Impact of water deficit on growth, productivity, and water use efficiency in potato (*Solanum tuberosum* L.)

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# List of abbreviations

|  |  |
| --- | --- |
| Variable | Abbreviation |
| Soil Plant Analysis Development | spad |
| Plant height | hgt |
| Relative water content | rwc |
| Leaf osmotic potential | lop |
| Leaf dry weight | ldw |
| Stem dry weight | sdw |
| Root dry weight | rdw |
| Tuber dry weight | tdw |
| Tuber number | ntub |
| Root length | rdl |
| Total transpiration | trs |
| Leaf area | lfa |
| Total dry biomass | tdb |
| Harvest index | hi |
| Specif leaf area | sla |
| Water use efficiency | wue |
| Tuber water use efficiency | twue |

# Abstract

Drought stress is a serious constraint affecting yields of almost all crops worldwide. The problem is only expected to get worse with water deficits stemming from climate change and population expansion. In this study, we aim to find traits that can help understand the relation between traits and mechanisms of tolerance in potato, and provide useful information for selection of drought tolerance in potato breeding programs. In order to explore the different responses of potato under drought stress, we evaluated fifteen genotypes under well watered (WD) and water deficit (WD) conditions for a range of agro-physiological traits. Tolerant genotypes such as CIP397077.16, CIP398190.89, and CIP392797.22 (UNICA) were able to preferentially put limited water toward tuber production rather than biomass. Lower specific leaf area (sla) and relative water content (rwc) under WD, and that potato genotypes with the ability to maintain high harvest index (hi) and tuber water use efficiency (twue). We also found correlation between hi and twue was 0.92 with a euclidean distance 0.91 and a negative correlation with spad (-0.7) at 38 days after treatment application.

**Key words:** abiotic stress, harvest index, lisimeter, drought tolerance, SPAD

Include info about potato!

# Introduction

Water has become a scarce and precious resource and its efficient utilization in the production of food is a key challenge in agriculture worldwide. Yield losses due to water deficit are one of the global problems limiting production. Tracking the consequences of water deficit in plants is a difficult task, as it depends on the timing, intensity, type of crop, and duration of stress (Blum, [2011](#ref-blum2011Drought)). Besides this, abiotic stresses never come alone but are coupled in nature with other location-specific environmental stress factors, such as high irradiance and temperature, which makes describing the effect of one single stress in the field nearly impossible *cita*.

Potato is an important non-grain food crop and is a key component of world food security. Potato is known to be sensitive to water deficit because of its shallow root system, and its fast-closing leaf stomata that reduce transpiration and photosynthesis, considerably reducing tuber yields (Deblonde & Ledent, [2001](#ref-deblonde2001Effects)). Nevertheless, potato has a high harvest index in comparison with cereals and relatively low demand for water *cita*.

Tuber initiation is the most critical period of a potato’s life span in terms of water due to its high demand of around 400 to 600 L for 1kg of tuber dry matter (Stark et al., [2013](#ref-stark2013Potato)). Thus, an effective water-saving method is highly desirable trait for potato in semi-arid areas. To increase yield per unit of water, crop demand for water should be reduced or be used efficiently. Plants need to be bred for water use efficiency (wue) by capturing traits that help the plants develop faster, flower earlier, have a lower leaf area index, and be more efficient in capturing radiation (Blum, [2005](#ref-blum2005Drought); Hochman et al., [2009](#ref-hochman2009Potential)). In addition to the morphological changes, water use can be improved by maintaining low stomatal conductance (gs) during vegetative stages. This simple change is extremely beneficial, as the higher transpiration efficiency (TE) helps to postpone water use to late growing stages and alters the relationship between the dry matter produced and the quantity of soil water consumed (Carli et al., [2014](#ref-carli2014Effect); Condon et al., [2004](#ref-condon2004Breeding)). The management of water has a marked influence on plant behavior, tuber production, and quality. An important component of adaptation to WUE, the efficiency of the amount of water applied and used for transpiration that goes toward dry matter production. Enhanced WUE can reduce crop water requirements and increase crop yield significantly (Tolk & Howell, [2009](#ref-tolk2009Transpiration)). In this way, when a higher WUE under drought is maintained, the effects of water deficit are reduced and the competitiveness for water in drought conditions enhanced (Ogaya & Peñuelas, [2003](#ref-ogaya2003Comparative)).

The WUE was found to be greater in the summer due to the greater harvest index (HI) and more-efficient interception of solar radiation per unit of applied water by drought-exposed than by well-watered plots (Trebejo & Midmore, [1990](#ref-trebejo1990Effect)). In normal conditions when irrigation is sufficient to meet the transpiration needs of the crop, genotypes with higher stomatal conductance and low WUE, able to extract more water from the soil, will have higher yield. In contrast, when water is not sufficient, the low WUE arising from a high rate of transpiration leads to low yields in favor of dry matter partitioning to reproductive organs (Tuberosa, [2012](#ref-tuberosa2012Phenotyping)).

This study elucidate the mechanisms for drought tolerance and yield in fifteen advanced potato genotypes including two commercial varieties that are likely to arise in water-limited conditions, and explores the interrelationship between traits that help plants to mitigate yield losses under water-limited conditions. Chlorophyll content (spad), relative water content (rwc), osmotic potential (op), specific leaf area (sla), tuber water use efficiency (twue), harvest index (hi), among other traits, were evaluated to identify convenient indicators of plant water status that helps in the selection of clones with high tolerance to water deficit.

Indirect selection between HI vs TWUE vs SPAD!

Include in the intro

# Materials and Methods

## Plant material and experimental design

Thirteen potato clones were selected from advanced breeding population collection at International Potato Center (CIP) and two commercial varieties were grown in an environmentally controlled greenhouse at CIP (La Molina Experimental Station) at 28/15°C day/night with 70±5% average relative humidity. The experiment was carried out in complete randomize block design where the first factor was the two irrigation treatments: well-watered (WW), treatment where the moisture was maintained at field capacity and water deficit (WD) and the second factor were compound by the fifteen potato genotypes, Table (1).

## Relationship between transpiration rate and soil water supply

Single plants were grown in a greenhouse in 5 liters plastic pots and It was sown containing 5 kg of dry commercial Sogemix SM2 (75% Peat Moss, perlite, vermiculite, and limestone). Fertilization was done twice with ammonium nitrate; triple superphosphate and potassium sulphate, one before planting mixed with the substrate and the other applied at the surface at 40 days after planting (dap).

The pots from both well water (WW) and water deficit (WD) treatments were watered to soaking and then allowed to drain overnight. Next day, soil evaporation was minimized by sealed with a plastic bag and all the pots were weighed and it was defined as the initial pot weight. Water deficits were imposed at 45 dap that coincides with the beginning of the development of the stolons.

Transpiration was calculated by weighing the pots every two days in the between 13:00 and 15:00 hours (GMT -05:00). The transpiration of each plant was calculated by the procedure previously described by Bhatnagar-Mathur et al. ([2007](#ref-bhatnagar-mathur2007Stressinducible)) and Ray & Sinclair ([1998](#ref-ray1998effect)). The inter-daily transpiration rates of WD plants were normalized against WW plant rates to reduce the influence of day-to-day variation (). The normalization was achieved by dividing transpiration of each individual plant in the WD regime by the mean transpiration of the WW plants. For compare the transpiration between plants, a second normalization was done so that the normalized transpiration rate (NTR) of each plant was defined in 1.0 when the soil water content in each pot was at field capacity (Sinclair & Ludlow, [1986](#ref-sinclair1986Influence)). The available soil water or the fraction of transpirable soil water (ftsw), for each pot was calculated by dividing the pot weight minus the final pot weight by the transpirable soil water of that pot ().

## Evaluated traits

**Water use efficiency (wue).** is defined as a ratio of biomass accumulation, total crop biomass or crop grain yield, to water consumed, expressed as transpiration, evapo transpiration, or total water input to the system (Sinclair et al., [1984](#ref-sinclair1984WaterUse)). According to this concept we calculated the biomass water use efficiency (wue) and tuber water use efficiency (twue). The wue was calculated as the total biomass in dry weight produced divided by the cumulative water transpired (Dalla Costa et al., [1997](#ref-dallacosta1997Yield)) and for twue was used the dry weight from tuber production divide the cumulative water transpired (trs) during the treatment.

**Relative water content (rwc).** was determined by weighing the third leaflet (FW) from the third leaf from the apical part from the youngest fully expanded leaf of each plant. Each leaflet were placing in a 4x3 inch ziploc bag containing distilled water for 24 hours and after these time it was removed to taking turgid weight (TW) afterwards it was dried in an oven at 90 ºC for 24 hours and weighed (DW). The rwc was calculated according to Vasquez-Robinet et al. ([2008](#ref-vasquez-robinet2008Physiological)) by the formula .

**Leaf osmotic potential (lop).** was determined using a dew point microvoltmeter (HR-33T Wescor Inc., Logan, UT, USA) with leaf discs of 5 mm diameter, taken from the third fully extended leaf. The leaf discs were put in 1 ml cryogenic tubes and frozen in liquid nitrogen for further analysis. The frozen leaves were incubated at 22°C for 30 min in a sealed C-52 chamber (Wescor Inc., Logan, UT, USA).

**Chlorophyll content (spad).** The chlorophyll content of the plant was evaluated by taking SPAD measurements using a SPAD-502 chlorophyll meter (Konica Minolta Sensing, Inc., Osaka, Japan) from the third youngest fully expanded leaf from three points (upper, middle and lower leaflet of a leaf). Individual readings of leaflets were averaged to represent individual measurement of a leaf. The evaluations were done on light adapted leaves at 29, 59, 76, and 83 day after planting (dap).

**Post-harvest traits.** The harvest was at 90 dap. The plants were separated in four components: leaves, stems, roots and tubers. The dry weight (g) components were determined by drying them at 80°C for 3 days in a forced air oven: leaf (ldw), stem (sdw), root (rdw), tuber (tdw). The leaf area (lfa) of the plants was measured in cm2 by taking photographs of all the leaves arranged on a wooden board and analyzing the pictures using ImageJ software (Zárate-Salazar et al., [2018](#ref-zarate-salazar2018Comparacao)).

**Indices.** The harvest index (hi) was calculated as the ratio of tdw related to the total dry biomass (tdb) and specific leaf area (sla) was calculated by dividing the leaf area (lfa) with lead dry weight (ldw).

## Statistical analysis

The experiment was carried out in a complete randomize block design with two factors; the irrigation, well water (WW) and water deficit (WD) treatments and fifteen potato genotypes. Each treatment consisted of five replicates with one potato plant for each experimental unit. Statistical analysis and graphs were performed in the statistical software R (R Core Team, [2020](#ref-R-base)). The analysis of variance (ANOVA) was performed to evaluate the differences between the factors and the comparison of the means with the Student-Newman-Keuls test (p<0.05) with agricoale and GerminaR package (de Mendiburu, [2020](#ref-R-agricolae); Lozano-Isla et al., [2019](#ref-lozano-isla2019GerminaR)). For the multivariate analysis, correlation and principal components analysis were performed with FactoMineR and heatmaply package (Galili et al., [2018](#ref-galili2018heatmaply); Husson et al., [2020](#ref-R-FactoMineR)). The hierarchical clustering between treatments and genotypes were computed with the Euclidean distance (Lê et al., [2008](#ref-le2008FactoMineR)).

# Result

## Treatment application

The drought treatment were apply at 45 day after planting (dap) and the fraction of transpirable soil water (ftsw) shown differences 4 day since treatment application. Plants in WW were maintained the water availability in the pots more than 70% while the restriction in the water supply for the WD treatment decrease the water availability until the finalization of the experiment when the plant in WD in average had less than 10% of ftsw, Figure 1A. In the case of the transpiration the plants in WD reduce the transpiration rate 8 days after not water irrigation, Figure 1B.

## Agro-phisological traits

SPAD units taken over the course of plant development (29, 59, 76, and 83 dap) showed that at 29 dap all plants were at the same stress level as no treatment difference was found, Table 2. At 59, 76 and 83 the spad shown difference en each evaluation and at the end of the experiment the values were lower than at 29 dap and the WD values for all the genotypes were higher than the ones at WW conditions. The genotypes CIP398190.89 and CIP720088 had the lowest differences among treatments for spad at 83 dap (2.06 and 0.30, respectively), while CIP398203.244 and CIP398208.33 had the largest (14.48 and 17.54, respectively), Supplementary table ??.

Leaf relative water content (rwc) and leaf osmotic potential (lop) significantly (p<0.01) decreased in response to WD in all the genotypes, Table 2. The values ranged between 64.96% and 50.09% for CIP720088 and CIP398201.510, respectively.

The specific leaf area (sla) reduction was 48% under WD compared to WW, Table 2. CIP398190.89 together with CIP398203.5 were among the clones with lowest reduction (24 and 21% respectively), while CIP398208.219, CIP398098.119, and CIP398208.704 were among the clones with highest sla reduction wth 53, 65, and 64% respectively, Supplementary table ??.

Plant high (hgt), leaf dry weight (ldw), stem dry weight (std), leaf area (lfa) decrease significantly (p<0.01) under drought treatment, Table 2. In the case of lfa there was a drastic reduction with 65% in plants under WD compare with WW plants, Table 2. While the components such as number of tuber (ntub), root dry weight (rdw) and root length (rdl) did not shown differences between the treatments (p>0.5).

## Yield components

Differences existed among genotypes in total dry biomass (g) of well-watered (WW) plants at the end of the experiment, Table 2. Water deficit (WD) treatment had a significant effect (P<0.001) with an average reduction of around 32% in comparison with the well-watered treatment, Table 2.

In terms of productivity, WD decreased tuber yield across genotypes by an average of 40% (P< 0.001). CIP398190.89 had greater tuber dry weight (g) in WD compared to its yield in WW treatment with a 5% increase in biomass, while others genotypes like CIP398203.5 and CIP398203.244 presented up to 56% and 48% reduced tuber production, Supplementary table ??. The genotypes CIP398203.244, CIP398180.612, and CIP398201.510 were among the most sensitive genotypes at 31.56, 46.75 and 48.88% respectively under WD. For harvest index (hi), differences among genotypes (p<0.001) and treatments (p<0.02) were found, Table 2.

Water use efficiency (wue) was generally higher in WD than WW plants (p<0.001), Table 2. Under WD treatment, CIP397077.16, CIP398208.620, CIP392797.22 and CIP398190.89 showed the highest wue with 13.06, 12.03, and 11.59 g.L-1, respectively, Figure 2A. The lowest wue with 8.50 and 9.24 g.L-1 were presented by CIP398180.612 and CIP398203.5, respectively. For Tuber Water Use efficiency (twue) there is not difference between treatments (p=0.5), Table 2. The genotypes with better twue under WD were CIP397077.16, CIP392797.22, CIP720088 and CIP398208.620, Figure 1 and Supplementary table ??.

## Multivariate analysis

The Principal Component Analysis (PCA) the two first dimension explain 64.9% of the variance in the experiment. In the first dimension trs (r=0.90), lfa (r=0.89), tbd (r=0.84), sla (r=0.83), tdw (r=0.77) and rwc (r=0.71) show a high correlation and association with WW treatment, in the other side the spad\_76 (r=-0,77) shown an negatives correlation and association with WD treatment. In the second dimension the rdw (r=0.87), rdl (r=0.86) have a high correlation and associated at WD treatment and negate correlated with hi (-0.89) and twue (-0.9) and associated to WW treatment, Figure 2A.

The clustering analysis show 5 groups and it could be associated in 2 different ways. The first association could by classified by the treatment applied, the blue and cyan are the well water treatments (WW) and the black and red associated at the water deficit treatment (WD); and the second association in green, cyan and red color genotypes with tolerate to water stress, in addiction they shown a correlation with twue, hi and tdw, traits that are important in the yield component, Figure 2.

The association between the cluster an the variables shown that the genotypes in the cluster 1 are positive correlated with the spad, rdl and rdw and negative correlated to hi, tdw, twue, sla. The genoytpes in the cluster 2 are positive associated with the hi and negative associated with ldw, tdb, sdw. In the cluster 3 the genotypes are positive correlated at wue, twue and negative correlated for rwc, lop and sla. The cluster 4 positive association with rdw, ldw, lfa, sdw, trs and negative correlated with wue and twue. And the cluster 5 is associated with sla, tdw, rwc, lfa and negative associated with spad and rdw, Figure 2.

The values of tdb and trs were strongly and positively correlated with 0.93 (P<0.05) with Euclidean distance of 0.91, Figure 3. The spad value shown stronger correlation when the time it was taken is longer with 0.83 positive correlation between 76 and 83 dap with a euclidean distance 0.53. A negative correlation (r= -0.73) among rdw and hi was found with a euclidean distance of 4.21, Figure 3.

For correlation between hi and twue was strong (r=0.92) with an euclidean distance of 0.68, shown not only a good correlation but also a good association between these two variables, Figure 3. While tuber dry weight (tdw) shown better correlation with hi (r=0.61) and twue (r=0.55) than wue (r=0.05) with a euclidean distance of the traits 4.21, shown low association with tdw, Figure 2 and Figure 3.

Interesting association since the application of the drought treatment (Table 2) is between spad with tdw that have negative correlation (r=~0.60) and an euclidean distance of 4.21 shown no assoction between them. Apparently spad measure is sensitive to the detect the drought stress and it is related with the tuber production, Figure 2 and Figure 3.

# Dicussion

Water stress triggered a range of morphological and physiological mechanisms in the potato genotypes tested, leading to different yield penalties and indicating a variety of survival strategies by potato. Most characteristics measure showed differences between treatments, pointing to their value in evaluating the impact of drought. According to (Songsri et al. 2009), enhanced extraction of water and nutrients from the soil due to large root system and long roots is a drought resistance mechanism in potato. But in our study showed that the minimal yield losses in some genotypes like CIP398190.89 under WD could be related to its ability to increase its twue, by absorbing the limited water and nutrients available in the soil without changing have a high reduction in the final yield, Figure 2.

Plant biomass accumulation, and consequently yield, was shown to be inextricably linked to transpiration (Sinclair et al., [1984](#ref-sinclair1984WaterUse)). A drought resistance mechanism can be the reduction of transpiration achieved by the reduction of leaf area with thick leaves often have greater photosynthetic capacity than thin leaves, due to their higher chlorophyll per leaf area counts (Songsri et al. 2009). Sensitive genotypes such as CIP398203.244 and CIP398201.510 preferred to produce leaves and more roots in preference to tubers. A lower specific leaf area (SLA) under WD, principally explained by decreases in new leaf production, number of leaves, and leaf size. This decrease might have had allowed a reduction in leaf transpiration, saving water for tuber bulking as suggested by Lahlou, et al. (2003). Hence, potato genotypes with the ability to maintain low SPAD and high SLA under WD conditions, can maintain higher twue and increase the tuber production. SPAD is an indicator of the photosynthetically active light transmittance characteristics of the leaf, which is dependent on the unit amount of chlorophyll per unit leaf area. SPAD units have been correlated with chlorophyll and carotenoid content in potato and other crops (Ramírez et al. 2014: Marenco et al. 2009) and are used in selecting genotypes tolerant to drought in breeding programs.

We found root dry weight, spad and hi to be good indicators for tuber water use efficient and useful traits for drought tolerance breeding programs Figure 2. The genotypes like CIP398201.510 and CIP398203.244 with the longest roots showed the lowest yield and hi under both stressed and non-stressed conditions. In this genotype, the long roots seem to contribute to vegetative growth rather than yield components.

It is important to remember that under WW conditions, soil can supply water at a steady rate to meet the transpiration demand. However, as the soil becomes dry, water flux from soil to root surface decreases and cannot satisfy the demand of transpiration. Additionally, in WD conditions, mineralization and supply of nutrients, especially N, is reduced, forcing the plant to use their resources efficiently as the only solution to not compromise yield (Motalebifard et al. 2013). Payne et al. (1995) found that N uptake was linearly related to plant transpiration, and that about twice as much N is taken up per kg of transpiration in water-stressed plants than in non-water-stressed plants. In our study, we found that CIP397077.16 and CIP398208.620 could maintain turgor, which, combined with the reduction of SLA, helped them to conserve water. Additionally, increased amounts of RWC under WD treatment in CIP720088 may have been the result of higher stomata conductivity, since the root length of CIP720088 in WW and WD treated plants were comparable (Figure 3a).

The strong correlation between WUE in this experiment and tuber yield (r = 0 .78, p < .001) indicates direct association between them, and at the same time, reflected the conservative relationship between biomass production and WUE through a range of limited soil water availability. Reduced stomatal conductance can constrain the diffusion of CO2 for photosynthesis, and accordingly the average total biomass in the WD treatment was significantly lower than that of the corresponding genotypes in WW treatment. Different studies have measured WUE at the leaf, whole plant, and crop levels (Guoju et al. 2013; Hochman et al. 2009) and have found no significant differences at plant or crop levels (Deblonde et al. 1999). In this study, WUE is considered a critical trait that can affect yield and its increase can lead a plant to tolerate or avoid water deficit conditions.

This ratio is called harvest index (H) and has been found to be relatively stable for a particular cultivar over a fairly wide range of conditions (Donald and Hamblin 1976).

Evans (1980) suggested that one of the main variables for yield increases seen to date has been increases in harvest index.

Evans (1980) further suggested that additional large increases in harvest indices are unlikely. Therefore, further increases in water-use efficiency based on marketable yield are not likely from increasesin the harvest index.

Passioura (1977) and Fischer (1979) have argued that obtaining high harvest indexes underwater-limitedconditions is especially importantin obtaining high water-use efficiencies.

Passioura (1977) proposed that cereals for water-limited environments be developed with roots with restricted water uptake rates. Again, such an alteration would, in principle, conserve water during vegetative growth leaving more soil waterfor extraction during grain development. The key aspect of both strategies is that sustained reproductive growth is essential for a high harvest index.

However, a deeper and more extensive rooting system may have drawbacks. A greater root biomass would almost surely result in lowered harvest index (in potato can be advantage?)

Improved harvest index. As illustrated in equations(7) and(9) improvements in harvest index result directly in increased water-use efficiency. The difficulty is that for many crops it appears that further substantial improvements in harvest index are unlikely.

SPAD measurements of the leaf were used as an indicator of nitrogen status and leaf senescence.

SPAD a good indicator for select best genotypes, because it have negative correlation with the tdw

Menor contendido de clorofila –> mayor contenido de otros pigmentos que ayuden a luchar contra el stress por sequia???

Selection basado en genotipos de alto HI y mayor SPAD para selección de líneas promisorias!

SPAD Acompanhado de la senecencia o que sucede, buscar explicación??

Lo que desmuestra que se puede usar hi and spad para saleccionar papas con mayor efficiencia de uso de agua para formar tuberculos

# Conclusions

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Table 1: Potatos (*Solanum tuberosum* L.) genotypes used for water deficit experiment with 13 lines from advanced breeding population at International Potato Center (CIP) and two comercial varieties.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Number | Genotypes | Adaptability | Growning period | Heat tolerance | Dry matter (%) |
| G01 | CIP720088 (Achirana-INTA) |  | early |  | 19 |
| G02 | CIP392797.22 (UNICA) | Lowland and highland Tropics | Medium |  | 21 |
| G03 | CIP397077.16 | Lowland tropics | Medium |  | 20 |
| G04 | CIP398192.213 | Mid elevation tropics | Medium | Tolerant | 22 |
| G05 | CIP398180.612 |  | Medium |  |  |
| G06 | CIP398208.704 | Mid elevation tropics | Medium | Tolerant | 24 |
| G07 | CIP398098.119 | Mid elevation tropics | Medium | Tolerant | 26 |
| G08 | CIP398190.89 | Mid elevation tropics | Medium | Tolerant | 21 |
| G09 | CIP398192.592 | Mid elevation tropics | Medium | Tolerant | 21 |
| G10 | CIP398201.510 | Mid elevation tropics | Medium | Tolerant | 20 |
| G11 | CIP398203.244 | Mid elevation tropics | Medium | Tolerant | 20 |
| G12 | CIP398203.5 | Mid elevation tropics | Medium | Tolerant | 13 |
| G13 | CIP398208.219 | Mid elevation tropics | Medium | Tolerant | 22 |
| G14 | CIP398208.33 | Mid elevation tropics | Medium | Tolerant | 21 |
| G15 | CIP398208.620 | Mid elevation tropics | Medium | Tolerant | 21 |

Table 2: List of variables measured in 15 potato genotypes under well-watered (WW) and water deficit (WD) treatment. Where: Tuber dry weight (TDW), tuber number (NTUB), root dry weight (RWD), leaf area (LFA), harvest index (HI), tuber water use efficency (TWUE).

|  |  |  |  |
| --- | --- | --- | --- |
| **Characteristic** | **WD**, N = 75 | **WW**, N = 75 | **p-value** |
| **spad\_29** | 56.1 ± 4.9 | 56.7 ± 5.0 | 0.4 |
| **spad\_59** | 47.9 ± 4.4 | 45.8 ± 3.7 | 0.002 |
| **spad\_76** | 46.0 ± 5.4 | 41.7 ± 3.6 | <0.001 |
| **spad\_83** | 44.1 ± 5.9 | 39.7 ± 4.5 | <0.001 |
| **hgt** | 132 ± 15 | 150 ± 16 | <0.001 |
| **rwc** | 58 ± 6 | 69 ± 5 | <0.001 |
| **lop** | -2.84 ± 0.30 | -2.25 ± 0.29 | <0.001 |
| **ldw** | 12.0 ± 3.7 | 17.3 ± 5.5 | <0.001 |
| **sdw** | 11.6 ± 9.1 | 14.5 ± 6.1 | <0.001 |
| **rdw** | 3.67 ± 1.94 | 3.50 ± 1.96 | 0.6 |
| **tdw** | 24 ± 11 | 40 ± 19 | <0.001 |
| **ntub** | 12.0 ± 6.2 | 12.0 ± 4.9 | 0.8 |
| **trs** | 4.52 ± 1.22 | 7.85 ± 2.20 | <0.001 |
| **lfa** | 2488 ± 797 | 7100 ± 2380 | <0.001 |
| **rdl** | 33.1 ± 6.5 | 32.5 ± 5.8 | 0.4 |
| **tdb** | 51 ± 16 | 75 ± 24 | <0.001 |
| **hi** | 0.47 ± 0.16 | 0.53 ± 0.14 | 0.020 |
| **sla** | 218 ± 62 | 415 ± 82 | <0.001 |
| **wue** | 11.32 ± 2.15 | 9.53 ± 1.26 | <0.001 |
| **twue** | 5.31 ± 2.03 | 5.09 ± 1.75 | 0.5 |

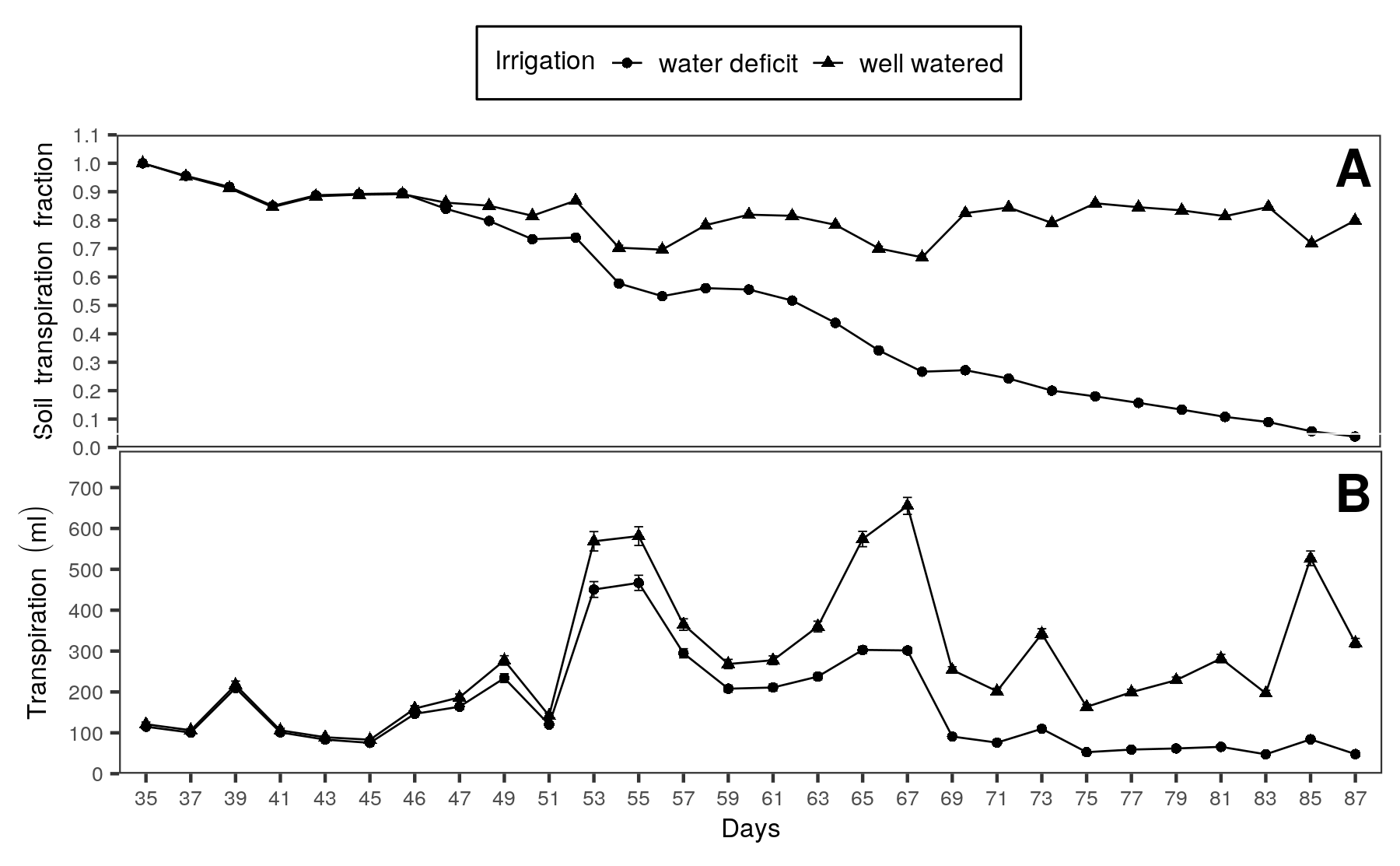


Figure 1: Soil transpiration fraction and transpiration during the experiment

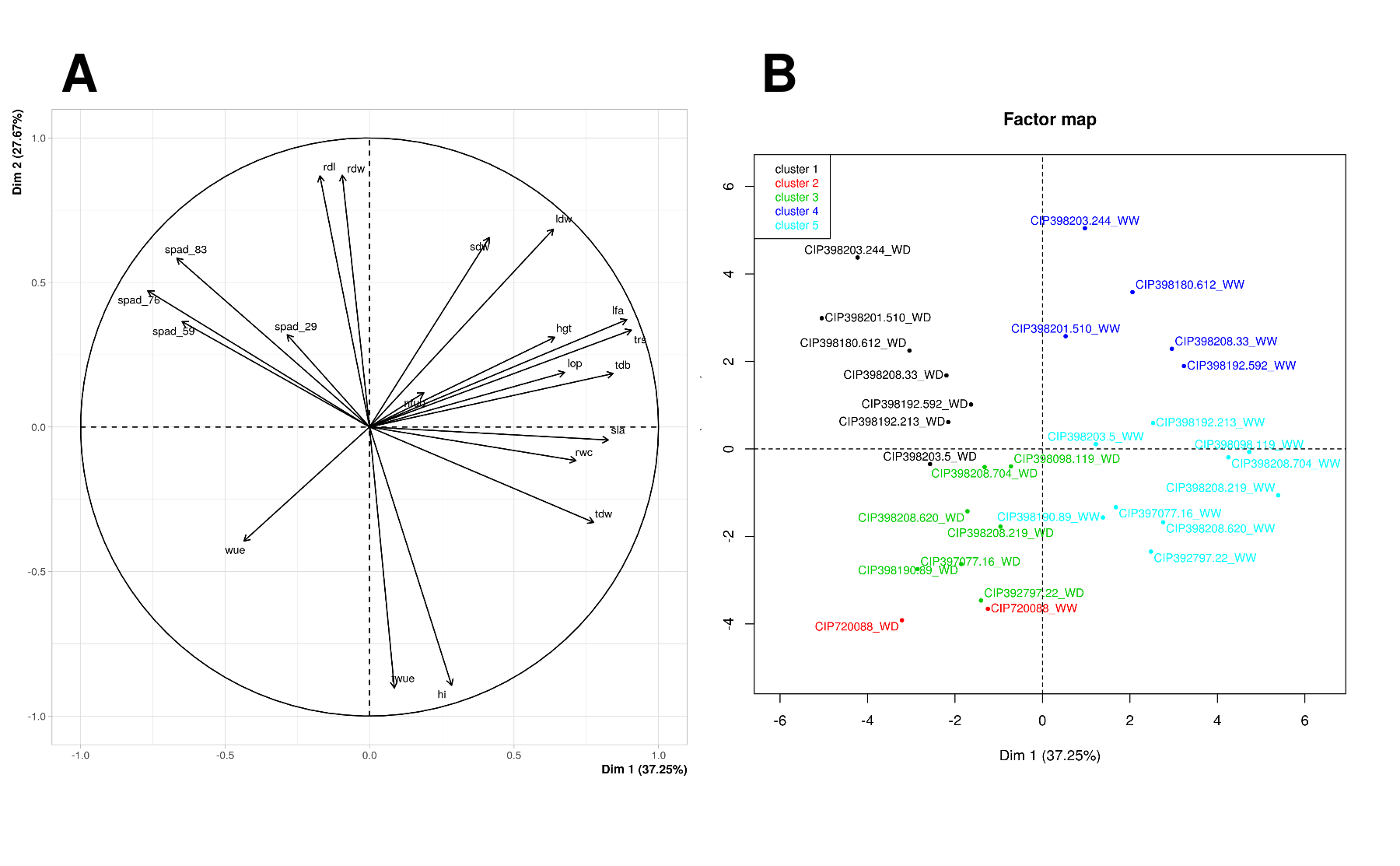


Figure 2: Principal component analysis

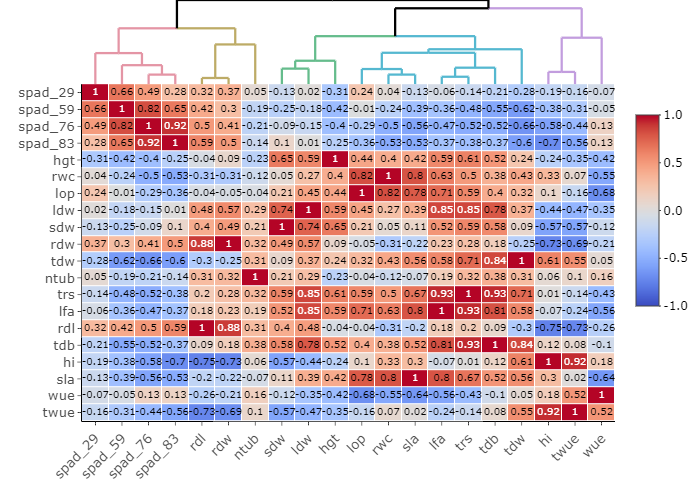


Figure 3: Correlation analysis