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

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# Abstract

Drought stress is one of the major causes of damage and subsequent reduction in yield all crops worldwide and the problem is only expected to get worse with water deficits stemming from climate change and population expansion so it is need to be bred plants for water use efficiency by capturing traits that help the plants develop faster and be more efficient using the resorces and improve the yields. Potato is one of most important food crop worldwide and modern cultivars are highly sensitive to soil drought. In this study, we aim to study the physiological responses of potato (*Solanum tuberosum* L) to soil drought at the tuberization phase under controlled condition and find traits that can help understand the relation between them 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 (wuet). We also found correlation between hi and wuet 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 and drought is one of the most uncontrollable and pervasive factors and one of the global problems limiting production (Obidiegwu et al., [2015](#ref-obidiegwu2015Coping)). 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)).

Potato (*Solanum tuberosum* L.) is the fourth most important food crop worldwide with an annual production of around 380 million tons [Birch et al. ([2012](#ref-birch2012Crops)); FAO 2017]. 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); Joshi et al., [2016](#ref-joshi2016Potato)) . In potato, tolerance to drought is a very complex trait (Anithakumari et al., [2012](#ref-anithakumari2012Genetic)) and about 2000 differentially expressed genes were revealed in potato in response to water deficit (Watkinson et al., [2006](#ref-watkinson2006Accessions)). Under field conditions, drought caused drastic losses in potato tuber yield and/or quality (Stark et al., [2013](#ref-stark2013Potato); Yang et al., [2016](#ref-yang2016Identification)).

Potato is sensitive to periodic water shortage and 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 (Monneveux et al., [2013](#ref-monneveux2013Drought), and @sprenger2016drought; Stark et al., [2013](#ref-stark2013Potato)) and management of water has a marked influence on plant behavior, tuber production, and quality. The modern potato cultivars are highly sensitive to soil drought and variability in response to soil drought is observed (Monneveux et al., [2013](#ref-monneveux2013Drought); Soltys-Kalina et al., [2016](#ref-soltys-kalina2016effect); Sprenger et al., [2016](#ref-sprenger2016drought)). Therefore, physiological behavior of the plants under this stress could provide information on their capacity to tolerate drought stress. Differences response have been observed in the effects caused by drought stress related to morphological, physiological, biochemical, and molecular changes among species and cultivars (Liu et al., [2005](#ref-liu2005ABA), [2006](#ref-liu2006Effects)). Climate change increases the need to identify potato genotypes that exhibit high tolerance to abiotic stresses (Monneveux et al., [2014](#ref-monneveux2014Drought)).

The present study elucidate the mechanisms for drought tolerance and yield in eleven 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 (wuet), 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.

# Materials and Methods

## Plant material

Thirteen potato clones were selected from advanced breeding population collection at International Potato Center (CIP) and two commercial varieties, Table (1). UNICA ( CIP392797.22) has a good response to warm and dry environments (Demirel et al., [2020](#ref-demirel2020Physiological); Gutiérrez-Rosales et al., [2007](#ref-gutierrez-rosales2007UNICA); Rolando et al., [2015](#ref-rolando2015Leaf)); and Achirana INTA (CIP720088) known for their earliness and drought tolerance (Schafleitner et al., [2007](#ref-schafleitner2007Field)).

## Experimental conditions

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). Each treatment consisted of five replicates with one potato plant for each experimental unit.

## Cultivation and management

The experiment was conducted at the International Potato Center (CIP) experimental station in Lima, Peru (12.1◦ S, 77.0◦ W, 244 m.a.s.l.). The plants were grown in an environmentally controlled greenhouse at 28/15°C day/night with 70±5% average relative humidity (HOBO U12 Outdoor/Industrial model, Onset Computer Corporation, Bourne, MA, USA). 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). The potato tubers were pre-sprouted for 2 weeks and planted at 5–7 cm depth. Fertilization was done twice with ammonium nitrate; triple super-phosphate and potassium sulphate, one before planting mixed with the substrate and the other applied at the surface at 40 days after planting (dap).

## Transpiration rate and soil water supply

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 (wueb) and tuber water use efficiency (wuet). 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 wuet was used the dry weight from tuber production divide the total 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 90ºC 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 concentration (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) to obtain the relative concentration of chlorophyll molecules per unit area of the leaf surface (Ling et al., [2011](#ref-ling2011Use)) in 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). SPAD values were highly significantly correlated with a + b chlorophyll concentration per unit leaf area (g cm−2) (Lichtenthaler & Wellburn, [1983](#ref-lichtenthaler1983Determinations)).

**Post-harvest traits.** The harvest was at 90 dapand 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 (Rueden et al., [2017](#ref-rueden2017ImageJ2); 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

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)). A t-student test between well water and water deficit treatment (p<0.05). 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 method for compute the hierarchical clustering between treatments and genotypes was euclidean distance (Lê et al., [2008](#ref-le2008FactoMineR)). The code and statistical analysis for reproducible analysis are available in the following github repository <https://github.com/Flavjack/20130515LM>.

# 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 their transpiration rate 8 days after not water application, 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 spad 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), Figure 2F.

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 with 53, 65, and 64% respectively, Figure 2B.

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, Figure 2A. 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.

Biomass water use efficiency (wueb) 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 wueb with 13.06, 12.03, and 11.59 g.L-1, respectively, Figure 3A. The lowest wueb with 8.50 and 9.24 g.L-1 were presented by CIP398180.612 and CIP398203.5, respectively. For Tuber Water Use efficiency (wuet) there is not difference between treatments (p=0.5), Table 2. The genotypes with better wuet under WD were CIP397077.16, CIP392797.22, CIP720088 and CIP398208.620, Figure 1 and Figure 2D.

## 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 wuet (-0.9) and associated to WW treatment, Figure 3A.

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 wuet, hi and tdw, traits that are important in the yield component, Figure 3.

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, wuet, 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 wueb, wuet and negative correlated for rwc, lop and sla. The cluster 4 positive association with rdw, ldw, lfa, sdw, trs and negative correlated with wueb and wuet. And the cluster 5 is associated with sla, tdw, rwc, lfa and negative associated with spad and rdw, Figure 3.

The values of tdb and trs were strongly and positively correlated with 0.93 (P<0.05) with Euclidean distance of 0.91, Figure 4. 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 4.

For correlation between hi and wuet 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 4. While tuber dry weight (tdw) shown better correlation with hi (r=0.61) and wuet (r=0.55) than wueb (r=0.05) with a euclidean distance of the traits 4.21, shown low association with tdw, Figure 3 and Figure 4.

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 association between them. Apparently spad measure is sensitive to the detect the drought stress and it is related with the tuber production, Figure 3 and Figure 4.

# Dicussion

Likewise, under drought stress, the tolerance of some genotypes has been associated with rapid recuperation after rehydration (Hu et al., 2010; Zegada-Lizarazu and Monti, 2013).

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. 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). 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 wuet, by absorbing the limited water and nutrients available in the soil without changing have a high reduction in the final yield, Figure 3.

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). 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. Hence, potato genotypes with the ability to maintain low SPAD and high SLA under WD conditions, can maintain higher wuet 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.

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.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 3. 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.

High correlation between tdw with wuet and hi than wueb indicates direct association between them, and at the same time, reflected the conservative relationship between biomass production and wueb through a range of limited soil water availability. 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 3. SPAD measurements of the leaf were used as an indicator of nitrogen status and leaf senescence. 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 water for 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.

Evans (1980) suggested that one of the main variables for yield increases seen to date has been increases in harvest index. Harvest index (hi) and has been found to be relatively stable for a particular cultivar over wide range of conditions (Donald and Hamblin 1976). Passioura (1977) and Fischer (1979) have argued that obtaining high harvest indexes underwater-limited conditions is especially important obtaining high water-use efficiencies even if many crops it appears that further substantial improvements in harvest index are unlikely [Evans (1980)].

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

At all growth stages, water stress reduces photosynthetic efficiency, but drought during tuber initiation and bulking has the most drastic effect on yield (Yuan et al., 2003; Onder et al., 2005).

Previous studies have shown that reduced soil water availability at diff erent growth stages results in earlier crop maturity (Karafyllidis et al., 1996) and decreased plant growth, tuber yield, tubers per plant and tuber size and quality (Lynch et al., 1995; Dalla Costa et al., 1997; Yuan et al., 2003).

The 80% treatment was more efficient or equally efficient compared with the 100 and 120% treatments, and had higher WUE in the first year; thus, this level of irrigation can be recommended as a good strategy in situations with limited water supplies or high water costs. The 80% treatment was more efficient or equally efficient compared with the 100 and 120% treatments, and had higher WUE in the first year; thus, this level of irrigation can be recommended as a good strategy in situations with limited water supplies or high water costs (Camargo et al., [2015](#ref-camargo2015Potato)).

The leaf chlorophyll content was lower in the high-WUE group indicating that the higher net photosynthesis rate was not due to higher leaf-N status (Kaminski et al., [2015](#ref-kaminski2015Contrasting)).

The leaf chlorophyll content was lower in the high-WUE group indicating that the higher net photosynthesis rate was not due to higher leaf-N status (Kaminski et al., [2015](#ref-kaminski2015Contrasting)).

Agriculture accounts for around 85 % of global water consumption (Shiklomanov and Rodda 2003), and the amount of water used for crop irrigation is predicted to double by 2050 (Tilman et al. 2002).

It is therefore essential for future studies to focus, in addition to improving the agricultural irrigation systems, on breeding crops with increased water-use efficiency (WUE), also at well-watered conditions (Kaminski et al., [2015](#ref-kaminski2015Contrasting)).

The regulation of potato (Solanum tuberosum subsp. tuberosum) stomatal conductance has been of special interest, as this crop is sensitive to drought and closes its stomata at relatively mild soil moisture deficits (Lynch et al. 1995, Sadras and Milroy 1996, Porter et al. 1999, Onder et al. 2005) resulting in considerable yield loss (Porter et al. 1999). An appropriate irrigation is therefore necessary to achieve desirable yield and quality (Liu et al. 2006). It has been shown that partial root zone drying (PRD), a technique where water is supplied alternately to two spatially separated parts of the potatoes root system, saves 30 % of irrigation water without reducing the overall yield (Shahnazariet al. 2007).

(ABA) based root-to-shoot chemical signalling system has been found to be effective in increasing WUE by partial stomatal closure, where water losses due to transpiration decrease significantly yet not affecting the photosynthetic potential of potato (Liu et al. 2005, 2006).

Potatoes use water more efficiently than cereals. The potato harvest index is approximately 0.75 and can reach as high as 0.86 (Shahnazari et al. 2007), in contrast to cereals for which it oscillates around 0.5 (Vreugdenhil and Bradshaw 2007).

Breeding potato with increased WUE is essential to meet the demand of a continuously increasing world population with little possibility to include previously unexploited arable land. However, phenotyping WUE is not a simple process due to cost, space and labour requirements (Kaminski et al., [2015](#ref-kaminski2015Contrasting)).

The physiological mechanisms of potato plants response to various environmental conditions require deeper understanding. In addition, potato is an autotetraploid (2n = 4x = 48) and suffers from acute inbreeding depression (Potato Genome Sequencing Consortium 2011), which contributes to a significant barrier for traditional breeding approaches (Kaminski et al., [2015](#ref-kaminski2015Contrasting)).

(Rolando et al., [2015](#ref-rolando2015Leaf)){

However, in the three genotypes tested, an increase in greenness was noted one week after the initiation of water restriction and maintained for 4–6 weeks.

In our work, a decrease in leaf growth a week after the initiation of water restriction coincided with the leaf greenness increase. Reduced leaf growth under water restriction was evidenced by both reduced leaf length and total above ground biomass accumulation, the latter measured three weeks after the restriction started.

Unica had the highest DSI, its final TB under water restriction was higher than Désirée. DSI compares the ratio between TB under water restricted and control treatments, thus Unica higher DSI is the result of a much higher TB under control treatment than Désirée. This higher TB, among other reasons, is a result of a longer vegetative period during which the crop accumulated biomass (Tardieu, 2013).

Finally, as the increase of greenness promoted by water stress likely depends on the stage of application and intensity of water restriction, further research on the timing effect of drought stress on the senescence process and its impact on the photosynthetic apparatus should be considered.

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Drought stress reduce the harvest index in 11% for WD plants, similar results were found in potato *(Schafleitner et al., 2007)* with 14% under terminal drought and more drastic with 57% Jerusalem artichoke (Ruttanaprasert et al., [2016](#ref-ruttanaprasert2016Effects)) showing that potato have moderate reduction under drought stress including in the present study that the number of tuber did not have variation between treatments.

*Jefferies (1992)* found that long term drought stress increased harvest index of potato in some early maturity varieties (from 0.41 to 0.50) but reduced one late maturity variety (from 0.54 to 0.25).

Nevertheless, harvest index of a tuber crop is an important trait determining yield under drought conditions *(Deguchi et al., 2010)*.

(Saravia et al., [2016](#ref-saravia2016Yield)){

UNICA was the most efficient genotype at using the N present in the soil and tolerating drought stress, while Achirana-INTA was most affected by drought in terms of NUE.

Both UNICA and CIP397077.16 tolerated drought in terms of yield maintenance and used the N present in the soil more efficiently, also under drought, than Achirana-INTA.

Saravia et al. ([2016](#ref-saravia2016Yield)) show that UNICA and CIP397077.16 while they did not have difference for harvest index under well water and drought treatment the Chlspad can discriminate the relation between the tuber yield under drought stress with less Chlspad shown that Chlspad could allow to discriminate drought tolerance genotypes under field conditions.

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A fast screening tool would be helpful in selecting valuable genotypes with defined growth strategies that translate to drought tolerance and are suitable for experiments and/or breeding (Soltys-Kalina et al., [2016](#ref-soltys-kalina2016effect)).

Differentiation of the architecture of the potato root system were found in several potato cultivars in the field (Zarzyńska et al., [2017](#ref-zarzynska2017Differences)). but in our case root lengt and root dry weight have the no statistical differences. In our tent experiment, root growth of all cultivars was limited by the volume of plastic bags, in which plants were grown. Among tested potato cultivars no large differences in plant architecture or canopy size were observed (Soltys-Kalina et al., [2016](#ref-soltys-kalina2016effect)).

The closure of stomata also reduces the rate of transpiration and results in the retention of water by the plant. Taken together, lowered rates of transpiration and photosynthesis directly affect water use efficiency (WUE) and drought tolerance (Chaerle, Saibo, & van der Straeten, 2005).

From an agronomical point of view, maintaining yield levels during drought is crucial for breeders, and thus, the drought tolerance of cultivars has been quantified from tuber yield under irrigated and soil drought conditions (Boguszewska-Mańkowska et al., [2018](#ref-boguszewska-mankowska2018Divergent)).

In the potato, yield is more affected by water deficiency during tuber formation than any other developmental stage (Ierna & Mauromicale, 2012; Obidiegwu et al., 2015).

Among the earliest plant responses to soil water deficiency is stomatal closure protecting the plant against excessive loss of water but it concomitantly restricts CO2 gas exchange (Feller & Vaseva, 2014; Obidiegwu et al., 2015).

A substantial increase in the efficiency of water use by Gwiazda was achieved by early stomata closure, and the sensitivity to ABA resulted in a significant reduction in transpiration rate.

The fluorescence quantum yield (Fv/Fm), the most widely used photosystem II efficiency indicator, did not change in tolerant potato cultivars (Gwiazda and Tajfun) under drought, but a small decrease in the Fv/ Fm ratio was associated with a lower drought tolerance in sensitive cultivars (Owacja and Oberon) (Boguszewska-Mańkowska et al., [2018](#ref-boguszewska-mankowska2018Divergent)).

Potato genotypes did not show differences in Fv/Fm values even at relative water deficits below 40% (Tourneux, Devaux, Camacho, Mamani, & Ledent, 2003) and during field drought, which were sufficient to lower the yield of tubers (Schafleitner et al., 2007). This indicates that photosystem II was unaffected by water deficiency, which implies that chlorophyll fluorescence measurements were unable to distinguish between drought-tolerant and -susceptible potato cultivars (Boguszewska-Mańkowska et al., [2018](#ref-boguszewska-mankowska2018Divergent)).

Young leaves generally have the highest metabolic activity and presumably the highest photosynthetic capacity under drought as they are less affected by turgor losses than older ones. Hence, synthesis of drought-adaptive proteins such as dehydrins and heat shock proteins is preferentially maintained in younger leaves contributing to increasing total protein contents (Meise et al., [2018](#ref-meise2018Impact)).

High N contents in leaves were negatively correlated with RWC. Therefore, an excess of leaf N promoted turgor decline under drought emphasizing the importance of a well-balanced N fertilization under water limitation (Meise et al., [2018](#ref-meise2018Impact); Saravia et al., [2016](#ref-saravia2016Yield)).

breeding of potatoes with advanced drought tolerance by improvement of OA is considered doubtful. Other traits with relevance for drought tolerance as possibly proline accumulation and extended root systems appear more promising for improving drought tolerance in potatoes (Meise et al., [2018](#ref-meise2018Impact)).

In potato plant, an optimal xylem-phloem transport interaction is critical considering the competition for photoassimilates between the above-ground and underground tissues (Kooman and Rabbinge 1996).

Drought conditions interfere with stem structure and availability of transport materials (Banik et al. 2016; Zheng et al. 2009).

However, our fndings (Aliche et al., [2020](#ref-aliche2020Morphological)) support the hypothesis that stem growth reduction during dehydration may also serve an advantageous purpose for the plants—to reduce transport distance (Koch et al. 2004). This suggests that stem growth reduction under limited water availability can facilitate an efcient water and nutrient transport in plants.

The stomatal closure of source leaves under dehydration in our greenhouse study as was observed in Biogold and Hansa (Aliche et al., [2020](#ref-aliche2020Morphological)) may imply that the sink leaves needed to adapt carbon fxation rate, as was shown in another study where younger leaves maintained their stomatal conductance and photosynthesis despite the decline of these attributes in older leaves (Vos and Oyarzun 1987).

ABA signalling is induced by osmotic stress, and is also known to induce the expression of dehydrins (osmoprotectants), which function as chaperones in plant drought responses (Hanin et al., 2011). In our study, we observed that the expression of a dehydrin gene, TAS14, was upregulated under drought up to several hundred-folds (Aliche et al., [2020](#ref-aliche2020Morphological)).

In our study (Aliche et al., [2020](#ref-aliche2020Morphological)), however, the chlorophyll fluorescence of drought-stressed plants did not significantly differ from those of the irrigated plants. Jefferies (1994) demonstrated in field grown potato (cv. Maris Piper) that drought had no significant effect on PSII function because excess light energy was dissipated by photorespiration.

The dark green-coloured drought-stressed leaves also had higher chlorophyll density (Aliche et al., [2020](#ref-aliche2020Morphological)).

Chlorophyll Content of Source leaves and Chlorophyll Content of Sink leaves have a positive relation with non-iirgated plant and negative relation with tuber dry weight (Aliche et al., [2020](#ref-aliche2020Morphological)). Chlorophyll Content could be interesting tool for screen drought tolerance genotypes.

Profiling of drought-resistance mechanisms and identification of drought-resistance genes are helpful ways to achieve this goal (Chen et al., [2020](#ref-chen2020Transcriptome)).

Twenty-three drought-responsive genes were identified by comparing the transcriptomes of drought-tolerant and drought-sensitive potato varieties under water stress (Chen et al., [2020](#ref-chen2020Transcriptome)).

Some genes will have memory effect on stress in this process and will show higher expression level when drought occurs again (Chen et al., [2020](#ref-chen2020Transcriptome)).

Diploid potato species have a wide genetic background, making it easier to isolate drought-resistant genes and analyze the molecular mechanisms of drought resistance, which can be as an effective material for drought resistance research in potato (Khan et al., [2015](#ref-khan2015Multiple); Yang et al., [2019](#ref-yang2019Transcriptome)).

The decrease in the expression level of the photosynthesis-related genes of JSY under drought stress indicates that plant water deficiency inhibits photosynthesis, and the degree of decline is greater with the increase of plant dehydration (Chen et al., [2020](#ref-chen2020Transcriptome)).

Transcript profiling highlighted a decrease in the abundance of transcripts encoding proteins associated with PSII light harvesting complex in stress tolerant cultivars (Demirel et al., [2020](#ref-demirel2020Physiological)).

Stress tolerant cultivars exhibited stronger expression of genes associated with plant growth and development, hormone metabolism and primary and secondary metabolism than stress susceptible cultivars (Demirel et al., [2020](#ref-demirel2020Physiological))

single and multiple abiotic stress tolerance in potato is associated with a maintenance of CO2 assimilation and protection of PSII by a reduction of light harvesting capacity.he data further suggests that stress tolerant cultivars suppress cell death and maintain growth and development via fine tuning of hormone signaling, and primary and secondary metabolism (Demirel et al., [2020](#ref-demirel2020Physiological)).

Tuber yield under limited water conditions is influenced by a combination of morphological and physiological processes including, photosynthesis, leaf expansion, and senescence, assimilate partitioning, tuber initiation, and tuber bulking (van Loon, 1981).

There is therefore a clear need to understand the responses to combined abiotic stresses under real-world conditions, to elucidate molecular mechanisms by which crops can maintain yield and quality in the face of abiotic stress and to define markers that can be efficiently applied in breeding to generate potato varieties that are more tolerant to combined abiotic stress (Demirel et al., [2020](#ref-demirel2020Physiological)).

Desiree and Unica (heat tolerant) both exhibited a significant reduction in the abundance of transcripts associated with PSII, particularly transcripts encoding light harvesting chlorophyllprotein complex components, when exposed to drought and heat (Demirel et al., [2020](#ref-demirel2020Physiological))

(Demirel et al., [2020](#ref-demirel2020Physiological)) These data suggest that tolerant cultivars acclimate to stress by reducing their light harvesting capacity thereby minimizing the potential for cellular damage resulting from the production of excessive ROS in the photosynthetic electron transport chain. Similarly, only the stress tolerant genotypes exhibited an elevated leaf temperature under heat and drought stress in comparison with heat alone. This would be consistent with the induction of non-photochemical quenching of chlorophyll fluorescence and the increased radiation of absorbed light energy as heat (Ruban, 2016)

(Demirel et al., [2020](#ref-demirel2020Physiological)) The transcription factor ABI5 is a key regulator of ABA signaling and stress responses and its function is modulated by AFP2 (Garcia et al., 2008). This provides a mechanism for fine-tuning stress responses and so its differential expression between heat tolerant and heat sensitive potato varieties is highly significant.

(Demirel et al., [2020](#ref-demirel2020Physiological)) We chose to impart stress treatments at the tuber initiation stage as this has been shown to limit foliage, stolon and tuber development and yield (Obidiegwu et al., 2015).

(Demirel et al., [2020](#ref-demirel2020Physiological)) These experiments indicate that stress tolerant cultivars respond to stress by i) reducing light harvesting capacity and increasing non-photochemical quenching and ii) maintaining capacity for growth and development in part by iii) rerouting metabolism to compensate for reduced photosynthesis. This is achieved by a fine tuning of hormonal signaling. The responses of cultivars with contrasting abiotic stress tolerance provided information on genes/classes of compounds that may be used as targets for future studies aimed at enhancing multi-stress tolerance in potato.

(Li et al., [2020](#ref-li2020Enhanced)) The transgenic potato plants showed normal phenotypes under drought stress, while the non-transgenic plants appeared withered. Results of physiological parameters assays showed that malondialdehyde, relative water content, and chlorophyll content in the transgenic potato plants were higher than that of non-transgenic plants. Upon rehydration after two weeks of drought, proline and soluble sugar contents of the transgenic potato plants were significantly higher than those of non-transgenic plants. These results combined demonstrate that the StProDH1 is a key player in the process of potato response to drought stress.

(Li et al., [2020](#ref-li2020Enhanced)) we cloned two potato ProDH genes StProDH1 and StProDH2 from the potato cultivar ‘Favorita’, and silencing the StProDH1 gene by the amiRNA technology. Our results suggested that the proline content increased in the transgenic potato plants and was companied by an enhanced tolerance to drought. This result expands our understanding of the role of ProDH in potato.

(Li et al., [2020](#ref-li2020Enhanced)) proline to be a compatible osmolyte, carbon, nitrogen storage, and ROS scavenger (Hare and Cress. 1997). In addition, proline accumulation may be involved in stress signaling response (Smirnoff and Cumbes. 1989). ProDH is a rate litmiting enzyme in proline catabolism, and is found a universally enzyme in all kingdoms of life (Servet et al., 2012).

(Li et al., [2020](#ref-li2020Enhanced)) the transgenic potato plants with improved drought tolerance were successfully generated by silencing the StProDH1 gene. The transgenic plants showed enhanced proline and soluble sugar content, photosynthesis efficiency and membrane stability under drought stress.

Potato (Solanum tuberosum L.) is the third most important crop species worldwide after rice and wheat in terms of human consumption, and its global production exceeds 388 million metric tons per year (Deuvax et al. 2014, FAOSTAT 2019)

(Plich et al., [2020](#ref-plich2020Relations)) It is well known that photosynthetic activity is reduced when plants are exposed to environmental stress (Retuerto et al. 2006; Prinzenberg et al. 2018). Drought stress reduces plant growth by reducing photosynthesis, which is mainly caused by stomatal limitation. Decreases in stomatal conductance reduce water loss through transpiration, but it also decreases carbon dioxide uptake, reducing the production of photoassimilates and plant growth.

(Plich et al., [2020](#ref-plich2020Relations)) These results suggest that measurements of chlorophyll a fluorescence may serve as a useful tool for estimating the level of tolerance to drought stress in potato.

With the change in environment and the scarcity of resources, abiotic stress has become an important factor which restricts the growing development of plants, having serious impact on quality of the agricultural products (Thao and Tran, 2012).

(Qi et al., [2020](#ref-qi2020potato)) In this study, it found that the StRFP2 gene was significantly up-regulated during drought stress which shows similar result as in previous transcriptome studies in potato under drought stress.

(Reddy et al., [2020](#ref-reddy2020Leaf)) Increased water use efficiency (WUE) by virtue of higher carbon assimilatory capacity can significantly circumvent this trade-off. Here, we report leaf mass area (LMA) has an important canopy architecture trait which when combined with superior carboxylation efficiency (CE) would achieve higher water productivity in rice.

(Reddy et al., [2020](#ref-reddy2020Leaf)) Increased WUE through improved chloroplast capacity to fix carbon has a greater relevance in enhancing water productivity in rice.

The increase in Chl content found in Es could be associated with the decrease in leaf growth and water turgor loss, as has been described in potato (Teixeira and Pereira, 2007; Ramírez et al., 2014; Rolando et al., 2015)

The Car/Chl ratio in all cultivars under drought stress was also higher than that in WW plants (Rodríguez-Pérez et al., [2017](#ref-rodriguez-perez2017Drought)). The Car content and Car/Chl ratio are correlated with the capacity of light protecting mechanisms (Boardman, 1977).

The Chl content increased in the Es cultivar under DS from 5 to 7 DAT compared to WW plants (Rodríguez-Pérez et al., [2017](#ref-rodriguez-perez2017Drought)).

decrease in the photosynthetic rate under water deficit conditions has been reported in plants such as potato (Solamun tuberosum L.) (Moorby et al., 1975 Schapendonk et al., 1989; Ierna and Mauromicale, 2006; Liu et al., 2006; Ramírez et al., 2016).

Stomatal and non-stomatal limitations cause an imbalance between the two phases of photosynthesis and an increase in the production of reactive oxygen species (ROS) (Sanchez-Rodríguez et al., 2010; Farhad et al., 2011).

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)).

The decrease in photosynthesis resulting from drought stress reduces growth, affecting parameters such as foliar area, total dry mass, and distribution of photoassimilates within the plants (Chaves et al., 2002; Lahlou et al., 2003).

A previous study reported that chlorophyll was a useful factor for assessing environmental stress resistance (Gao et al., 2015).

# Conclusions

The genotypes with high hi, low spad content under WD present mechanisms for drought avoiding. Additionally, tolerant genotypes like CIP398208.620, CIP398098.119. CIP397077.16 and CIP392797.22 (UNICA) preferentially use available water for tuber production rather than above ground biomass represented by their high wuet. Traits like spad and hi are associated to tuber yield under drought stress and could be useful as selection criteria for first stage breeding programs because are easy and chip to measure in large populations. However, there are additional strategies of the below-ground plant parts that need to be explored for their role in yield stability under water stress conditions.

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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: Treatment comparison for seventeen variables between Well-Watered (WW) and Water Deficit (WD) in 15 potato genotypes. Where: Tuber dry weight (tdw; g), Specific Leaf Area (sla; cm2g-1), Harvest Index (hi), Tuber Water Use Efficiency (wuet; gl-1), Chlorophyll Concentration (spad), Plant height (hgt; cm), Relative water content (rwc; %), Leaf osmotic potential (lop; MPa), Leaf dry weight (ldw; g), Stem dry weight (sdw; g), Root dry weight (rdw; g), Tuber number (ntub; N°), Root length (rdl; cm), Total transpiration (trs; ml), Leaf area (lfa; cm2), Total dry biomass (tdb; g), Biomass water use efficiency (wueb; gl-1). The vales are represented by the mean ± standard deviation with the significance under T-test with their respective p-values.

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable** | **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 |
| **wueb** | 11.32 ± 2.15 | 9.53 ± 1.26 | <0.001 |
| **wuet** | 5.31 ± 2.03 | 5.09 ± 1.75 | 0.5 |

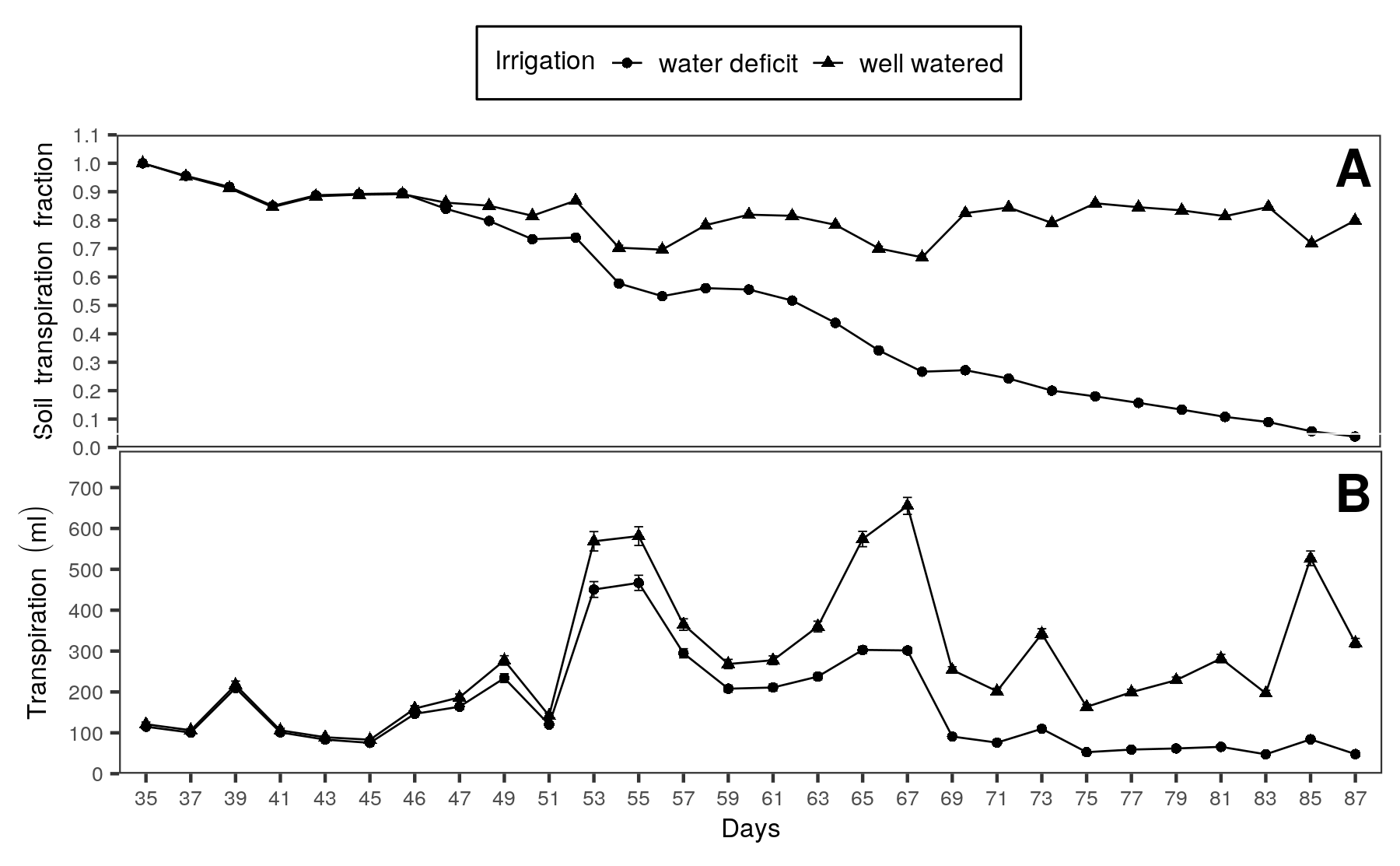


Figure 1: (A) Soil transpiration fraction (ftsw; %) and (B) Daily transpiration in 15 potato genotypes under well-watered (WW) and water deficit (WD) experiment.

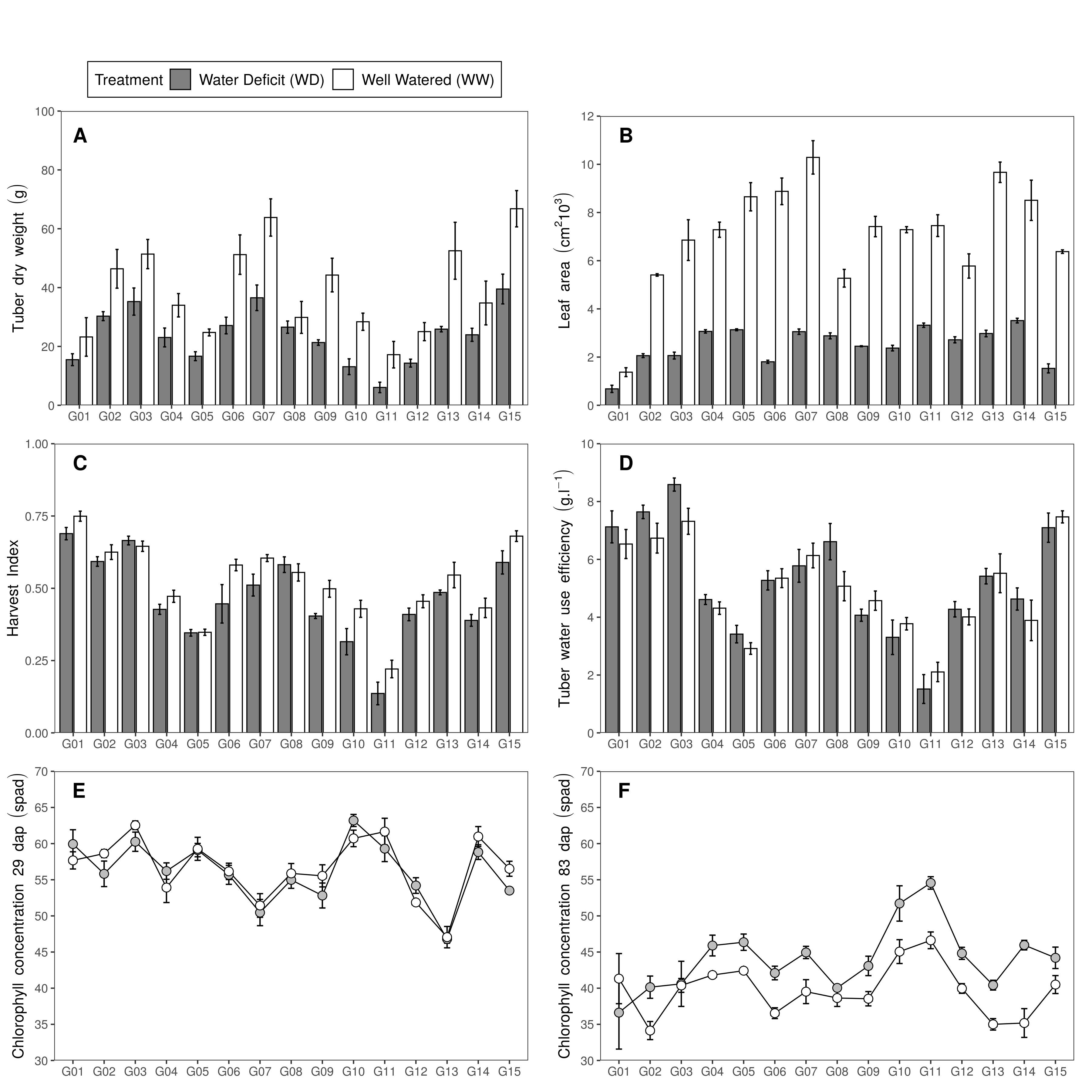


Figure 2: Variables measured in 15 potato genotypes under well-watered (WW) and water deficit (WD) treatment. (A) Tuber dry weight (tdw; g). (B) Leaf Area (lfa; cm2). (C) Harvest Index (hi). (D) Tuber Water Use Efficiency (wuet; gl-1). D-E Chlorophyll Concentration (spad). Error bars indicate standard error (n = 5). dap is days after planting.

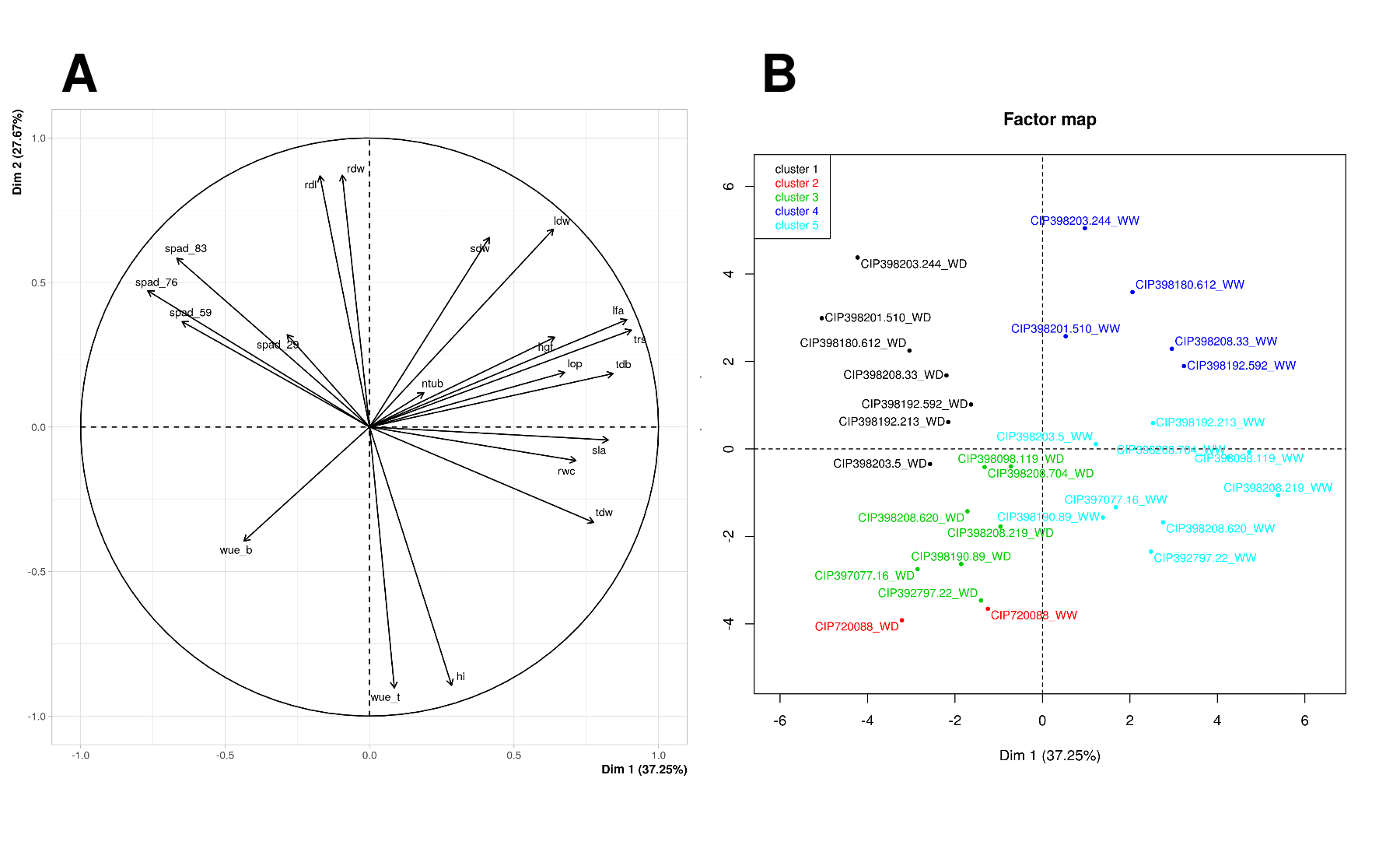


Figure 3: Principal Component Analysis (PCA) from variables measured in 15 potato genotypes under well-watered (WW) and water deficit (WD) treatment. (A) PCA for the variables. (B) PCA for the genotypes under WW and WD. Where: Tuber dry weight (tdw; g), Specific Leaf Area (sla; cm2g-1), Harvest Index (hi), Tuber Water Use Efficiency (wuet; gl-1), Chlorophyll Concentration (spad), Plant height (hgt; cm), Relative water content (rwc; %), Leaf osmotic potential (lop; MPa), Leaf dry weight (ldw; g), Stem dry weight (sdw; g), Root dry weight (rdw; g), Tuber number (ntub; N°), Root length (rdl; cm), Total transpiration (trs; ml), Leaf area (lfa; cm2), Total dry biomass (tdb; g), Biomass water use efficiency (wueb; gl-1).

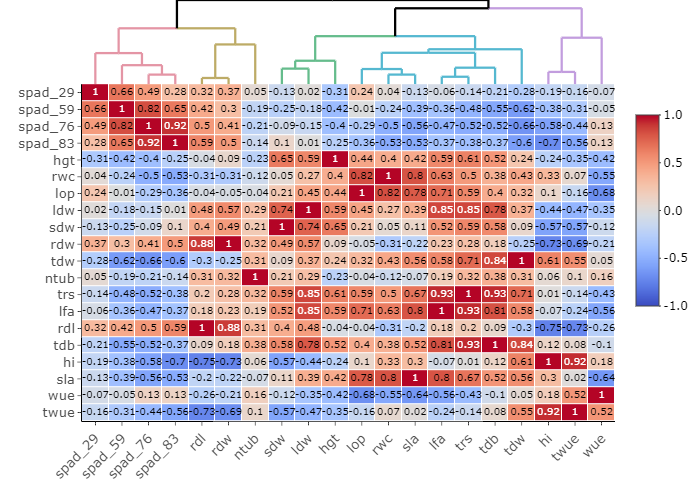


Figure 4: Correlation and cluster analysis from variables measured in 15 potato genotypes under well-watered (WW) and water deficit (WD) treatment. Where: Tuber dry weight (tdw; g), Specific Leaf Area (sla; cm2g-1), Harvest Index (hi), Tuber Water Use Efficiency (wuet; gl-1), Chlorophyll Concentration (spad), Plant height (hgt; cm), Relative water content (rwc; %), Leaf osmotic potential (lop; MPa), Leaf dry weight (ldw; g), Stem dry weight (sdw; g), Root dry weight (rdw; g), Tuber number (ntub; N°), Root length (rdl; cm), Total transpiration (trs; ml), Leaf area (lfa; cm2), Total dry biomass (tdb; g), Biomass water use efficiency (wueb; gl-1).