		Tritordeum vs Trit. durum	-22,3	0,03133
		Trit. durum vs H. chilense	394,8	0,00000
	med	Tritordeum vs H. chilense	236,8	0,00003
		Tritordeum vs Trit. durum	-49,4	0,00000
		Trit. durum vs H. chilense	565,2	0,00000
	dry	Tritordeum vs H. chilense	255,8	0,00006
		Tritordeum vs Trit. durum	-39,7	0,00018
		Trit. durum vs H. chilense	490,0	0,00000

R^2 = 0,948	Specific Leaf Area Summary			p-value
	Species			0,00000
	Treatment			0,00088
	SPEC*TREAT			0,03218
			difference (%)	
Effect of treatment	H. chilense	moist vs med	6,5	n.s.
		moist vs dry	26,1	0,01135
		med vs dry	18,4	n.s.
	Trit. durum	moist vs med	16,0	0,03880
		moist vs dry	9,7	n.s.
		med vs dry	-5,4	n.s.
	Tritordeum	moist vs med	12,7	0,02312
		moist vs dry	17,6	0,00537
		med vs dry	4,4	n.s.
Effect of species	moist	H. chilense vs Tritordeum	136,8	0,00000
		Tritordeum vs Trit. durum	-3,4	n.s.
		H. chilense vs Trit. durum	128,9	0,00000
	med	H. chilense vs Tritordeum	150,5	0,00000
		Tritordeum vs Trit. durum	-0,5	n.s.
		H. chilense vs Trit. durum	149,3	0,00000
	dry	H. chilense vs Tritordeum	121,0	0,00000
		Tritordeum vs Trit. durum	-9,9	n.s.
		H. chilense vs Trit. durum	99,1	0,00000

R^2 = 0,931	Leaf Area Ratio Summary			p-value
	Species			0,00000
	Treatment			0,04841
	SPEC*TREAT			0,47603
			difference (%)	
Effect of treatment	H. chilense	moist vs med	8,5	n.s.
		moist vs dry	24,8	n.s.
		med vs dry	15,1	n.s.
	Trit. durum	moist vs med	50,0	0,02251
		moist vs dry	53,0	0,01882
		med vs dry	2,0	n.s.
	Tritordeum	moist vs med	22,7	n.s.
		moist vs dry	21,5	n.s.
		med vs dry	-1,0	n.s.
Effect of species	moist	H. chilense vs Tritordeum	281,3	0,00000
		Tritordeum vs Trit. durum	58,6	n.s.
		H. chilense vs Trit. durum	504,7	0,00000
	med	H. chilense vs Tritordeum	331,3	0,00000
		Tritordeum vs Trit. durum	93,9	n.s.
		H. chilense vs Trit. durum	736,1	0,00000
	dry	H. chilense vs Tritordeum	271,1	0,00000
		Tritordeum vs Trit. durum	99,7	n.s.
		H. chilense vs Trit. durum	641,3	0,00000

R^2 = 0,843	Shoot/Root Ratio Summary			p-value
	Species			0,00000
	Treatment			0,58845
	SPEC*TREAT			0,26373
			difference (%)	
Effect of treatment	H. chilense	moist vs med	5,0	n.s.
		moist vs dry	-5,4	n.s.
		med vs dry	-10,0	n.s.
	Trit. durum	moist vs med	26,9	n.s.
		moist vs dry	4,0	n.s.
		med vs dry	-18,0	n.s.
	Tritordeum	moist vs med	-14,9	n.s.
		moist vs dry	-8,7	n.s.
		med vs dry	7,3	n.s.
Effect of species	moist	Tritordeum vs H. chilense	176,7	0,00316
		Tritordeum vs Trit. durum	-52,5	0,00001
		Trit. durum vs H. chilense	482,5	0,00000
	med	Tritordeum vs H. chilense	241,5	0,00025
		Tritordeum vs Trit. durum	-29,2	0,02080
		Trit. durum vs H. chilense	382,2	0,00000
	dry	Tritordeum vs H. chilense	186,7	0,00120
		Tritordeum vs Trit. durum	-45,9	0,00007
		Trit. durum vs H. chilense	429,7	0,00000

R^2 = 0,885	Leaf Weight Ratio Summary			p-value
	Species			0,00000
	Treatment			0,36660
	SPEC*TREAT			0,22357
			difference (%)	
Effect of treatment	H. chilense	moist vs med	0,7	n.s.
		moist vs dry	-3,5	n.s.
		med vs dry	-4,2	n.s.
	Trit. durum	moist vs med	12,9	0,01380
		moist vs dry	32,5	0,00010
		med vs dry	17,4	0,00659
	Tritordeum	moist vs med	2,4	n.s.
		moist vs dry	2,4	n.s.
		med vs dry	0,0	n.s.
Effect of species	moist	H. chilense vs Tritordeum	10,7	n.s.
		Tritordeum vs Trit. durum	52,9	0,00000
		H. chilense vs Trit. durum	69,4	0,00000
	med	H. chilense vs Tritordeum	12,6	0,04894
		Tritordeum vs Trit. durum	68,5	0,00000
		H. chilense vs Trit. durum	89,8	0,00000
	dry	H. chilense vs Tritordeum	17,6	0,00786
		Tritordeum vs Trit. durum	97,8	0,00000
		H. chilense vs Trit. durum	132,5	0,00000

R^2 = 0,974	Stem Weight Ratio Summary			p-value
	Species			0,00000
	Treatment			0,61863
	SPEC*TREAT			0,31517
			difference (%)	
Effect of treatment	H. chilense	moist vs med	11,8	n.s.
		moist vs dry	2,0	n.s.
		med vs dry	-8,8	n.s.
	Trit. durum	moist vs med	8,7	0,00715
		moist vs dry	6,0	n.s.
		med vs dry	-2,5	n.s.
	Tritordeum	moist vs med	-4,7	n.s.
		moist vs dry	-4,4	n.s.
		med vs dry	0,3	n.s.
Effect of species	moist	Tritordeum vs H. chilense	287,5	0,00000
		Tritordeum vs Trit. durum	-30,0	0,00000
		Trit. durum vs H. chilense	453,5	0,00000
	med	Tritordeum vs H. chilense	354,5	0,00000
		Tritordeum vs Trit. durum	-20,2	0,00004
		Trit. durum vs H. chilense	469,5	0,00000
	dry	Tritordeum vs H. chilense	313,1	0,00000
		Tritordeum vs Trit. durum	-22,5	0,00001
		Trit. durum vs H. chilense	432,7	0,00000

R^2 = 0,953	Ear Weight Ratio Summary			p-value
	Species			0,00000
	Treatment			0,01109
	SPEC*TREAT			0,01789
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-	-
		moist vs dry	-	-
		med vs dry	-	-
	Trit. durum	moist vs med	-17,2	0,02830
		moist vs dry	-32,0	0,00022
		med vs dry	-18,0	0,00878
	Tritordeum	moist vs med	-18,8	n.s.
		moist vs dry	-19,8	n.s.
		med vs dry	-1,2	n.s.
Effect of species	moist	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	249,2	0,00000
		Trit. durum vs H. chilense	-	-
	med	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	242,5	0,00000
		Trit. durum vs H. chilense	-	-
	dry	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	312,3	0,00000
		Trit. durum vs H. chilense	-	-

R^2 = 0,93	Root Weight Ratio Summary			p-value
	Species			0,00000
	Treatment			0,61186
	SPEC*TREAT			0,80267
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-2,4	n.s.
		moist vs dry	3,1	n.s.
		med vs dry	5,6	n.s.
	Trit. durum	moist vs med	-17,6	n.s.
		moist vs dry	-5,4	n.s.
		med vs dry	14,8	n.s.
	Tritordeum	moist vs med	7,0	n.s.
		moist vs dry	6,9	n.s.
		med vs dry	-0,1	n.s.
Effect of species	moist	H. chilense vs Tritordeum	92,2	0,00000
		Tritordeum vs Trit. durum	82,2	0,00031
		H. chilense vs Trit. durum	250,1	0,00000
	med	H. chilense vs Tritordeum	110,6	0,00000
		Tritordeum vs Trit. durum	40,3	0,02050
		H. chilense vs Trit. durum	195,5	0,00000
	dry	H. chilense vs Tritordeum	99,3	0,00000
		Tritordeum vs Trit. durum	61,3	0,00300
		H. chilense vs Trit. durum	221,4	0,00000

R^2 = 0,647	Root Dry Weight Summary			p-value
	Species			0,00000
	Treatment			0,02114
	SPEC*TREAT			0,56605
			difference (%)	
Effect of treatment	H. chilense	moist vs med	32,6	n.s.
		moist vs dry	47,4	n.s.
		med vs dry	11,1	n.s.
	Trit. durum	moist vs med	-11,6	n.s.
		moist vs dry	29,8	0,04979
		med vs dry	46,8	0,00609
	Tritordeum	moist vs med	4,8	n.s.
		moist vs dry	44,4	n.s.
		med vs dry	37,8	n.s.
Effect of species	moist	Tritordeum vs H. chilense	132,1	0,00006
		Tritordeum vs Trit. durum	78,9	0,00107
		Trit. durum vs H. chilense	29,8	n.s.
	med	Tritordeum vs H. chilense	193,7	0,00002
		Tritordeum vs Trit. durum	50,8	0,01267
		Trit. durum vs H. chilense	94,7	0,01650
	dry	Tritordeum vs H. chilense	136,8	0,00256
		Tritordeum vs Trit. durum	60,7	0,03870
		Trit. durum vs H. chilense	47,4	n.s.

$R^2 = 0,774$	**Senescent Leaf Fraction Summary**				p-value
	Species				0,00000
	Treatment				0,56643
	SPEC*TREAT				0,93320
				difference (%)	
Effect of treatment	H. chilense	moist vs med		-7,6	n.s.
		moist vs dry		39,6	n.s.
		med vs dry		34,6	n.s.
	Trit. durum	moist vs med		-16,2	n.s.
		moist vs dry		-7,4	n.s.
		med vs dry		10,6	n.s.
	Tritordeum	moist vs med		-11,4	n.s.
		moist vs dry		-0,6	n.s.
		med vs dry		12,1	n.s.
Effect of species	moist	Tritordeum vs H. chilense		1350,5	0,00004
		Tritordeum vs Trit. durum		-12,1	n.s.
		Trit. durum vs H. chilense		1550,1	0,00001
	med	Tritordeum vs H. chilense		1413,4	0,00001
		Tritordeum vs Trit. durum		-16,9	n.s.
		Trit. durum vs H. chilense		1720,8	0,00000
	dry	Tritordeum vs H. chilense		782,0	0,00007
		Tritordeum vs Trit. durum		-18,0	n.s.
		Trit. durum vs H. chilense		976,3	0,00000

$R^2 = ,798$	**Leaf Dry Matter Content Summary**				p-value
	Species				0,00000
	Treatment				0,00000
	SPEC*TREAT				0,37924
				difference (%)	
Effect of treatment	H. chilense	moist vs med		-6,7	n.s.
		moist vs dry		-22,3	0,00230
		med vs dry		-16,7	0,01174
	Trit. durum	moist vs med		-18,0	0,04271
		moist vs dry		-23,6	0,00915
		med vs dry		-6,7	n.s.
	Tritordeum	moist vs med		-19,6	0,00069
		moist vs dry		-24,9	0,00007
		med vs dry		-6,6	n.s.
Effect of species	moist	Tritordeum vs H. chilense		25,2	0,00886
		Tritordeum vs Trit. durum		-6,7	n.s.
		Trit. durum vs H. chilense		34,2	0,00069
	med	Tritordeum vs H. chilense		45,3	0,00001
		Tritordeum vs Trit. durum		-4,9	n.s.
		Trit. durum vs H. chilense		52,8	0,00000
	dry	Tritordeum vs H. chilense		29,6	0,00022
		Tritordeum vs Trit. durum		-5,0	n.s.
		Trit. durum vs H. chilense		36,5	0,00002

$R^2 = 0,962$	**Water Use Efficiency Summary**				p-value
	Species				0,00000
	Treatment				0,08230
	SPEC*TREAT				0,35203
				difference (%)	
Effect of treatment	H. chilense	moist vs med		7,5	n.s.
		moist vs dry		-16,0	n.s.
		med vs dry		-21,9	n.s.
	Trit. durum	moist vs med		-6,3	n.s.
		moist vs dry		-6,3	n.s.
		med vs dry		0,0	n.s.
	Tritordeum	moist vs med		-12,1	0,01228
		moist vs dry		-7,1	n.s.
		med vs dry		5,7	n.s.
Effect of species	moist	Tritordeum vs H. chilense		292,3	0,00000
		Tritordeum vs Trit. durum		-3,9	n.s.
		Trit. durum vs H. chilense		308,1	0,00000
	med	Tritordeum vs H. chilense		379,9	0,00000
		Tritordeum vs Trit. durum		2,5	n.s.
		Trit. durum vs H. chilense		368,2	0,00000
	dry	Tritordeum vs H. chilense		254,6	0,00000
		Tritordeum vs Trit. durum		-3,1	n.s.
		Trit. durum vs H. chilense		265,8	0,00000

$R^2 = 0,894$	**Relative Growth Rate Summary**				p-value
	Species				0,00000
	Treatment				0,04705
	SPEC*TREAT				0,94692
				difference (%)	
Effect of treatment	H. chilense	moist vs med		2,1	n.s.
		moist vs dry		-3,5	n.s.
		med vs dry		-1,4	n.s.
	Trit. durum	moist vs med		0,7	n.s.
		moist vs dry		3,8	0,00002
		med vs dry		3,0	0,00013
	Tritordeum	moist vs med		-0,2	n.s.
		moist vs dry		3,6	0,00014
		med vs dry		3,8	0,00010
Effect of species	moist	Tritordeum vs H. chilense		23,8	0,00000
		Tritordeum vs Trit. durum		-0,2	n.s.
		Trit. durum vs H. chilense		24,1	0,00000
	med	Tritordeum vs H. chilense		26,6	0,00000
		Tritordeum vs Trit. durum		0,7	n.s.
		Trit. durum vs H. chilense		25,8	0,00000
	dry	Tritordeum vs H. chilense		-23,7	0,00000
		Tritordeum vs Trit. durum		-0,1	n.s.
		Trit. durum vs H. chilense		-23,8	0,00000

Part Final Harvest

$R^2 = 0,965$	**Total Dry Biomass**			p-value
	Species			0,00000
	Treatment			0,00000
	SPEC*TREAT			0,37911
			difference (%)	
Effect of treatment	H. chilense	moist vs med	31,9	0,00012
		moist vs dry	107,7	0,00000
		med vs dry	57,5	0,00004
	Trit. durum	moist vs med	28,9	0,00001
		moist vs dry	77,3	0,00000
		med vs dry	37,6	0,00002
	Tritordeum	moist vs med	22,3	0,00014
		moist vs dry	70,6	0,00000
		med vs dry	39,4	0,00002
Effect of species	moist	Tritordeum vs H. chilense	28,7	0,00000
		Tritordeum vs Trit. durum	-8,1	0,00499
		Trit. durum vs H. chilense	40,0	0,00000
	med	Tritordeum vs H. chilense	38,7	0,00000
		Tritordeum vs Trit. durum	-3,2	n.s.
		Trit. durum vs H. chilense	43,3	0,00000
	dry	Tritordeum vs H. chilense	56,7	0,00000
		Tritordeum vs Trit. durum	-4,4	n.s.
		Trit. durum vs H. chilense	63,9	0,00000

$R^2 = 0,854$	**Water Use Efficiency Summary**			p-value
	Species			0,00000
	Treatment			0,19857
	SPEC*TREAT			0,35295
			difference (%)	
Effect of treatment	H. chilense	moist vs med	0,9	n.s.
		moist vs dry	2,8	n.s.
		med vs dry	1,9	n.s.
	Trit. durum	moist vs med	4,6	n.s.
		moist vs dry	-1,8	n.s.
		med vs dry	-6,1	0,02887
	Tritordeum	moist vs med	-0,4	n.s.
		moist vs dry	-8,3	n.s.
		med vs dry	-7,9	n.s.
Effect of species	moist	Tritordeum vs H. chilense	29,6	0,00002
		Tritordeum vs Trit. durum	-11,2	0,00868
		Trit. durum vs H. chilense	46,0	0,00000
	med	Tritordeum vs H. chilense	31,2	0,00001
		Tritordeum vs Trit. durum	-6,8	n.s.
		Trit. durum vs H. chilense	40,8	0,00000
	dry	Tritordeum vs H. chilense	45,3	0,00000
		Tritordeum vs Trit. durum	-4,9	n.s.
		Trit. durum vs H. chilense	52,8	0,00000

$R^2 = 0,990$	**Relative Growth Rate Summary**			p-value
	Species			0,00000
	Treatment			0,00000
	SPEC*TREAT			0,00000
			difference (%)	
Effect of treatment	H. chilense	moist vs med	0,9	n.s.
		moist vs dry	44,2	0,00002
		med vs dry	43,0	0,00003
	Trit. durum	moist vs med	583,8	0,00043
		moist vs dry	748,7	-0,00005
		med vs dry	194,9	n.s.
	Tritordeum	moist vs med	375,4	0,00013
		moist vs dry	313,1	0,00008
		med vs dry	22,6	n.s.
Effect of species	moist	H. chilense vs Tritordeum	817,9	0,00000
		Tritordeum vs Trit. durum	-29,2	n.s.
		H. chilense vs Trit. durum	549,4	0,00000
	med	H. chilense vs Tritordeum	2606,2	0,00000
		Tritordeum vs Trit. durum	-275,7	0,04581
		H. chilense vs Trit. durum	4302,7	0,00000
	dry	H. chilense vs Tritordeum	1456,0	0,00000
		Tritordeum vs Trit. durum	-115,4	n.s.
		H. chilense vs Trit. durum	3020,5	0,00000

$R^2 = 0,965$	**Root Dry Weight Summary**			p-value
	Species			0,00000
	Treatment			0,00000
	SPEC*TREAT			0,00000
			difference (%)	
Effect of treatment	H. chilense	moist vs med	38,0	0,00019
		moist vs dry	116,3	0,00000
		med vs dry	56,8	0,00027
	Trit. durum	moist vs med	24,3	0,04334
		moist vs dry	16,3	n.s.
		med vs dry	-6,4	n.s.
	Tritordeum	moist vs med	21,2	0,02848
		moist vs dry	104,1	0,00003
		med vs dry	68,4	0,00075
Effect of species	moist	H. chilense vs Tritordeum	66,4	0,00000
		Tritordeum vs Trit. durum	190,8	0,00000
		H. chilense vs Trit. durum	383,8	0,00000
	med	H. chilense vs Tritordeum	46,2	0,00000
		Tritordeum vs Trit. durum	198,2	0,00000
		H. chilense vs Trit. durum	335,8	0,00000
	dry	H. chilense vs Tritordeum	57,0	0,00009
		Tritordeum vs Trit. durum	65,7	0,00354
		H. chilense vs Trit. durum	160,1	0,00000

	Shoot/Root Ratio Summary			p-value
R^2 = 0,952	Species			0,00000
	Treatment			0,01112
	SPEC*TREAT			0,00003
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-10,7	n.s.
		moist vs dry	-8,9	n.s.
		med vs dry	2,1	n.s.
	Trit. durum	moist vs med	3,0	n.s.
		moist vs dry	56,9	0,00362
		med vs dry	52,3	0,00590
	Tritordeum	moist vs med	0,9	n.s.
		moist vs dry	-21,2	n.s.
		med vs dry	-21,8	n.s.
Effect of species	moist	Tritordeum vs H. chilense	301,3	0,00262
		Tritordeum vs Trit. durum	-75,0	0,00000
		Trit. durum vs H. chilense	1502,9	0,00000
	med	Tritordeum vs H. chilense	255,1	0,00401
		Tritordeum vs Trit. durum	-74,4	0,00000
		Trit. durum vs H. chilense	1288,7	0,00000
	dry	Tritordeum vs H. chilense	363,9	0,00015
		Tritordeum vs Trit. durum	-50,2	0,00001
		Trit. durum vs H. chilense	831,1	0,00000

	Leaf Weight Ratio Summary			p-value
R^2 = 0,949	Species			0,00000
	Treatment			0,00383
	SPEC*TREAT			0,00188
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-4,7	n.s.
		moist vs dry	-3,1	n.s.
		med vs dry	1,7	n.s.
	Trit. durum	moist vs med	14,5	0,00456
		moist vs dry	0,9	n.s.
		med vs dry	-11,9	0,00673
	Tritordeum	moist vs med	-8,6	n.s.
		moist vs dry	-19,0	0,00093
		med vs dry	-11,4	0,01759
Effect of species	moist	H. chilense vs Tritordeum	-3,8	n.s.
		Tritordeum vs Trit. durum	78,3	0,00000
		H. chilense vs Trit. durum	71,5	0,00000
	med	H. chilense vs Tritordeum	-7,7	n.s.
		Tritordeum vs Trit. durum	123,2	0,00000
		H. chilense vs Trit. durum	106,0	0,00000
	dry	H. chilense vs Tritordeum	-19,5	0,00000
		Tritordeum vs Trit. durum	121,9	0,00000
		H. chilense vs Trit. durum	78,5	0,00000

	Stem Weight Ratio Summary			p-value
R^2 = 0,966	Species			0,00000
	Treatment			0,00680
	SPEC*TREAT			0,00213
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-13,9	n.s.
		moist vs dry	-14,2	n.s.
		med vs dry	-0,3	n.s.
	Trit. durum	moist vs med	-6,7	n.s.
		moist vs dry	-20,7	0,00011
		med vs dry	-15,0	0,00106
	Tritordeum	moist vs med	14,1	n.s.
		moist vs dry	3,8	n.s.
		med vs dry	-9,0	n.s.
Effect of species	moist	Tritordeum vs H. chilense	363,5	0,00000
		Tritordeum vs Trit. durum	20,1	0,00084
		Trit. durum vs H. chilense	286,0	0,00000
	med	Tritordeum vs H. chilense	249,8	0,00000
		Tritordeum vs Trit. durum	-1,8	n.s.
		Trit. durum vs H. chilense	256,2	0,00000
	dry	Tritordeum vs H. chilense	283,4	0,00000
		Tritordeum vs Trit. durum	-8,2	n.s.
		Trit. durum vs H. chilense	317,8	0,00000

	Ear Weight Ratio Summary			p-value
R^2 = 0,981	Species			0,00000
	Treatment			0,00020
	SPEC*TREAT			0,00030
			difference (%)	
Effect of treatment	H. chilense	moist vs med	-	-
		moist vs dry	-	-
		med vs dry	-	-
	Trit. durum	moist vs med	0,1	n.s.
		moist vs dry	35,2	0,00086
		med vs dry	35,0	0,00088
	Tritordeum	moist vs med	-13,7	n.s.
		moist vs dry	36,4	n.s.
		med vs dry	58,0	n.s.
Effect of species	moist	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	717,2	0,00000
		Trit. durum vs H. chilense	-	-
	med	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	604,7	0,00000
		Trit. durum vs H. chilense	-	-
	dry	Tritordeum vs H. chilense	-	-
		Trit. durum vs Tritordeum	724,7	0,00000
		Trit. durum vs H. chilense	-	-

	Root Weight Ratio			p-value
R^2 = 0,982	Species			0,00000
	Treatment			0,74776
	SPEC*TREAT			0,00875
			difference (%)	
Effect of treatment	H. chilense	moist vs med	4,7	n.s.
		moist vs dry	3,7	n.s.
		med vs dry	-0,9	n.s.
	Trit. durum	moist vs med	-4,0	n.s.
		moist vs dry	-34,2	0,00398
		med vs dry	-31,5	0,00640
	Tritordeum	moist vs med	-0,5	n.s.
		moist vs dry	20,5	n.s.
		med vs dry	21,1	n.s.
Effect of species	moist	H. chilense vs Tritordeum	112,9	0,00000
		Tritordeum vs Trit. durum	217,4	0,00000
		H. chilense vs Trit. durum	575,6	0,00000
	med	H. chilense vs Tritordeum	102,3	0,00000
		Tritordeum vs Trit. durum	206,4	0,00000
		H. chilense vs Trit. durum	519,9	0,00000
	dry	H. chilense vs Tritordeum	147,3	0,00000
		Tritordeum vs Trit. durum	73,3	0,00002
		H. chilense vs Trit. durum	328,5	0,00000