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Defining biological thresholds associated to plant water status for monitoring water restriction effects: Stomatal conductance and photosynthesis recovery as key indicators in potato

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ABSTRACT

The definition of irrigation schedules depends on the understanding of the response of key plant traits to different water restriction characteristics with the aim to avoid physiological impairment. In this study, different timings (at tuber initiation and bulking) and intensities (four soil moisture levels) of water restriction were tested in the potato crop. The temporal patterns of mid-morning or maximum, light saturated stomatal conductance (g_{s_max}), recovery of net photosynthesis ($A_{recovery}$), stem water potential (Ψ_{stem}), carbon isotope discrimination in tubers (Δ_{tuber}), plant water concentration (*PWC*), photochemical reflectance index (*PRI*) and crop water stress index (*CWSI*) were analyzed. Early-severe water restriction caused a drastic yield reduction, with low recovery of physiological responses (g_{s_max}, Δ_{tuber}, Ψ_{stem}, *CWSI*, $A_{recovery}$) after 15 days of post-restriction irrigation and even a continued reduction of some of them (*PWC*, *PRI*). It also caused a prolonged g_{s_max} reduction below 0.05 mol H_2O m^{-2} s^{-1} ($\approx$5 µmol CO_2 m^{-2} s^{-1} of net photosynthesis) suggesting that this value defines a physiological severity threshold in potato, under which a metabolic impairment occurs. *CWSI* and *PRI* showed a close linear (R^2 = 0.76) and no linear (natural logarithm function, R^2 = 0.67) relationship with g_{s_max} respectively. In cloudless dry environments, irrigation schedules in potato should aim to avoiding *CWSI* values higher than 0.4, especially until before of maximum canopy cover establishment. A close relationship between $A_{recovery}$ at maximum stress moment and yield reduction was found. The strong relationship between the measured traits (except *PWC* and Ψ_{stem}) and final yield at maximum stress moment found in the present study warrants further research on drought phenotyping immediately before post-restriction irrigation or when the defined severity threshold in potato is reached.

1. Introduction

Potato, the fourth most important edible crop in the world (FAO, 2016) is expanding to drought prone areas affected by climate change (Monneveux et al., 2013). Because it has a high water requirement, which amounts to an estimated 3500–6500 m^3 ha^{-1} (Sood and Singh, 2003), strategies for saving water while maintaining yields are needed. Several irrigation techniques such as deficit irrigation, partial root-zone drying and drip irrigation conserve water and increase water use efficiency with no significant yield reduction compared to conventional, water wasteful irrigation methods (Erdem et al., 2006; Liu et al., 2006; Sasani et al., 2006; Shahnazari et al., 2007, 2008; Saeed et al., 2008; Kumar et al.,

Abbreviations: A_n, net photosynthesis; A_{max}, Average maximum net photosynthesis; $A_{recovery}$, Recovery of net photosynthesis; *D*, duration of irrigation; DAP, days after planting; *CWSI*, crop water stress index; g_s, stomatal conductance; g_{s_max}, maximum light-saturated stomatal conductance; *IWQ*, irrigated water quantity; *PRI*, photochemical reflectance index; *PWC*, plant water concentration; T_{canopy}, Canopy temperature; T_{dry}, dry temperature (7 °C over the dry bulb temperature); T_{wet}, wet artificial reference surface temperature; VPD, vapour pressure deficit; Δ_{tuber}, carbon isotope discrimination in tubers; Ψ_{stem}, stem water potential; θ_v, soil volumetric water content; θ_{vT}, the target θ_v established for each treatment.

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2009; Ahmadi et al., 2010; Jensen et al., 2010; Jovanovic et al., 2010; Ati et al., 2012; Xie et al., 2012; Yactayo et al., 2013). In general, soil-based water content methods (potential evapotranspiration, pan evaporation, soil moisture or tensiometers) are used for determining irrigation schedules. However, using physiological descriptors of plant water status for a more precise definition of optimal irrigation timing has been suggested (Medici et al., 2014). Since mid-morning or maximum, light-saturated stomatal conductance (g_{s_max}) response integrates a complex interaction between internal and external plant factors (Medrano et al., 2002), Flexas et al. (2004) postulated that this trait is a more appropriate indicator of water stress intensity than either leaf potential or relative water content. Thus, g_{s_max} values between 0.1 and 0.15 mol H_2O m^{-2} s^{-1} have been proposed as an optimum threshold at which to irrigate the crop (Flexas et al., 2004, 2006). Highly variable physiological traits have been used as indicators of plant water status for managing irrigation in potato (Byrd et al., 2014; Zakaluk and Ranjan, 2006; Zakaluk and Sri Ranjan, 2008; Rud et al., 2014) but assessing g_{s_max} for scheduling irrigation in this crop is still a pending issue.

Photosynthesis recovery after an irrigation pulse is another physiological descriptor that has been proposed for monitoring water demand by the crop (Flexas et al., 2004, 2006, 2012). However, photosynthesis recovery depends on the timing, duration and intensity of water restriction before the water pulse (Xu et al., 2010). In potato, carbon isotope discrimination measured in tubers (Δ_{tuber}) is an integrative trait that reflects photosynthetic carbon balance over time (Jefferies and MacKerron, 1997) and it has proven to be useful for assessing the physiological performance of potato under both well-watered and water restriction conditions (Ramírez et al., 2015a). As the relationship between g_{s_max} thresholds and the recovery of photosynthesis (Flexas et al., 2004) is not thoroughly studied, Δ_{tuber} is so far the most reliable indicator of physiological processes affected by water restriction and the way for maximizing potato water use efficiency.

Canopy temperature (T_{canopy}), detected by proximal sensing methods has been proposed to analyse drought tolerance in potato (Stark et al., 1991; Prashar et al., 2013). On the other hand, T_{canopy}-based Crop Water Stress Index (*CWSI*) closely correlates with stomatal conductance, a key trait affected by the water status of the plant (Rud et al., 2014). The water restriction effect on potato depends on its timing, intensity and duration and their combination (Jefferies, 1995), thus severe water restriction can negatively affect tuber yield if it occurs just before or during tuber initiation (Mackerron and Jefferies, 1986; Monneveux et al., 2013) or bulking (Van Loon, 1981). In this study, the effects of the timing (water restriction starting at tuber initiation and bulking) and intensity (from well-irrigated to no watered plants) of water stress on physiological traits (g_{s_max}, Ψ_{stem}, Δ_{tuber}, plant water content) commonly used to test drought effects in potato, and their relationship with indexes based on proximal sensed T_{canopy} and reflectance were assessed. The study was carried out in a desert area to avoid the interfering effect of rainfall. The planted variety was UNICA, previously used to test irrigation techniques (Yactayo et al., 2013) and drought tolerance in potato (Ramírez et al., 2014, 2015a, 2015b; Rolando et al., 2015). The objectives of the study were to: i) define a threshold value of a plant physiological trait that indicates water restriction but at a level that precludes physiological impairment and yield reduction, ii) compare the reliability of the identified physiological trait with proximal sensed indexes as indicators for monitoring plant water status, and iii) analyse photosynthesis recovery after early drought and its relationship with yield. As metabolic impairment has been observed in crops other than potato when g_{s_max} drops below 0.05 mol H_2O m^{-2} s^{-1} (Flexas et al., 2004, 2006), it is hypothesized that this value could represent a physiological threshold in potato, which if surpassed during sensitive phenological stages, no recovery of plant water status and photosynthesis will occur, leading to a subsequent tuber yield reduction.

2. Materials and methods

2.1. Study area and plant material

The field trial was carried out at the "Santa Rita de Siguas" Experimental Station from September to December 2014. The station, owned by the Peruvian National Institute of Agrarian Innovation, is located in the Arequipa Region – Southern Peru (16° 29.6′S, 72° 05.7′W, 1292 m.a.s.l.)- in a desert area on the western flanks of the Andes. The area has an average yearly precipitation and monthly air temperature of 0 mm $year^{-1}$ and 17.7 ± 1.4 °C respectively, with maximum (27.6 ± 0.48 °C) and minimum (10.0 ± 0.34 °C) monthly temperatures during November and July, respectively (data for 2011–2014, from La Joya Meteorological Station, 16° 35′ 33″S, 71° 55′ 9″W). During the trial, the average air temperature, global solar radiation, relative atmospheric humidity and vapour pressure deficit (VPD) were 19.1 ± 0.16 °C, 26.04 ± 0.24 MJ m^{-2} day^{-1}, 49.7 ± 1.36% and 1.14 ± 0.08 kPa respectively (data recorded with a HOBO U12 Outdoor/Industrial Model and Silicon pyranometer sensor S-LIB-M003 Model, Onset Computer Corporation, Bourne, MA, USA, see details in Table 1). The maximum hourly VPD recorded ranged between 3.3 and 4.4 kPa. The textural soil class was loamy sand (880 g kg^{-1} of sand and 60 g kg^{-1} of clay and silt) with 4.35 ± 0.17 dS m^{-1}, 0.65 ± 0.03%, 1.61 g cm^{-3} and 0.14 m^3 m^{-3} average water electrical conductivity, soil organic matter content, soil bulk density and volumetric water content (θ_v) at field capacity, respectively. The planted potato variety was UNICA (CIP code: 392797.22), a genotype adapted to the Peruvian coast drylands with resistance to virus and heat, and slightly tolerant to salinity (Gutiérrez-Rosales et al., 2007).

2.2. Experimental design

A randomized complete block design, with 7 treatments repeated in 4 blocks was used. The factorial treatments included two water restriction timings (early and late) and three intensity levels (low, medium, severe) along with one fully irrigated control. Each plot (14.0 m × 3.2 m) contained 120 plants sown at a distance of 0.38 m in-row spacing and 0.80 m between rows. Plots were further sectioned into 6 sub-plots (3.2 m × 1.5 m) for sequential plant samplings throughout the season. Each sub-plot was comprised of five plants in each of four rows, for a total of 20 plants. The cen-

Table 1
Environmental conditions during the experimental period 2014. Average daily values ± standard error. VPD = Vapour pressure deficit.

	September	October	November	December
Minimum Temperature (°C)	11.1 ± 0.43	11.5 ± 0.35	10.6 ± 0.43	11.5 ± 0.29
Maximum Temperature (°C)	26.3 ± 0.77	27.7 ± 0.41	26.9 ± 0.28	26.8 ± 0.37
Average Temperature (°C)	18.7 ± 0.46	19.6 ± 0.30	18.8 ± 0.29	19.1 ± 0.28
Average Relative Humidity (%)	45.3 ± 3.10	39.3 ± 2.11	53.6 ± 2.31	58.9 ± 2.02
Global Solar Radiation (MJ m^2 d^{-1})	23.1 ± 0.81	25.8 ± 0.29	27.3 ± 0.29	26.8 ± 0.32
Average VPD (kPa)	1.21 ± 0.09	1.41 ± 0.07	1.03 ± 0.06	0.93 ± 0.05
Maximum VPD recorded (kPa)	3.59	4.14	3.27	3.26