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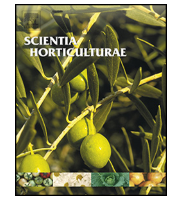

Chlorophyll concentration in leaves is an indicator of potato tuber yield in water-shortage conditions

D.A. Ramírez[a,*], W. Yactayo[a], R. Gutiérrez[a], V. Mares[a], F. De Mendiburu[a,b], A. Posadas[a], R. Quiroz[a]

[a] *International Potato Center (CIP), P.O. Box 1558, Lima 12, Peru*
[b] *Universidad Nacional Agraria La Molina (UNALM), Av. La Molina, Lima 12, Peru*

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ABSTRACT

The phenotyping of secondary characters is a common practice in breeding programs aiming at finding physiological mechanism related to drought tolerance. However, the dynamics of these characters depend on crop phenology, levels of water shortage, and other factors that affect their relationship with yield and limit their capacity to be used for predictive purposes. In this work, we compared tuber yield with the temporal trend (using accumulated thermal time) of chlorophyll concentration (Chl_{SPAD}), osmotic potential, and relative water content under water restriction. UNICA, a potato variety characterized by its low drought susceptibility was tested under full irrigation (as a control) and different treatments of partial root-zone drying and deficit irrigation in greenhouse and field conditions. Chl_{SPAD} was the only trait showing a concurrent changing trend (slope) with yields, particularly in field conditions. The rate of greenness loss or senescence was slower in the higher water restriction treatments, which indicates that the stay-green effect (delayed senescence) occurs in some potato varieties. Chl_{SPAD} at the loss of half the maximum plant cover during senescence (between 1040 and 1170 °C days) was high and negatively correlated with final yield in all irrigation treatments. Our findings suggest that during senescence, chlorophyll increment is not related to a rise of carbon assimilation (non-functional stay-green), but could be associated with an oxidative stress occurrence, ultimately reducing yield.

1. Introduction

The identification and measurements of morphological, physiological and phenological traits related to plant fitness (growth, reproduction and dispersion), is a crucial aspect in plant functional biology (Garnier and Navas, 2012). The monitoring of plant traits named "phenotyping of secondary characters" is a common practice in breeding programs aiming at finding physiological mechanism related to the response of stressors e.g. drought tolerance (Blum, 2011). Notwithstanding, changes in crop phenology, levels of water restriction and other factors, affect the relationship of commonly assessed traits with integrative variables such as yield, and limit their capacity to be used for predictive purposes (Tuberosa, 2012). Thus, the assessment of the dynamics of physiological changes under water restriction, through high-throughput phenotyping techniques, becomes important (Berger et al., 2010).

Expansion of potato cultivation to drought prone areas and the likely increase of water shortages for agriculture, driven by climate change and competing demands for other uses, highlight the importance of the irrigation water saving methods (Monneveux et al., 2013). Partial root-zone drying (PRD) and deficit irrigation are promising techniques conducive to water savings without tuber yield reductions (Liu et al., 2006a,b; Jensen et al., 2010; Xie et al., 2012; Yactayo et al., 2013). PRD is considered a false water stress (Xu et al., 2011) and is better regarded as a simulated or induced mild drought situation (Tardieu, 2012). It has been pointed out that under these conditions, an "opportunistic" or "risky" physiological strategy (maintaining photosynthesis and stomatal opening) allows the crop to take advantage of water pulses with a concomitant increased growth during periods of restricted water supply (Tardieu, 2012). This risky physiological response facilitates an effective use of water *vis a vis* water use efficiency

Abbreviations: ANOVA, analysis of variance; CIP, International Potato Center; Chl_{SPAD}, chlorophyll concentration measured by SPAD; DI, deficit irrigation; *E*, daily plant transpiration; FI, full irrigation; LHC, loss of half the maximum plant cover; MC, maximum plant cover; MTB, maximum tuber bulking; PRD, partial root-zone drying; RWC, relative water content; π, osmotic potential; ΣTT, accumulated thermal time.

* Corresponding author. Tel.: +51 1 3175312; fax: +51 1 317 5329.
E-mail address: d.ramirez@cgiar.org (D.A. Ramírez).

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(Blum, 2009) which is driven by drought avoidance mechanisms (stomatal closure) and penalizes plant yield. However, to test these recent paradigms appropriate crop phenotyping is required, which depends on the identification of key plant traits and the appropriate timing of their monitoring through crop phenology. Concerning the latter, accumulated thermal time (ΣTT) or daily temperature above a temperature threshold (degree days) during crop development (Wang, 1960), has been proven suitable for predicting crop phenological stages (McMaster and Wilhelm, 1997). In crops in which agronomical organs growth belowground, ΣTT represents a non-destructive method appropriated to predict rooting or tubertization stages as has been demonstrated in sweetpotato (*Ipomoea batatas* (L.) Lam.) (Villordon et al., 2009a,b, 2010) and potato (*Solanum tuberosum* L.) (Jefferies and MacKerron, 1987; Streck et al., 2007; but see De Paula et al., 2005). Although Streck et al. (2007) pointed out the importance of distinguishing cardinal temperatures (minimum, optimum and maximum) for each developmental phase when calculating thermal time in potato, this approach has not yet been used to determine when to carry out the phenotyping under water restriction in this crop.

The greenness degree measured through chlorophyll concentration, transmittance measurements (SPAD) or reflectance by remote sensing, is a plant trait frequently monitored under water stress to assess stay-green effect (delayed senescence) in some crops (Blum, 2009; Tuberosa, 2012). In potato, chlorophyll content has been used to assess the yield response to water restriction under PRD (Jensen et al., 2010; Yactayo et al., 2013) and correlated results were observed by the latter authors. As for osmotic potential (π), it is the main driver of water potential whose reduction leads to turgor loss, which in turn, is the major determinant of water stress in plants (Bartlett et al., 2012). Osmotic adjustment, which is considered as a drought tolerance mechanism (Nilsen and Orcutt, 1996), is caused by the accumulation of low-molecular organic substances driving osmotic intake of water into cell compartments (Larcher, 2003). Osmotic potential and relative water content (RWC) are used in osmotic adjustment estimation (Morgan, 1983, 1992) which highlights their importance in the assessment of crop response to water restriction. In this study we assessed the dynamics of three physiological traits (chlorophyll content, π and RWC) in a potato variety (UNICA) with lower drought susceptibility index than the average value of *S. tuberosum* landraces (Cabello et al., 2012) under two water saving techniques (deficit irrigation and PRD) in greenhouse and field conditions. Our objectives were to: —compare the temporal trend of physiological traits with tuber yield under water restriction; —identify the crop phase along the accumulated thermal time when a phenotyped trait shows the closest correspondence with final tuber yield.

2. Materials and methods

2.1. Study area and potato variety

Two trials were carried out at the International Potato Center (CIP) experimental station in Lima, Peru (12.1°S; 77.0°W, 244 m asl) located in a desert environment. The trials were conducted under greenhouse (September–December 2008) and field conditions (June–November 2009). The accumulated precipitation, minimum–maximum temperatures, monthly average atmospheric humidity and global radiation for the growth season during 2008 and 2009 were: 0.0 and 42.7 mm, 13.4–27.4 and 13.9–20.4 °C, 88.1 and 85.0%, and 15.7 and 10.7 MJ m^{-2} h^{-1}, respectively (CIP Meteorological Station, see details for the growing season during the field trial in Table 1). The variety studied was UNICA (CIP code No. 392797.22) an early material with good acclimation to warm and dry environments (Gutiérrez et al., 2007).

Table 1
Mean monthly values of meteorological variables during 2009 growth period (Source: CIP Meteorological Station).

	July	Aug.	Sept.	Oct.
Relative humidity (%)	85.6	85.4	85.5	83.4
Rainfall (mm)	10.0	18.0	8.0	2.0
Global Radiation (MJ m^{-2} h^{-1})	7.0	9.4	10.3	16.0
Maximal temperature (°C)	18.9	18.6	18.6	20.4
Minimal temperature (°C)	15.3	13.9	14.1	14.5
Mean temperature (°C)	17.1	16.3	16.3	17.5

2.2. Greenhouse trial experimental design

Tubers were planted in pots (5.8 l) filled with 1.2 kg of PRO-MIX (Premier Tech Horticulture, Canada), a humic soil substrate with a high water retention capacity (a field capacity of 30.8% of volumetric water content). At planting, each pot received 12 g of a mixture of granular fertilizers composed by urea (46% N), KCl (60% K_2O) and $(NH_4)_3PO_4$ (18% N and 46% P_2O_5) with a ratio of 2:1:2, respectively. In addition, 500 ml of a solution (1 g l^{-1}) (Peter fertilizer, Everris International B.V., Geldermalsen, The Netherlands) with 15% (N)–2% (P_2O_5)–20% (K_2O) was applied in each pot by three times, before the beginning of the water restriction period. A solution (1.33 g l^{-1}) of fungicide (Farmathe, Farmex S.A., Peru) was applied twice before the beginning of the treatments. Before the experiment each pot filled with dry PRO-MIX (DSW) was weighted and water was added until water saturation (when it began to drain). The weight of the pot at field capacity (FCW) was determined when water drainage stopped and the amount of water at field capacity was determined by subtracting FCW–DSW (~1800 g of water). The substrate was maintained at water saturated conditions until 28 days after planting. A completely randomized design with 5 replicates (pots) was used in this trial. At 28 days after planting two watering treatments (deficit irrigation—DI and partial root-zone drying—PRD) with three levels of daily water reposition each (60%, 45% and 30% of transpired water) were applied. The average volumetric water of the tested level of water reposition was: 19.4 ± 0.7%, 16.0 ± 0.8% and 10.5 ± 0.6% corresponding to 60%, 45% and 30% of transpired water, respectively. Full Irrigation (FI) with 100% of transpired water reposition was the control. The soil volume in the PRD pots were divided into two sections by a plastic membrane (1 mm thick), fixed to the pot with silicone to prevent water filtration from one side to another. After emergence all pots were covered with a plastic film to prevent evaporation from the soil. This cover was removed and replaced before and after irrigations. For FI, daily water supplied replaced the daily transpiration (E), which was calculated gravimetrically as the weight difference of potted plants during 24 h. The average E in plants belonging to FI treatments served as reference for the calculation of water needs of the plants assigned to DI and PRD treatments. However, if any plant transpired less than the average E of FI plants at a given date its own transpired water quantity was provided. The irrigation shift of each half-soil volume in the PRD treatments was carried out when the substrate was at 50% field capacity, determined gravimetrically from DSW and corrected with the dry weight of a substrate sample.

2.3. Field trial experimental design

The soil of the experimental field was a sandy loam (50, 32 and 18% of sand, silt and clay, respectively) with 19.7% of volumetric water content at field capacity, 1.4 g cm^{-3} of bulk density, 7.6 pH in water and 2.4 dS m^{-1} of electric conductivity (Laboratorio de Análisis de Suelos, Plantas, Aguas y Fertilizantes–Universidad Nacional Agraria La Molina, Lima, Peru). Fertilizers were applied with concentrations of 200, 140 and 160 kg ha^{-1} of N (urea), P (P_2O_5) and K (K_2O), respectively. A randomized complete block design with