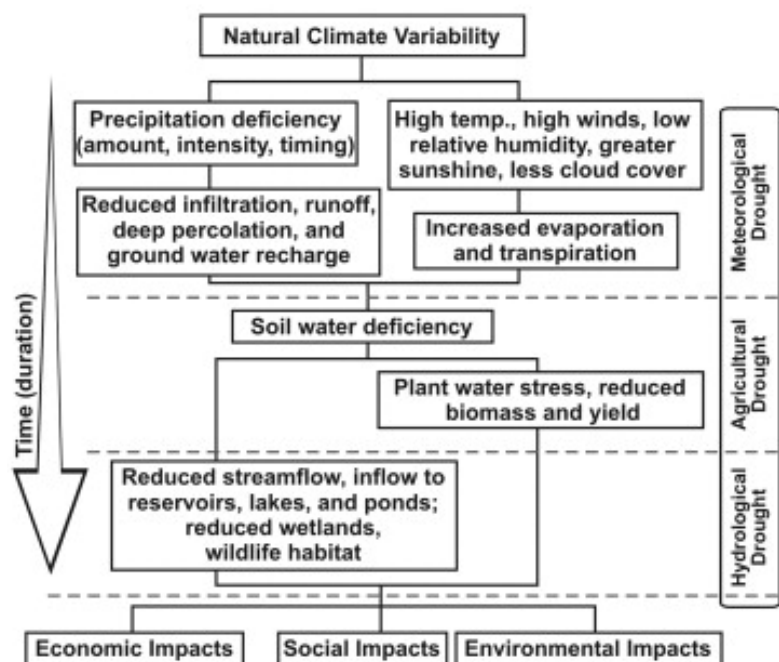


## Resource allocation of *Arabidopsis thaliana* during drought

### Introduction

Plants are subjected to a plethora of environmental stresses in the field (Mittler, 2006). Manipulating abiotic factors such as water availability (Turnbull et al., 2001; Abbate et al., 2004), temperature (Paulsen, 1994; Wigge, 2013), salinity (Gupta and Huang, 2014), soil composition (Farrell et al., 2013) have been used to induce plant stress to understand the underlying mechanisms of plant response to such constraints. It is predicted that there will be a 5.8°C temperature rise by the end of the 21<sup>st</sup> century (Houghton et al., 2001) which will consequently lead to more frequent, intense and longer drought events.

Meteorological drought leads to agricultural drought (Figure 1) which has direct impact on plant growth (Trenberth et al., 2014). In 1967–2007, extreme drought events lasted longer than extreme heat events. From 1980 to 2008, that maize production decreased by 3.8%, wheat by 5.5% (Lobell et al., 2011), and during 1964–2007 the cereal production decreased by 10.1% globally (Lesk et al., 2016) caused mainly by drought. Over 40% of global food production already depends on irrigation systems (Chaves and Oliveira, 2004) and with the growing human population, food production has to increase by manifold. However, it is predicted that by 2050, 6.5 billion people will be living in countries facing chronic water shortage and 36% of the total population will be living in countries that will not be self-sufficient in terms of food production (Rockström et al., 2009). Therefore, it is crucial to understand how much and for how long water deficit can be tolerated by crops to plan future climate change resilient food production systems (Teixeira et al., 2013; Challinor et al., 2014).

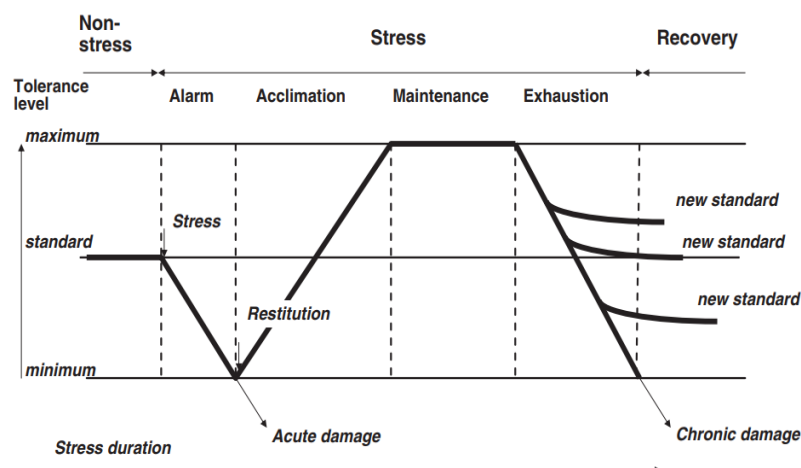


**Figure 1.** The causation of different types of drought due to climate change has not only environmental but economic and social impact too (Wilhite et al., 2014). Agriculture is one of the most well-known sector to be affected by droughts however, many other sectors (e.g. transportation, energy production) are negatively affected as well.

The state of water deficit in plants can induce stomatal closure (Muller et al., 2011) and also resource allocation between reproductive and non-reproductive tissues (Herms and Mattson, 1992; Munne-Bosch and Alegre, 2004). The extent of change depends on both intensity and duration of the stress (Figure 2). This partitioning aims to lead to an optimal shift in biomass allocation to increase survival (McConnaughay and Coleman, 1999). In many crop and vegetable species this leads to a decrease in leaf dry mass ratio to the plant's total dry mass, which has an enormous economic impact in food production (Boogaard et al., 1996; Liu and Stutzel, 2004). The root:shoot ratio, which acts as a balance for nitrogen and photosynthesis (Ågren and Ingestad, 1987), has been extensively studied but controversial results have been observed in different species (Gedroc et al., 1996; Mokany et al., 2006; Anjum et al., 2011). In comparative studies, lower root:shoot ratio described the better performing plants, such as new wheat (Siddique et al., 1990) and rice varieties (Nada and Abogadallah, 2016) compared to older varieties. This ratio has been used for versatile purposes, for example for estimating belowground carbon stocks by IPCC (1996), and characterising biomes (Mokany et al., 2006) and plant growth forms (Schenk and Jackson, 2002).

Previous studies have used leaf and root biomass along with root:shoot ratios to investigate the drought effect on plants, however multivariate analyses reveal more detailed patterns in terms of plant growth for *Arabidopsis thaliana* (Qaderi et al., 2006; Hummel et al., 2010; Vile et al., 2012). This model organism has been widely studied (Rhee et al., 2003), therefore extensive amount of data is available to understand its regulatory mechanisms and responses. However, previous studies had directional hypotheses and did not quantify the change in plant structures during drought. Genomics and transcriptomics can identify the genes and levels of their expression (Cattivelli et al., 2008) but first, it is crucial to understand the overall change in plant structures in terms of stress response.

In this study, we studied the effect of drought using *Arabidopsis thaliana* by comparing control plants to 'drought treated' plants induced by chronic water retention for three weeks. The first prediction was that there will be an overall decrease in biomass in the treated plants which will focus on survival more than growth. Second prediction was that pattern of root:shoot ratio will increase which will be a sign of resource allocation. The overall variation of different plant structures and their importance was investigated using multivariate analysis.



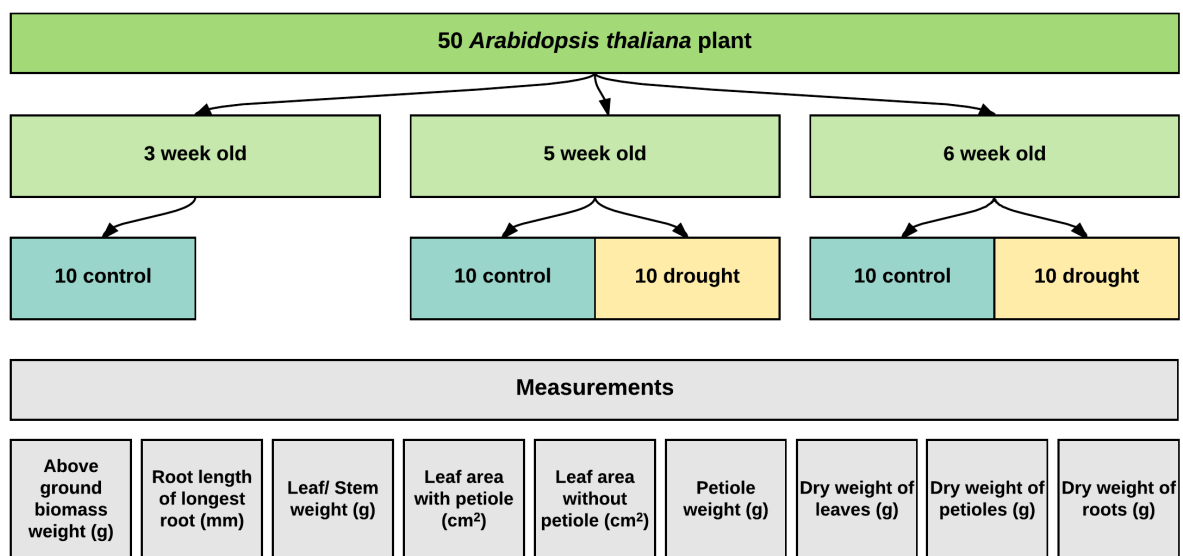
**Figure 2.** The plant enters an alarm stage induced by an abiotic stress (Kosová et al., 2011). According to the intensity and duration of the stress, it might be able to acclimate and recover, or it suffers chronic or acute damage which leads to plant death. Each stage is controlled by different signalling pathways and biosynthesis mechanisms.

## Materials and methods

Fifty *Arabidopsis thaliana* plants were used for six biomass measurements with three dry weight recording. All plants were grown in glasshouse environment in 20°C average temperature. Plants were grown in multipurpose compost in 100 ml pots. Control plants were regularly watered by glasshouse technicians (T0 treatment, 500 ml up to three times per week) while the plants under 'drought' treatment (T1) were not watered. The first measurements were taken of ten, three week old, control plants (Figure 2). Two weeks later, ten control and ten drought treated plants (T2) were measured. The following week another ten control and ten drought treated plants were measured. Therefore, the total of 30 control plant and 20 drought treated plants were measured in three weeks.

The aboveground biomass was removed, measured (total leaf and stem weight with 0.001 g accuracy). The module weight was measured afterwards (soil and pot weight, with 0.01 g accuracy). The root system was removed, rinsed and dried by blotting. The total length was measured of the longest, primary root with 0.1 mm accuracy. The leaves were cut at the end of the petiole, the total leaf area was measured with 0.01 cm<sup>2</sup> accuracy and then the petioles were removed from the leaves. The total leaf area was measured again without the petioles and the total weight of the petioles was also determined. The leaf and petiole areas were measured by leaf area measurement system. The samples were labelled individually, and students measured one character at a time to ensure uniform measuring. The petioles, leaves and roots were baked in an oven at 60°C for 80-90 hours. The dry weights were measured afterwards with 0.001 g accuracy.

The root:shoot ratio for dry weights and the ratio between leaf:biomass of dry weights were calculated in Excel. As the data set was not normally distributed, Kruskal-Wallis, nonparametric test was used with Dunn testing. The data grouping separated the different treatments (T0, T1, and T2) and also weeks (W3, W5, and W6). Principal Component Analysis

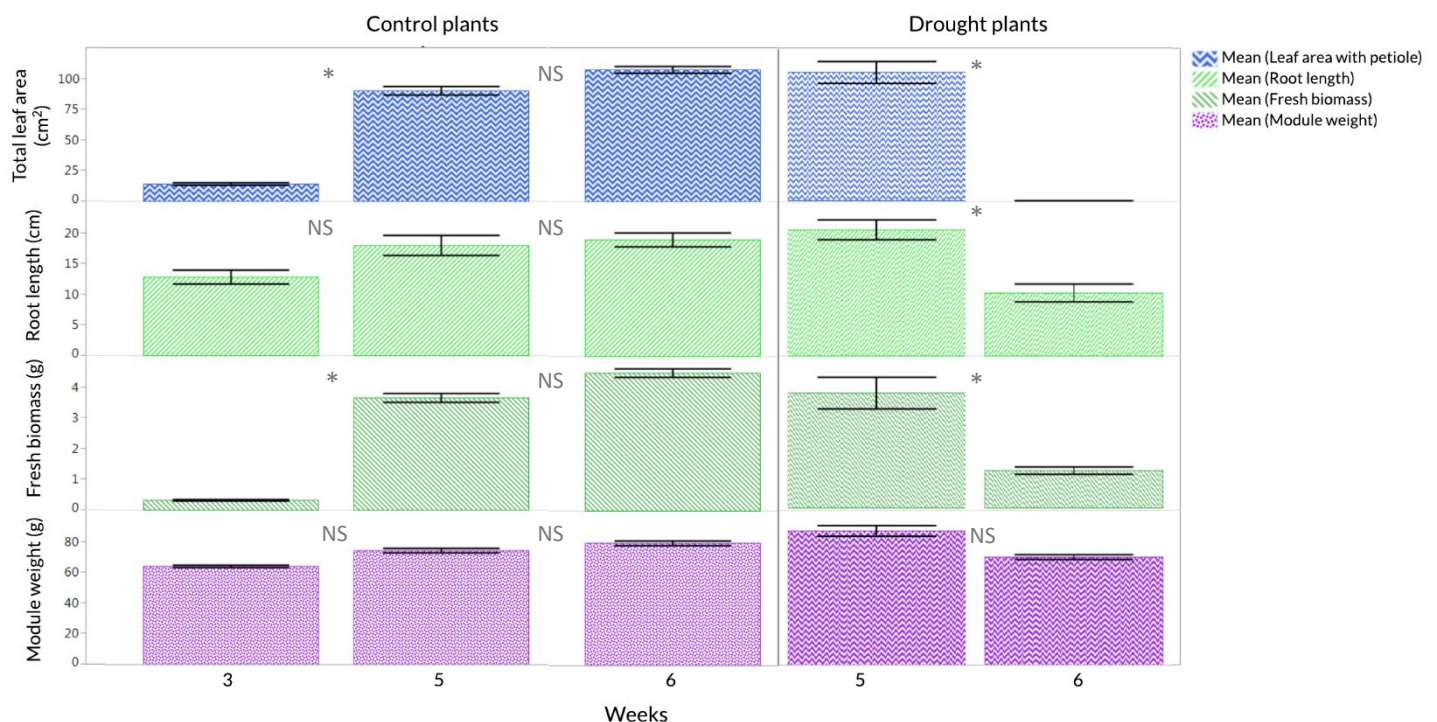


**Figure 3.** Experimental design of studying the drought effect (T1) on *Arabidopsis* plants. Many measurements were taken to test which plant organ (leaf, petiole, or root) is affected by the T1 treatment.

(PCA) was used to retain the most variation of the data with FactoMineR package in R (R Development Core Team, 2008), and the contribution of each measurement to the variance in the data was calculated. A log+1 transformation increased the linearity assumed by the PCA. After the visualisation of variable correlation plot, the highly positively correlated variables were omitted from the PCA. Seven outliers (ID11, 14, 18, 21, 23, 37, 50) were removed with the mvoutlier package, based on chisq-quantile calculations from the 2.5% and 97.5% quartile.

## Results

Descriptive statistics showed an overall decrease of the weight of the stressed plants in comparison to the control plants (Figure 4). All Kruskal Wallis tests were highly significant ( $P < .000$ , Table 1) for all variables between treatments. The Dunn pairwise test showed that there were significant differences between T1 plants' ( $n_1=20$ ) module weight ( $P=.001$ ), fresh biomass ( $P=.047$ ), petiole weight ( $P=.010$ ), and leaf dry weight ( $P=.028$ ) compared to T0 plants ( $n_2=20$ , Table 2). In week six, all measurements were highly significant ( $P < 0.005$ ) except the leaf:biomass dry weight ratio ( $P=.345$ ) between T0 and T2. Comparison between T1 and T2 plants also showed significant changes of fresh biomass ( $P=.021$ ), root length ( $P=.010$ ), leaf area ( $P=.005$ ), root dry weight ( $P=.029$ ) and the root:shoot ratio of dry weights ( $P=.002$ ). Comparing T2 plants to week three control plants, significant differences were found between module weight ( $P=.006$ ), petiole weight ( $P=.002$ ), leaf dry weight ( $P=.033$ ), and petiole dry weight ( $P=.035$ ) but no difference between root measurements. The ratio of the of root length:shoot increased in treated plants (Figure 5) and so did root:shoot of dry weights. This was an opposite shift to the control plants.



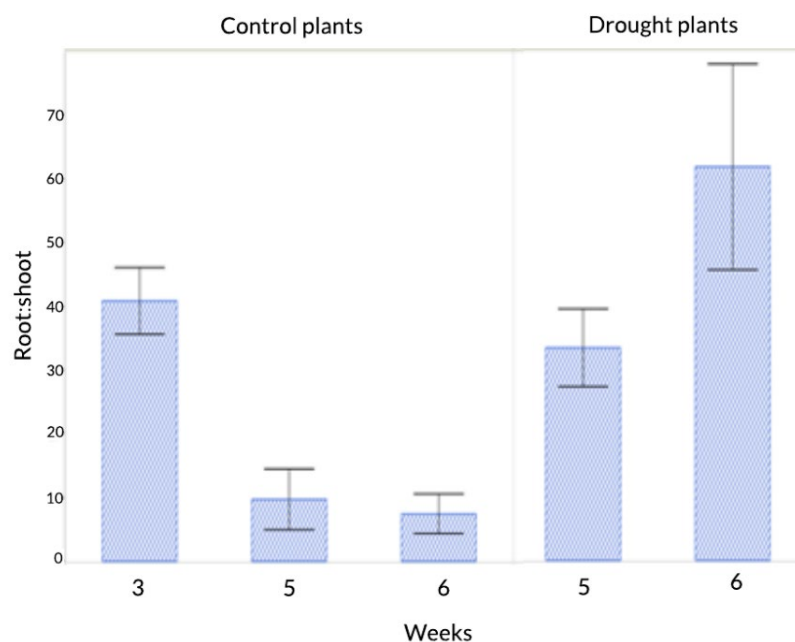
**Figure 4.** The different responses in module weight (purple), fresh biomass (dark green), root length (light green) and total leaf area (blue) of 30 control and 20 drought treated plant with calculated standard error of the mean. The biomass of T1 and T2 plants overall decreased while T0 plants' biomass increased. Significant differences according to Dunn testing (\*,  $P < .05$ ; NS,  $P > .05$ ) are shown.

**Table 1.** Kurskal-Wallis test shows highly significant differences between all variables throughout the two weeks between treated and control plants.

n=40	$\chi^2_{(4)}$	P	95% CI
Module weight	44.914	<b>.000</b>	52.321 - 58.991
Fresh biomass	43.964	<b>.000</b>	1.652 - 3.189
Root length	29.321	<b>.000</b>	2.466 - 8.987
Leaf area with petiole	45.827	<b>.000</b>	35.625 - 67.004
Leaf area without petiole	45.735	<b>.000</b>	38.494 - 4.741
Fresh petiole weight	42.649	<b>.000</b>	0.682 - 0.935
Dry leaf weight	44.563	<b>.000</b>	0.144 - 0.233
Dry petiole weight	36.377	<b>.000</b>	0.057 - 0.094
Dry root weight	38.228	<b>.000</b>	1.318 - 5.277
Dry root:shoot ratio	32.824	<b>.000</b>	3.457 - 15.480
Dry leaf:biomass	21.925	<b>.000</b>	9.144 - 5.216

**Table 2.** The Dunn pairwise tests between different weeks (W3, W5, W6), and treatments (T0, T1, T2) reveal which variables are significant (shown in bold). Control plants differed the most from week three to week five (green). Treated plants compared to control plants different in almost all variables in week six (orange). From week five to week six, the treated plants significantly differed by six variables (yellow).

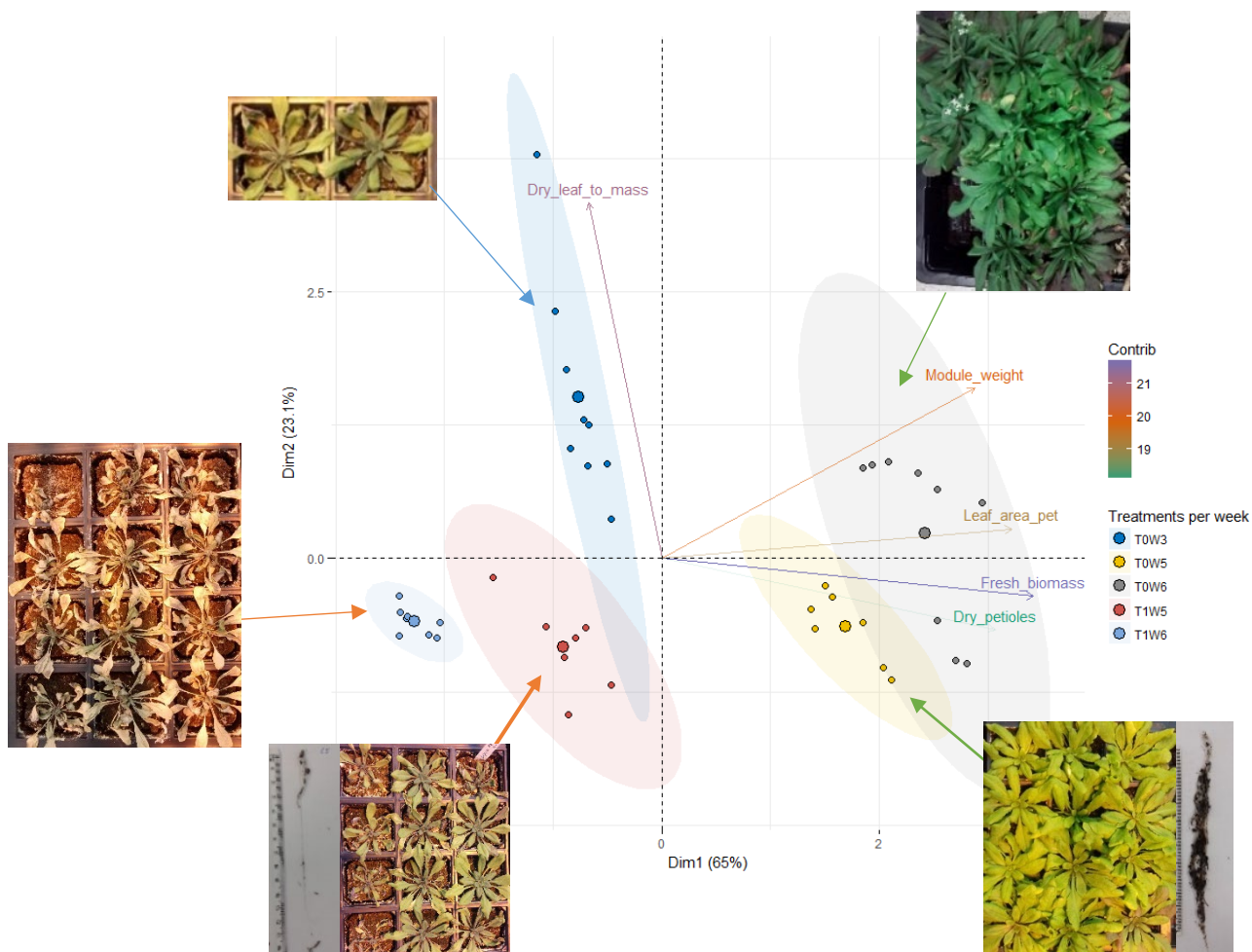
Dunn test	Module weight	Fresh biomass	Root length	Leaf area + petiole	Leaf area without petiole	Fresh petiole weight	Dry leaf weight	Dry petiole weight	Dry root weight	Dry root:shoot ratio	Dry Leaf: biomass
<b>T0W3 T0W5</b>	.092	<b>.013</b>	.064	<b>.006</b>	<b>.004</b>	0.390	<b>.000</b>	<b>.000</b>	<b>.010</b>	.759	<b>.000</b>
<b>T0W3 T0W6</b>	<b>.010</b>	<b>.000</b>	<b>.017</b>	<b>.000</b>	<b>.000</b>	<b>.025</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	.382
<b>T0W5 T0W6</b>	.365	.197	.529	.195	.242	.143	.156	.406	<b>.013</b>	<b>.001</b>	<b>.006</b>
<b>T0W3 T1W5</b>	.126	.560	.482	.254	.218	.073	<b>.028</b>	<b>.008</b>	<b>.003</b>	.077	<b>.007</b>
<b>T0W5 T1W5</b>	<b>.001</b>	<b>.047</b>	.247	.096	.092	<b>.010</b>	<b>.035</b>	.128	.690	.111	.330
<b>T0W6 T1W5</b>	<b>.000</b>	<b>.001</b>	.079	<b>.004</b>	<b>.005</b>	<b>.000</b>	<b>.000</b>	<b>.022</b>	<b>.033</b>	.109	.068
<b>T0W3 T2W6</b>	<b>.006</b>	.069	.059	.102	.120	<b>.002</b>	<b>.033</b>	<b>.035</b>	.371	.214	.083
<b>T0W5 T2W6</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.031</b>	<b>.032</b>	.068	.134	.061
<b>T0W6 T2W6</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.000</b>	<b>.005</b>	<b>.000</b>	<b>.000</b>	.345
<b>T1W5 T2W6</b>	.208	<b>.021</b>	<b>.010</b>	<b>.007</b>	<b>.005</b>	.157	.866	.519	<b>.029</b>	<b>.002</b>	.375



**Figure 5.** The root length:shoot ratio clearly increased in the treated plants (right) while it was decreasing in the control plants (left).



After removing positively correlated variables, the PCA used five variables (module weight, fresh biomass, leaf area with petiole, dry petiole weight, dry leaf:biomass ratio) which revealed separate clusters according to control *versus* treated and smaller clusters according to different weeks (Figure 6). Axis one (PC1) explained 64.475% of the total variance in the data set, axis two (PC2) represented 22.308% while PC3 contained 9.026% of the total variance (Table 3). The fresh biomass contributed 29.105% to axis one while the dry weight of leaf:biomass ratio represented 81.222% to the total variance explained by PC2 (Table 3). Thus, the two groups' difference can be mostly explained by fresh biomass and the leaf:biomass ratio but also the leaf area (contributed 26.023% to PC1) explained most of the variation in the data set. Week three T0 plants formed a cluster closer to the T1 plants than to the other controls. Dry petiole weight contributed 44.546% to PC3, however it did not separate neither the treatment nor the different weeks.



**Figure 6.** PCA scatterplots with 95% confidence ellipses, coloured according to treatments per weeks. The colour and length of the five variables' arrows indicate their contribution to the total variance on the PC axes and their relative location indicates their correlation (same direction is positively correlated, opposite direction is negatively correlated). Pictures of the actual plants and roots help visualise the differences between the clusters.

**Table 3.** Posterior eigenvalue distribution on PC axes and the total variance explained by the axes. Most of the variance is loaded onto the first three axes.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.224	1.115	0.451	0.163	0.047
%of variance explained	64.475	22.308	9.026	3.256	0.935

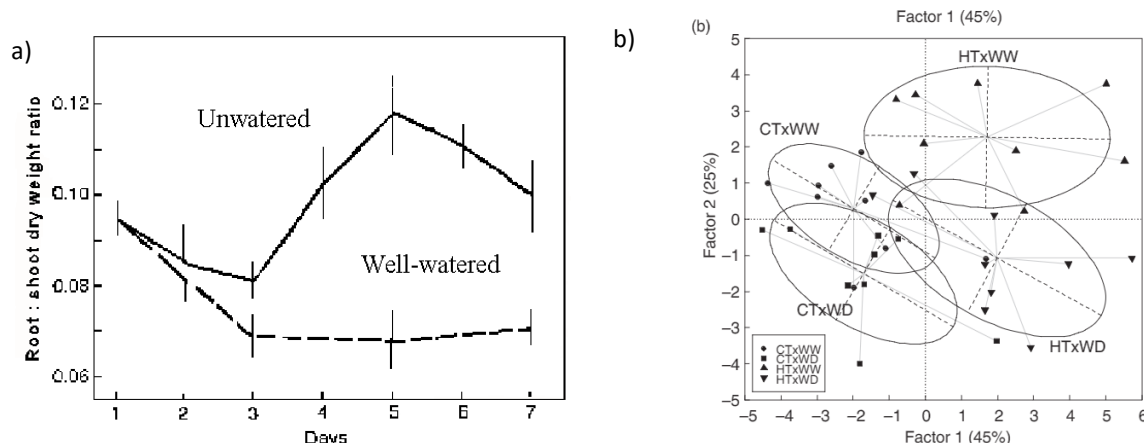
**Table 4.** Variable contribution (%) to the PC axes explain the clusters positions on the PCA scatter plots.

	PC1	PC2	PC3	PC4	PC5
Module weight	20.675	14.993	23.066	36.948	4.318
Fresh biomass	29.105	0.772	4.752	0.980	64.392
Leaf area with petiole	26.023	0.352	13.737	57.873	2.015
Dry petiole weight	23.410	2.661	44.546	0.747	28.636
Dry leaf:biomass ratio	0.788	81.222	13.898	3.453	0.640

## Discussion

In this study we investigated the response of *Arabidopsis* plants exposed to water retention for three weeks. We showed how multivariate methods with non-parametric test provide quantitative insight to which plant structures are affected by drought. The plants lost turgidity in the basal, larger leaves in week five and throughout the following week, the leaves were rapidly turning yellow, became more wrinkled and eventually died off. We found an overall decrease in plant biomass of plants exposed to drought which coincided with our first prediction (Figure 3, Table 1). There was a significant decrease between the different duration of treatment, especially for fresh biomass, root length, leaf area, root dry weight and the root:shoot ratio of dry weights (Table 3). This pattern was similar to previous studies done on *Arabidopsis* or closely related *Brassica* species (Chaves et al., 2002; Qaderi et al., 2006; Müller et al., 2010; Husen et al., 2014).

We observed fewer lateral roots from week five to six as a result of drought stress. *Arabidopsis* mutants have been observed to decrease the number of lateral roots or alter their morphology with decreasing soil moisture, but have the ability to recover with rehydration (Vartanian et al., 1994; Schnall and Quatrano, 1992). We had difficulties removing all the soil without damaging the root system, but in comparison to Vaughan et al.'s (2011) images, it can be assumed that other studies met the same difficulties, and the additional amount of soil did not compromise our findings. The root:shoot ratio increased while it was decreasing for the control plants which was similar in previous studies (Sharp and Davies, 1979; Chavez et al., 2002; Dhanda et al., 2004; Hummel et al., 2010; Vile et al., 2012) and therefore confirmed our second hypothesis (Figure 7a). This could reflect on optimisation of water uptake (Blum, 1996; Vile et al., 2012). Interestingly, the leaf:biomass ratio of dry



**Figure 7.** a) A seven day long drought experiment conducted on *Zea mays* in their fourth leaf stage showing the increase of root:shoot ratio in un-watered plants showing similar pattern to this study (Sharp and Davies, 1979). b) PCA scatterplot clustering according to high temperature (HT), control air temperature (CT), water deficit (WD), and well-watered (WW) treatments (Vile et al., 2012).

weights was not significant between treatments, only throughout the development of the control plants (Table 2). This ratio can be more indicative for CO<sub>2</sub> and light treatments (Oren et al., 1986) but is used for horticultural crop harvest predictions (Marcelis, 1998).

The main aim of this study was to investigate which plant structure is most susceptible to drought stress. The PCA provided a reliable method to reveal that the most of the variable contribution was explained by leaf biomass rather than roots. Five variables led to the separation of both treatments and weeks on the plants' response to drought (Figure 6, Table 4). A PCA by Vile et al. (2012) (Figure 7b) showed similar clustering according to water and temperature treatments for *Arabidopsis*. So did Hummel et al. (2010), explaining how different intensity and duration of drought treatments clearly separate plant biomass and enzyme production. Root length and dry weight did not contribute to the variance in the data and these were only significantly different in the stressed plants in week six. Therefore, it can be concluded that the plants' response to drought mostly happened aboveground.

In our study, we only manipulated the watering regime for a model organism however, it is important to consider drought effect at different developmental stages as water consumption fluctuates throughout development (Müller et al., 2010). Early flowering has been shown to be an adaptation to natural drought (Franks, 2011) which also causes an increase in root:shoot ratio (Wilson, 1988). Also, in the field, there can be different durations of drought followed by precipitation, which enables plant recovery (Müller et al., 2010; Husen et al., 2014). Drought events might also coincide with high temperatures events (Angadi et al., 2000; Vile et al., 2012). In order to predict plant growth in the future, the effect of increasing CO<sub>2</sub> levels (Qaderi et al., 2006) and UVB radiation also has to be understood on different plant structures (Teramura et al., 1991; Larsson et al., 1998; Alexieva et al., 2001;). Although, extensive meta-analyses have been done on plant growth in different biomes and under different treatments (Schenk and Jackson, 2002; Mokany et al., 2005; Vicente-Serrano et al., 2013), the experimental designs vary, and a consortium on drought study methods would enable cross validation between studies (Gilbert and Medina, 2016). It is also crucial to consider agricultural fields in terms of ecosystem services besides crop production and their sustainability (Zhang et al., 2007). Studies using manipulative experimental designs which simulate climate change, enable us to plan for the challenging future of food production relying on the resilience of plants.



**Figure 8.** Combining studies on weeds (Ziska et al., 2004), microbial organisms and endophytic fungi (Worchel et al., 2013), herbivory (Mattson and Haack, 1987), herbicide and insecticide usage (Waite et al., 1992), pollination (Herrero and Johnson, 1981), and other abiotic factors enables us to understand the interactions occurring on agricultural fields. As it is a both spatially and temporally complex system, changes in one interaction caused by climate change, will result in shift of all other interactions.





## References

- Abbate, P.E., Dardanelli, J.L., Cantarero, M.G., Maturano, M., Melchiori, R.J.M. and Suero, E.E., 2004. Climatic and water availability effects on water-use efficiency in wheat. *Crop Science*, 44(2), pp.474-483
- Ågren, G.I. and Ingestad, T., 1987. Root: shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment*, 10(7), pp.579-586
- Alexieva, V., Sergiev, I., Mapelli, S. and Karanov, E., 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant, Cell and Environment*, 24(12), pp.1337-1344
- Angadi, S.V., Cutforth, H.W., Miller, P.R., McConkey, B.G., Entz, M.H., Brandt, S.A. and Volkmar, K.M., 2000. Response of three *Brassica* species to high temperature stress during reproductive growth. *Canadian Journal of Plant Science*, 80(4), pp.693-701
- Anjum, S.A., Xie, X.Y., Wang, L.C., Saleem, M.F., Man, C. and Lei, W., 2011. Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research*, 6(9), pp.2026-2032
- Blum, A., 1996. Crop responses to drought and the interpretation of adaptation. *Plant Growth Regulation*, 20(2), pp.135-148
- Boogaard, R.V.D., Veneklaas, E.J. and Lambers, H., 1996. The association of biomass allocation with growth and water use efficiency of two *Triticum aestivum* cultivars. *Functional Plant Biology*, 23(6), pp.751-761
- Challinor, A.J., Watson, J., Lobell, D.B., Howden, S.M., Smith, D.R. and Chhetri, N., 2014. A meta-analysis of crop yield under climate change and adaptation. *Nature Climate Change*, 4(4), pp.287-291
- Chaves, M.M. and Oliveira, M.M., 2004. Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. *Journal of Experimental Botany*, 55(407), pp.2365-2384
- Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osório, M.L., Carvalho, I., Faria, T. and Pinheiro, C., 2002. How plants cope with water stress in the field? Photosynthesis and growth. *Annals of Botany*, 89(7), pp.907-916
- Dhanda, S.S., Sethi, G.S. and Behl, R.K., 2004. Indices of drought tolerance in wheat genotypes at early stages of plant growth. *Journal of Agronomy and Crop Science*, 190(1), pp.6-12
- Farrell, C., Ang, X.Q. and Rayner, J.P., 2013. Water-retention additives increase plant available water in green roof substrates. *Ecological Engineering*, 52, pp.112-118
- Franks, S.J., 2011. Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. *New Phytologist*, 190(1), pp.249-257
- Gedroc, J.J., McConnaughay, K.D.M. and Coleman, J.S., 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both?. *Functional Ecology*, 10(1), pp.44-50

- Gilbert, M.E. and Medina, V., 2016. Drought adaptation mechanisms should guide experimental design. *Trends in Plant Science*, 21(8), pp.639-647
- Gupta, B. and Huang, B., 2014. Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. *International Journal of Genomics*, 2014(701596), pp.18
- Hermes, D.A. and Mattson, W.J., 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, 67(3), pp.283-335
- Herrero, M.P. and Johnson, R.R., 1981. Drought stress and its effects on maize reproductive systems. *Crop Science*, 21(1), pp.105-110
- Houghton, J.T., Ding, Y.D.J.G., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. and Johnson, C.A., 2001. Climate change 2001: The Scientific Basis. The Press Syndicate of the University of Cambridge
- Hummel, I., Pantin, F., Sulpice, R., Piques, M., Rolland, G., Dauzat, M., Christophe, A., Pervent, M., Bouteillé, M., Stitt, M. and Gibon, Y., 2010. *Arabidopsis* plants acclimate to water deficit at low cost through changes of carbon usage: an integrated perspective using growth, metabolite, enzyme, and gene expression analysis. *Plant Physiology*, 154(1), pp.357-372
- Husen, A., Iqbal, M. and Aref, I.M., 2014. Growth, water status, and leaf characteristics of *Brassica carinata* under drought and rehydration conditions. *Brazilian Journal of Botany*, 37(3), pp.217-227
- IPCC 1996. Land-Use Change and Forestry. In: *Revised 1996 IPCC Guidelines for National Greenhouse Gas Inventories: Reference Manual*, Intergovernmental Panel on ClimateChange Geneva, Switzerland. Available at: [http://www.ipcc-nggip.iges.or.jp/public/gpplulucf/gpplulucf\\_files/GPG\\_LULUCF\\_FULL.pdf](http://www.ipcc-nggip.iges.or.jp/public/gpplulucf/gpplulucf_files/GPG_LULUCF_FULL.pdf)
- Kosová, K., Vítámvás, P., Prášil, I.T. and Renaut, J., 2011. Plant proteome changes under abiotic stress—contribution of proteomics studies to understanding plant stress response. *Journal of Proteomics*, 74(8), pp.1301-1322
- Larsson, E.H., Bornman, J.F. and Asp, H., 1998. Influence of UV-B radiation and Cd<sup>2+</sup> on chlorophyll fluorescence, growth and nutrient content in *Brassica napus*. *Journal of Experimental Botany*, 49(323), pp.1031-1039
- Lesk, C., Rowhani, P. and Ramankutty, N., 2016. Influence of extreme weather disasters on global crop production. *Nature*, 529(7584), pp.84-87.
- Liu, F. and Stützel, H., 2004. Biomass partitioning, specific leaf area, and water use efficiency of vegetable amaranth (*Amaranthus* spp.) in response to drought stress. *Scientia Horticulturae*, 102(1), pp.15-27
- Lobell, D.B., Schlenker, W. and Costa-Roberts, J., 2011. Climate trends and global crop production since 1980. *Science*, 333(6042), pp.616-620
- Marcelis, L.F.M., Heuvelink, E. and Goudriaan, J., 1998. Modelling biomass production and yield of horticultural crops: a review. *Scientia Horticulturae*, 74(1), pp.83-111

- Mattson, W.J. and Haack, R.A., 1987. The role of drought stress in provoking outbreaks of phytophagous insects. *Insect Outbreaks*, pp.365-407
- McConnaughay, K.D.M. and Coleman, J.S., 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology*, 80(8), pp.2581-2593
- Mittler, R., 2006. Abiotic stress, the field environment and stress combination. *Trends in Plant Science*, 11(1), pp.15-19
- Mokany, K., Raison, R. and Prokushkin, A.S., 2006. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology*, 12(1), pp.84-96
- Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. and Gibon, Y., 2011. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, 62(6), pp.1715-1729
- Müller, T., Lüttschwager, D. and Lentzsch, P., 2010. Recovery from drought stress at the shooting stage in oilseed rape (*Brassica napus*). *Journal of Agronomy and Crop Science*, 196(2), pp.81-89
- Munné-Bosch, S. and Alegre, L., 2004. Die and let live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology*, 31(3), pp.203-216
- Nada, R.M. and Abogadallah, G.M., 2016. Restricting the above ground sink corrects the root/shoot ratio and substantially boosts the yield potential per panicle in field-grown rice (*Oryza sativa* L.). *Physiologia plantarum*, 156(4), pp.371-386
- Oren, R., Schulze, E.D., Matyssek, R. and Zimmermann, R., 1986. Estimating photosynthetic rate and annual carbon gain in conifers from specific leaf weight and leaf biomass. *Oecologia*, 70(2), pp.187-193
- Paulsen, G.M., 1994. High temperature responses of crop plants. *Physiology and Determination of Crop Yield*, Chapter 14A [via American Society of Agronomy], pp.365-389
- Qaderi, M.M., Kurepin, L.V. and Reid, D.M., 2006. Growth and physiological responses of canola (*Brassica napus*) to three components of global climate change: temperature, carbon dioxide and drought. *Physiologia Plantarum*, 128(4), pp.710-721
- R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rhee, S.Y., Beavis, W., Berardini, T.Z., Chen, G., Dixon, D., Doyle, A., Garcia-Hernandez, M., Huala, E., Lander, G., Montoya, M. and Miller, N., 2003. The Arabidopsis Information Resource (TAIR): a model organism database providing a centralized, curated gateway to *Arabidopsis* biology, research materials and community. *Nucleic Acids Research*, 31(1), pp.224-228
- Rockström, J., Falkenmark, M., Karlberg, L., Hoff, H., Rost, S. and Gerten, D., 2009. Future water availability for global food production: the potential of green water for increasing resilience to global change. *Water Resources Research*, 45(7), W00A12



- Schenk, H.J. and Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90(3), pp.480-494
- Schnall, J.A. and Quatrano, R.S., 1992. Absciscic acid elicits the water-stress response in root hairs of *Arabidopsis thaliana*. *Plant physiology*, 100(1), pp.216-218
- Sharp, R.E. and Davies, W.J., 1979. Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta*, 147(1), pp.43-49
- Siddique, K.H.M., Belford, R.K. and Tennant, D., 1990. Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. *Plant and Soil*, 121(1), pp.89-98
- Teixeira, E.I., Fischer, G., van Velthuisen, H., Walter, C. and Ewert, F., 2013. Global hot-spots of heat stress on agricultural crops due to climate change. *Agricultural and Forest Meteorology*, 170, pp.206-215
- Teramura, A.H., Ziska, L.H. and Sztein, A., 1991. Changes in growth and photosynthetic capacity of rice with increased UV-B radiation. *Physiologia Plantarum*, 83(3), pp.373-380
- Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. and Sheffield, J., 2014. Global warming and changes in drought. *Nature Climate Change*, 4(1), pp.17-22
- Turnbull, M.H., Whitehead, D., Tissue, D.T., Schuster, W.S., Brown, K.J. and Griffin, K.L., 2001. Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiology*, 21(9), pp.571-578
- Vartanian, N., Marcotte, L. and Giraudat, J., 1994. Drought rhizogenesis in *Arabidopsis thaliana* (differential responses of hormonal mutants). *Plant Physiology*, 104(2), pp.761-767
- Vaughan, M.M., Tholl, D. and Tokuhisa, J.G., 2011. An aeroponic culture system for the study of root herbivory on *Arabidopsis thaliana*. *Plant Methods*, 7(1), p.5
- Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno, J.I., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J. and Morán-Tejeda, E., 2013. Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences*, 110(1), pp.52-57
- Vile, D., Pervent, M., Belluau, M., Vasseur, F., Bresson, J., Muller, B., Granier, C. and Simonneau, T., 2012. Arabidopsis growth under prolonged high temperature and water deficit: independent or interactive effects? *Plant, Cell and Environment*, 35(4), pp.702-718
- Waite, D.T., Sommerstad, H., Grover, R., Kerr, L. and Westcott, N.D., 1992. Pesticides in ground water, surface water and spring runoff in a small Saskatchewan watershed. *Environmental Toxicology and Chemistry*, 11(6), pp.741-748
- Wigge, P.A., 2013. Ambient temperature signalling in plants. *Current Opinion in Plant Biology*, 16(5), pp.661-666
- Wilhite, D.A., Sivakumar, M.V. and Pulwarty, R., 2014. Managing drought risk in a changing climate: The role of national drought policy. *Weather and Climate Extremes*, 3, pp.4-13

- Wilson, J.B., 1988. A review of evidence on the control of shoot: root ratio, in relation to models. *Annals of Botany*, 61(4), pp.433-449
- Worchel, E.R., Giaque, H.E. and Kivlin, S.N., 2013. Fungal symbionts alter plant drought response. *Microbial Ecology*, 65(3), pp.671-678
- Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. and Swinton, S.M., 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics*, 64(2), pp.253-260
- Ziska, L.H., Faulkner, S. and Lydon, J., 2004. Changes in biomass and root: shoot ratio of field-grown Canada thistle (*Cirsium arvense*), a noxious, invasive weed, with elevated CO<sub>2</sub>: implications for control with glyphosate. *Weed Science*, 52(4), pp.584-588