

Transpiration and leaf growth of potato clones in response to soil water deficit

André Trevisan de Souza, Nereu Augusto Streck*, Arno Bernardo Heldwein, Dilson Antonio Bisognin, José Eduardo Minussi Winck, Thiago Schmitz Marques da Rocha, Alencar Junior Zanon

Federal University of Santa Maria/CCR – Dept. of Plant Science, Av. Rorâima, 1000, Prédio 77 – 97105-900 – Santa Maria, RS – Brazil.

*Corresponding author <nstreck2@yahoo.com.br>

Edited by: Gerrit Hoogenboom

Received May 29, 2013

Accepted December 05, 2013

ABSTRACT: Potato (*Solanum tuberosum* ssp. *Tuberosum*) crop is particularly susceptible to water deficit because of its small and shallow root system. The fraction of transpirable soil water (FTSW) approach has been widely used in the evaluation of plant responses to water deficit in different crops. The FTSW 34 threshold (when stomatal closure starts) is a trait of particular interest because it is an indicator of tolerance to water deficit. The FTSW threshold for decline in transpiration and leaf growth was evaluated in a drying soil to identify potato clones tolerant to water deficit. Two greenhouse experiments were carried out in pots, with three advanced clones and the cultivar Asterix. The FTSW, transpiration and leaf growth were measured on a daily basis, during the period of soil drying. FTSW was an efficient method to separate potato clones with regard to their response to water deficit. The advanced clones SMINIA 02106-11 and SMINIA 00017-6 are more tolerant to soil water deficit than the cultivar Asterix, and the clone SMINIA 793101-3 is more tolerant only under high solar radiation.

Introduction

The shortage of water in the soil has been, for a long time, the environmental factor that most limits crop yield worldwide (Oliveira et al., 1982; Shao et al., 2008). Potato (*Solanum tuberosum* ssp. *Tuberosum*) crop is particularly susceptible to soil water deficit because of its small and shallow root system (Weisz et al., 1994).

The fraction of transpirable soil water (FTSW) approach has been widely used for the evaluation of plant response to water deficit (Bindi et al., 2005; Davatgar et al., 2009; Muchow and Sinclair, 1991; Ray and Sinclair, 1997). The FTSW threshold indicates the timing of stomatal closure in response to soil water deficit (Ray and Sinclair, 1997; Sinclair and Ludlow, 1986) and the degree of tolerance to water deficit. Genotypes with delayed wilting during a soil drying cycle have a high FTSW threshold (Devi et al., 2009). The FTSW threshold has been determined for many annual agricultural crops (Amir and Sinclair, 1991; Davatgar et al., 2009; Devi et al., 2009; Gholipour et al., 2012; Lecoeur and Sinclair, 1996; Muchow and Sinclair, 1991; Ray and Sinclair, 1997; Sinclair and Ludlow, 1986), some perennial fruit crops, grapevine (*Vitis vinifera*) (Bindi et al., 2005), and some forest crops, *Eucalyptus grandis* and *Eucalyptus saligna* (Martins et al., 2008). Recently, researchers have shown genetic variations in FTSW threshold among cultivars of the same crop, such as soybean (*Glycine max*) (Hufstetler et al., 2007), peanut (*Arachis hypogaea*) (Devi et al., 2009), pearl millet (*Pennisetum glaucum*) (Kholova et al., 2010) and sorghum (*Sorghum bicolor*) (Gholipour et al., 2012).

The response of plant transpiration and growth parameters to FTSW has been previously studied for two potato cultivars in the Netherlands (Weisz et al., 1994) and two cultivars in Brazil (Lago et al., 2012). New potato clones are released almost annually and some of them were recently introduced in the State of Rio Grande do

Sul - RS (Bisognin et al., 2008), South Brazil, but their response to water deficit is unknown. Because there has been an increasing frequency of years with rainfall below normal in the first decade of this century in southern Brazil (Streck et al., 2009), an important step is to identify, from the already developed potato clones, those with a difference in the threshold fraction of transpirable water (FTSW).

The objective of this study was to evaluate the FTSW threshold for decline in transpiration and leaf growth in a drying soil to identify potato clones tolerant to water deficit.

Materials and Methods

Two greenhouse experiments (Experiment one – E1 and Experiment two – E2) were conducted in Santa Maria, RS, Brazil (29°43' S; 53°43' W; 95 m a.s.l.) during 2010 and 2011. The greenhouse was covered with double polycarbonate plates that have a transmissivity to incoming solar radiation of about 80 %. An automatic maximum temperature control system, was set at 32 °C, and the minimum temperature was not controlled.

The experiments were conducted in 8 L (24-cm diameter × 23-cm tall) plastic pots in the spring, planting starting on 08 Sept 2010 (E1), and in the fall, on 01 Apr 2011 (E2). The experimental design was completely randomized, with two treatments: irrigation (T1) and no irrigation (T2), and ten replicates (one pot with one plant)

Four potato genotypes were selected for this study based on the results of Bisognin et al. (2008) for genotype differences adapted to subtropical environments: cultivar Asterix and the advanced clones SMINIA 793101-3, SMINIA 00017-6 and SMINIA 02106-11. Asterix is an old cultivar developed in Europe, and currently extensively grown in south Brazil. The advanced clones SMINIA 793101-3 and SMINIA 00017-6 have good processing

quality, adaptation and high tuber yield in subtropical environments, and advanced clone SMINIA 02106-11 is adapted to temperate and subtropical environments (Bisognin et al., 2008). In a previous study, the advanced clone SMINIA 793101-3 was identified by Lago et al. (2012) as being tolerant to water deficit as compared with the Macaca, an old cultivar also used in South Brazil, and was, therefore, used in this study as a reference clone with tolerance to water stress. The response of the other genotypes to a drying soil is unknown.

The pots were painted white to reduce absorption of solar radiation by the outer walls, filled with A horizon soil samples of a Hapludalf, and placed on a 70 cm high bench. Soil contained 28 g kg⁻¹ organic matter, 0.092 mg g⁻¹ K, and 0.0084 mg g⁻¹ P using sodium dichromate (for organic matter) and Mehlich-1 (for K and P) extractors, respectively. The correction of soil nutrients and acidity was made according to soil analysis and local recommendations for potato. NPK rates applied were 0.56, 0.80 and 0.88 g per pot of N, P and K, respectively.

The seed tubers had high physiological and sanitary quality, with a diameter of about 30 mm. One tuber was planted per pot and the first sprout that emerged on the soil surface was regarded as the main stem, while the other sprouts were eliminated as soon as they emerged to standardize one stem (plant) per pot. All pots were maintained in a well-watered condition until the start of the experiment (Sinclair and Ludlow, 1986; Lago et al., 2012).

From a total of 40 pots planted with each clone, a selection was made of 20 pots per clone (to reduce plant variability), ten of them were used as control (T1), in which water deficit was not applied, and ten pots in which water deficit was applied (T2). In addition to the pots with plants, there were also six pots kept without plants, three of them had the evaporated water replenished (after weighing pots every day, see details below) whereas in the other three pots water was not replenished. The daily mean values of water lost by evaporation from the pots without plants were subtracted from the pots in T1 and T2, respectively, in order to ascertain the water lost by evaporation from the pots with plants, and, therefore, quantify plant transpiration only.

The soil drying experiment followed the protocol originally described by Sinclair and Ludlow (1986) that has been widely used in other studies (Muchow and Sinclair, 1991; Ray and Sinclair, 1997; Devi et al., 2009; Gholipoor et al., 2012). Prior to the application of water deficit, all pots were saturated with water (Sinclair and Ludlow, 1986; Ray and Sinclair, 1997) and allowed to drain for 23 h (Lago et al., 2012), when soil was assumed to be at field capacity. On completing the 23 h after saturation, all pots (with plant and with no plants) were covered with a white opaque plastic film, and the initial weight of each pot was determined. This day was the onset of the experiments (05 Oct 2010 in E1 and 03 May 2011 in E2). Thereafter, the water deficit was ap-

plied in the T2 pots, which were irrigated no further until the end of the experiment when transpiration of the plants in T2 was 10 % or lower as compared with plants in T1 (Sinclair and Ludlow, 1986; Muchow and Sinclair, 1991). Water deficit was applied when plants had nine to twelve leaves on the main stem (Weisz et al., 1994; Lago et al., 2012). The dehydration of the soil was slow and there was thus no need to add water to the drying pots, as is sometimes reported in experiments that use this protocol (Devi et al., 2009; Gholipoor et al., 2012).

Every day, starting at 16h00, all pots were weighed on an electronic scale with a capacity of 50 kg and an accuracy of 5 g. After the weighing, each pot in T1 was irrigated with the amount of water that had been transpired by the plant since the previous day, as determined by the difference between the weight of the pot on that specific day and the initial weight (Sinclair and Ludlow, 1986; Muchow and Sinclair, 1991).

Daily minimum and maximum air temperatures were measured during the two experiments inside a shelter located in the middle of the experiment. In the second experiment, the air vapor pressure deficit (DPV) was also measured daily at 15h00 with a psychrometer. Incoming solar radiation inside the greenhouse during the two experiments was estimated from solar radiation measured at a weather station located approximately 300 m from the greenhouse multiplied by a factor of 0.8.

The relative transpiration (TR) was calculated by the equation (Sinclair and Ludlow, 1986):

$$TR = \frac{MT2_j - MT2_{(j-1)}}{[\sum(MT1_j - MT1_{(j-1)})] / n} \quad (1)$$

where MT2 is the mass of each pot in T2 (g per pot), MT1 the mass of each pot T1 (g per pot), 'j' refers to the day, and 'n' represents the number of replicates (plants) in T1.

The experiments finished when all plants in T2 presented TR ≤ 0.1 (10 %), as recommended by the original protocol, assuming that below this rate of transpiration the stomata are closed and the water loss is due only to the epidermal conductance (Sinclair and Ludlow, 1986; Muchow and Sinclair, 1991). The final mass was the weight of the pot when TR ≤ 0.1.

After the end of each experiment, the FTSW for each T2 pot was calculated, each day, by the equation (Sinclair and Ludlow, 1986):

$$FTSW = \frac{MT2_j - MT2_{end}}{MT2_{initial} - MT2_{end}} \quad (2)$$

where MT2 is the mass of each pot in T2 (g per pot), 'j' refers to the day, 'initial' indicates MT2 on the starting day of the application of water deficit (beginning of the experiment) and 'end' indicates MT2 on the last day of the experiment.

Leaf area (LA) was determined daily throughout the experiment by measuring the longest length (L) and the largest width (W) of the apical leaflet of each leaf on the plant. The LA of each leaflet was calculated multiplying the length and width by a shape factor: LA = 0.7067*L*W ($r^2=0.994$), LA = 0.7189*L*W ($r^2 = 0.996$), LA = 0.6978*L*W ($r^2 = 0.994$) and LA = 0.7026*L*W ($r^2 = 0.993$), respectively, for clones SMINIA 00017-6, SMINIA 02106-11, SMINIA 793101-3 and Asterix. The shape factor for each clone was estimated using simple linear regression between L*W and the measured area (scanned and digitally measured) of 60 individual leaflets.

The LA of all leaflets was summed for each plant on each day and the daily relative leaf growth (LGR) for each clone was calculated by:

$$LGR = \frac{LAT2_j - LAT2_{j-1}}{[\sum(LAT1_j - LAT1_{j-1})] / n} \quad (3)$$

where LAT2 is the leaf area of all leaflets measured on each plant in T2 (cm² per plant), LAT1 is the leaf area of all leaflets measured on each plant in T1 (cm² per plant), 'j' refers to the day and 'n' represents the number of replications (plants) in T1.

The amount of water, in liters, necessary for the production of 1 kg of biomass (L kg⁻¹) of dry mass, is the coefficient of transpiration (CT), which is an indicator of the efficiency of the use of water by plants (Hsiao and Acevedo, 1974). Three plants of each clone for each experiment prior to application of water deficit and all plants at the end of the experiments were sampled and oven dried at 60 °C to determine the initial and final total dry biomass and root dry biomass. CT was determined by:

$$CT = \frac{TT}{BF - BI} \quad (4)$$

where TT is the total transpiration (L per plant), BF is the final total dry biomass (kg per plant) and BI is the initial total dry biomass (kg per plant).

The variables transpiration and leaf growth were subjected to two normalizations (Sinclair and Ludlow, 1986; Ray and Sinclair, 1997). The first normalization was the application of equations 1 and 3 to TR and LGR, respectively, so that TR and LGR varied from zero to one and enabled large daily environmental variations during the experimental periods to be minimized. The second normalization aimed to reduce variations between plants caused mainly by differences in plant size. For the second normalization, TR and LGR of individual plants were divided by the mean of TR and LGR before water stress developed in the soil for each plant, i.e. while FTSW was equal to or greater than 0.5 (Lago et al., 2012), as recommended by the protocol (Devi et al., 2009; Gholipour et al., 2012), resulting in the NTR and NLGR variables.

The NTR and NLGR data (after the second normalization) were fitted to the logistic-type equation $Y =$

$1/\{1 + \exp[-a(X - b)]\}$ (Sinclair and Ludlow, 1986; Ray and Sinclair, 1997), where Y is the dependent variable (NTR and NLGR), X is FTSW and "a" and "b" are empirical coefficients estimated by nonlinear regression analysis. As an indicator of tolerance to soil water deficit, the value of the FTSW threshold for NTR and NLGR was estimated as the value of FTSW when the NTR or NLGR from the logistic equation equaled 0.95 (Lago et al., 2012). This approach is similar to the two-segment linear regression approach used by Devi et al. (2009) and Gholipour et al. (2012).

The variables total transpiration (total water extracted by plants during the experiment, in g per plant), CT (L kg⁻¹ dry mass) and FTSW threshold for NTR and NLGR were analyzed according to a 4 × 2 factorial scheme with each plant being a replicate, A factors were the clones (four levels) and B factors were the soil water regime treatments (two levels = irrigated and non-irrigated). These data were subjected to analysis of variance (ANOVA) and means were compared by the Tukey test at 5 % probability of type I error. Normality of the data was tested with the Shapiro-Wilk test before performing ANOVA.

Results and Discussion

The maximum daily air temperature varied little during the experimental period, mainly in E1, due to the control system of the greenhouse that was set to 32 °C, while the daily minimum air temperature varied considerably (Figure 1A). The minimum temperatures varied from 9.2 to 20.0 °C in E1 and from 4.0 to 19.6 °C in E2, and the maximum temperatures varied from 26.4 to 32.0 °C in E1 and from 21.7 to 31.6 °C in E2.

The vapor pressure deficit (DPV) at 15h00 in E2 ranged from 1.0 to 4.6 hPa (Figure 1B), which is in the very low VPD range (below 15 hPa, Kiniry et al., 1998), indicating that the plants grew and developed in an atmosphere of low evaporative demand. The low levels of VPD in the afternoon are due to the maximum temperature control system in the greenhouse which, upon reaching the maximum temperature of 32 °C, flipped on a ventilation system that forced air to pass through a wall of soaked expanded clay, forcing moist air into the greenhouse. Even though not measured, similar afternoon VPDs are expected to occur during E1 because during this experiment the fan system turned on even more often than during E2 due to higher solar radiation and longer days during E1 as compared with E2 (Figure 1C). The meteorological conditions (temperature, photoperiod and solar radiation) during E1 and during E2 (Figure 1) are typical of field conditions when potato is grown during spring and fall, respectively, in this region (Bisognin et al., 2008).

Potato plant development is mainly driven by temperature (Streck et al., 2007). Due to higher minimum temperatures in E1 than E2 (Figure 1A), the length of the first experiment was shorter (24, 23, 23 and 25 days)

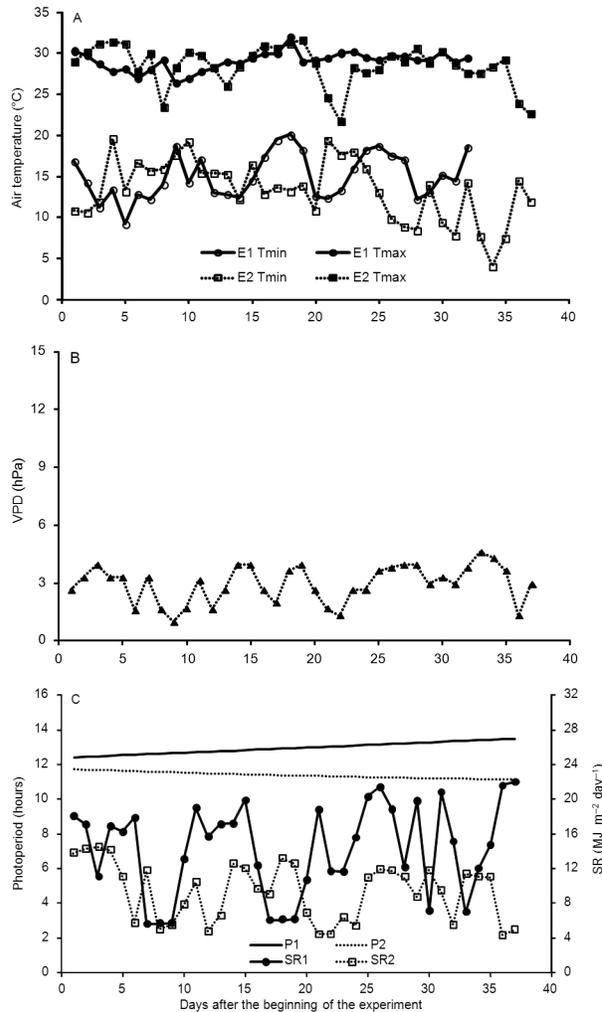


Figure 1 – (A) Daily minimum (Tmin) and maximum (Tmax) air temperatures during the two experiments (E1 and E2), (B) daily air vapor pressure deficit (VPD) at 3 p. m. during the second experiment (E2) and (C) photoperiod (P) and solar radiation (SR) during the two experiments (E1 and E2). Santa Maria, RS, Brazil, 2010-2011. Each experiment began the day after soil in the pots was water saturated.

than in the second experiment (32, 35, 36 and 33 days for clones SMINIA 02106-11, SMINIA 00017-6, SMINIA 793101-3 and Asterix, respectively).

For the transpiration and coefficient of transpiration (CT) variables there were no significant clone x soil water regime interactions (Table 1). There was no difference in total transpiration among clones, and plants without water deficit had higher transpiration than plants with water deficit, as expected. The coefficient of transpiration was lower in plants with water deficit in both experiments, indicating higher water use efficiency when plants were subjected to a drying soil. Among the clones, no differences were found in coefficient of transpiration when T1 and T2 values were

plotted, as indicated by ANOVA (interaction clones x soil water regimes was not significant). Looking at the CT values only in T2 (Table 1) clones SMINIA 00017-6 and SMINIA 793101-3 had lower CT than cultivar Asterix, indicating that these two clones are more water use efficient.

The small differences in CT among clones (Table 1) are probably due to the short period of water deficit (10 to 13 days) beyond the FTSW threshold. Defense mechanisms against water deficit in the long term such as increased root growth and leaf senescence need more time to act, the stomatal closure being the most effective mechanism to defend the plant from water deficit in the short term (Sinclair and Ludlow, 1986; Lago et al., 2011). In both experiments E1 and E2, dry root matter did not differ between irrigated and non-irrigated treatments (Table 1) and no leaf senescence was observed in non-irrigated plants, indicating that long-term defense mechanisms against soil water shortage were not activated in the plants.

The response of NTR to FTSW for the four potato clones in both experiments is shown in Figure 2. The variability of the data is high, especially in the FTSW range between 0.5 and 1.0, a common feature in experiments using the FTSW approach with other crops (Sinclair and Ludlow 1986; Ray and Sinclair, 1997; Sinclair et al., 2005; Wahbi and Sinclair, 2007; Martins et al., 2008). The lower the air temperature, solar radiation and VPD, the greater the variability of the NTR data (Lago et al., 2011).

Besides the variability in the data, the logistic equation described well the NTR response to the FTSW for the different clones and experiments (Figure 2). As FTSW decreases, the NTR varied around the maximum value, and after reaching an FTSW threshold, the NTR started to decrease due to stomatal closure (Ludlow and Sinclair, 1986), one of the key defense mechanisms that the plant uses to protect from soil water deficit in the short term (Taiz and Zeiger, 2006). Variability of the data was lower in the range of FTSW values between zero and 0.4, indicating that the response of NTR to FTSW in the range that causes stomata closure is well defined, even in a low VPD atmosphere. Therefore, the lower variability of the data at low FTSW indicates that the approach of using the FTSW threshold as an indicator for tolerance to water shortage is appropriate.

The FTSW threshold for NTR was higher in the spring experiment (E1) than in the fall experiment (E2) for all clones (Figure 2). The main hypothesis for the lower FTSW threshold in E2 was the lower availability of solar radiation this time of year, resulting in lower potential transpiration, as compared to E1, as plants in E2 took about 10 days longer to extract the water from the pots (duration of the experiment was, on the average of the four genotypes, 23 days and 33 days in E1 and E2, respectively).

Among the potato clones, in E1 the lowest FTSW threshold for NTR was for Asterix (0.28) and the highest for SMINIA 02106-11, SMINIA 00017-6 and SMINIA

Table 1 – Total transpiration, coefficient of transpiration and roots dry matter of potato clones SMINIA 02106-11, SMINIA 00017-6, SMINIA 793101-3 and cultivar Asterix, grown in treatments without water deficit (T1) and with water deficit (T2), in two experiments (E1 = water deficit started on 05 Oct 2010, E2 = 03 May 2011). Santa Maria, RS, Brazil, 2010-2011.

Genotype	E1			E2		
	T1	T2	Mean	T1	T2	Mean
	Transpiration (g per plant)					
SMINIA 02106-11	3678	1774	2726 A ⁽¹⁾	2732	1968	2350 A
SMINIA 00017-6	2942	1769	2356 A	3467	1901	2684 A
SMINIA 793101-3	3128	1747	2438 A	2677	1909	2293 A
Asterix	3614	1752	2683 A	2657	1864	2262 A
Mean	3341 a	1761 b		2883 a	1911 b	
CV (%)	18			28		
	Coefficient of transpiration (L kg ⁻¹ dry matter)					
SMINIA 02106-11	204	194	199 A	215	182	199 A
SMINIA 00017-6	197	162	180 A	174	161	168 A
SMINIA 793101-3	195	165	180 A	178	155	167 A
Asterix	215	179	197 A	174	179	177 A
Mean	203 a	175 b		186 a	164 b	
CV (%)	18			16		
	Roots dry matter (g per plant)					
SMINIA 02106-11	5.7	4.7	5.2 A	1.3	1.4	1.3 A
SMINIA 00017-6	4.8	4.6	4.7 A	1.6	1.4	1.5 A
SMINIA 793101-3	5.1	5.1	5.1 A	1.1	1.4	1.3 A
Asterix	6.5	5.7	6.1 A	0.6	1.0	0.7 B
Mean	5.5 a	5.0 a		1.1 a	1.3 a	
CV (%)	39			32		

¹Means followed by the same lowercase letters in rows and uppercase letters in columns are not differ (Tukey test, $p < 0.05$). CV = coefficient of variation.

793101-3 (0.34, 0.37 and 0.41) respectively, and in E2 the lowest FTSW threshold was for SMINIA 793101-3 (0.19), followed by Asterix (0.24), SMINIA 00017-6 (0.26) and SMINIA 02106-11 (0.28). The range of FTSW threshold values in this study (0.19 to 0.41) is slightly greater than the range of values found in other studies on potato, such as found in Weisz et al. (1994) (from 0.20 to 0.35) for cultivars BelRus and Katahdin, respectively, and overlaps partially the range reported by Lago et al. (2012) of 0.28 to 0.49 for the Macaca cultivar and for advanced clone SMINIA 793101-3, respectively. The advanced clone SMINIA 793101-3 had the highest FTSW threshold in E1 (Figure 2E) and the lowest FTSW threshold in E2 (Figure 2F).

The response of NLGR to FTSW for the four potato clones in both experiments is shown in Figure 3. The variability of the data is greater than in Figure 2. In previous studies with other crops, the leaf growth response to FTSW also had greater variability than the relative transpiration (Muchow and Sinclair, 1991; Lago et al., 2011). The FTSW threshold was higher in E1 than in E2, except for the cultivar Asterix. In E1, FTSW threshold for NLGR was the greatest for clone SMINIA 00017-6 (0.80) (Figure 3C) and the lowest for cultivar Asterix (0.31) (Figure 3G) whereas in E2 the lowest FTSW threshold was for clones SMINIA 02106-11 and SMINIA 793101-3 (0.29) (Figure 3B, 3F), followed by clone SMINIA 00017-6 (0.37) (Figure 3) and cultivar Asterix (0.88) (Figure 3H). The range of FTSW threshold values ob-

tained here (0.29-0.88) is higher than the range reported by Lago et al. (2012), from 0.29 to 0.49, and includes the 0.6 value obtained by Weisz et al. (1994), with clones adapted to temperate environments.

The NLGR began to decrease before (at a higher FTSW, Figure 3) NTR (at a lower FTSW, Figure 2), for all clones in both experiments except for the clone SMINIA 02106-11 in E1 (Figure 3A). This anticipation of the reduction in leaf growth compared to the reduction in transpiration in a drying soil indicates a passive hydraulic response of potato leaves to water deficit. A decrease in leaf cell turgor led to the activation of the stomatal closure mechanism, thus causing a reduction in leaf cell division and expansion and, consequently, reducing leaf growth (Marenco and Lopes, 2005; Taiz and Zeiger, 2006).

Tolerance to water deficit is a genotype-dependent trait. In a previous study, Lago et al. (2012) found a higher tolerance to soil water deficit in the clone SMINIA 793101-3, when compared with Macaca, an old cultivar but still widely used by potato producers in Rio Grande do Sul. In this study, the clone SMINIA 793101-3 had the highest FTSW threshold in E1 (Figure 3E), confirming results of Lago et al. (2012), but it had the lowest FTSW threshold in E2 (Figure 3F), which does not agree with results reported by Lago et al. (2012). In E2 solar radiation was lower than in E1 (figure 1C), typical of the fall weather in this location and it took more time for plants for depleting soil water than in E1.

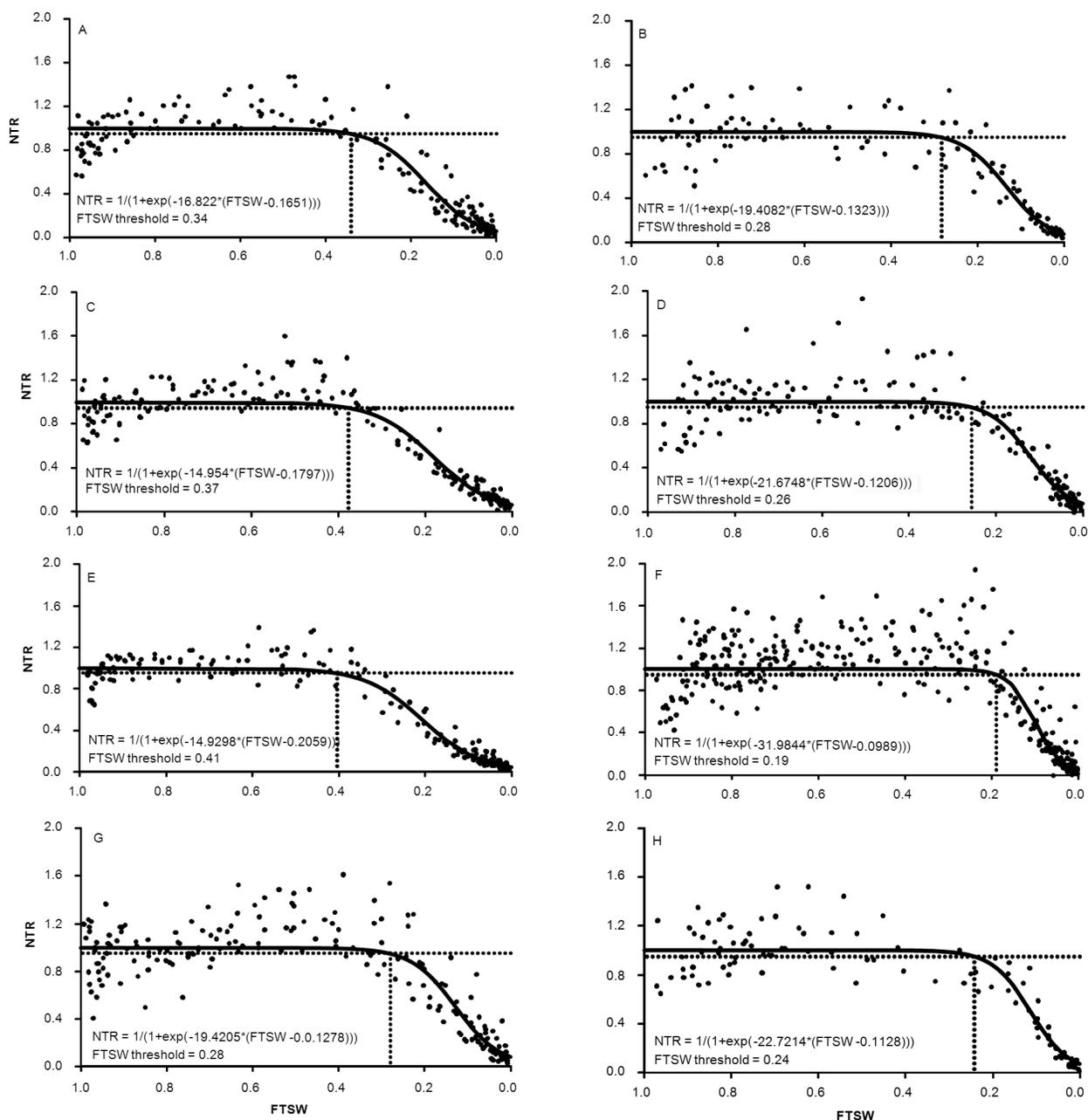


Figure 2 – Normalized relative transpiration (NTR) as a function of fraction of transpirable soil water (FTSW) for potato clones SMINIA 02106-11 (A, B), SMINIA 00017-6 (C, D), SMINIA 793101-3 (E, F) and cultivar Asterix (G, H) grown in a greenhouse in two experiments: E1 = water deficit started on 05 Oct 2010 (A, C, E, G), E2 = water deficit started on 03 May 2011 (B, D, F, H). Santa Maria, RS, Brazil, 2010-2011. Threshold FTSW: fraction of transpirable soil water when the NTR starts to decrease due to stomatal closure.

Lago et al. (2012) also found a lower FTSW threshold (0.33) for the clone SMINIA 793101-3 when the experiment was conducted in the fall (average solar radiation was $8.6 \text{ MJ m}^{-2} \text{ day}^{-1}$) as compared with the FTSW threshold (0.49) when their experiment was conducted in the spring (average solar radiation was $16.1 \text{ MJ m}^{-2} \text{ day}^{-1}$). Therefore, results from our experiments and those from Lago et al. (2012) consistently indicate that

when clone SMINIA 793101-3 grows under high solar radiation, stomata close at a higher FTSW whereas when it grows under low solar radiation, stomata close at a much lower FTSW than other clones.

Gholipour et al. (2012) evaluated sixteen sorghum genotypes and identified two groups of hypothesized traits: one group exhibited high FTSW thresholds for conserving water in a soil drying cycle, while another

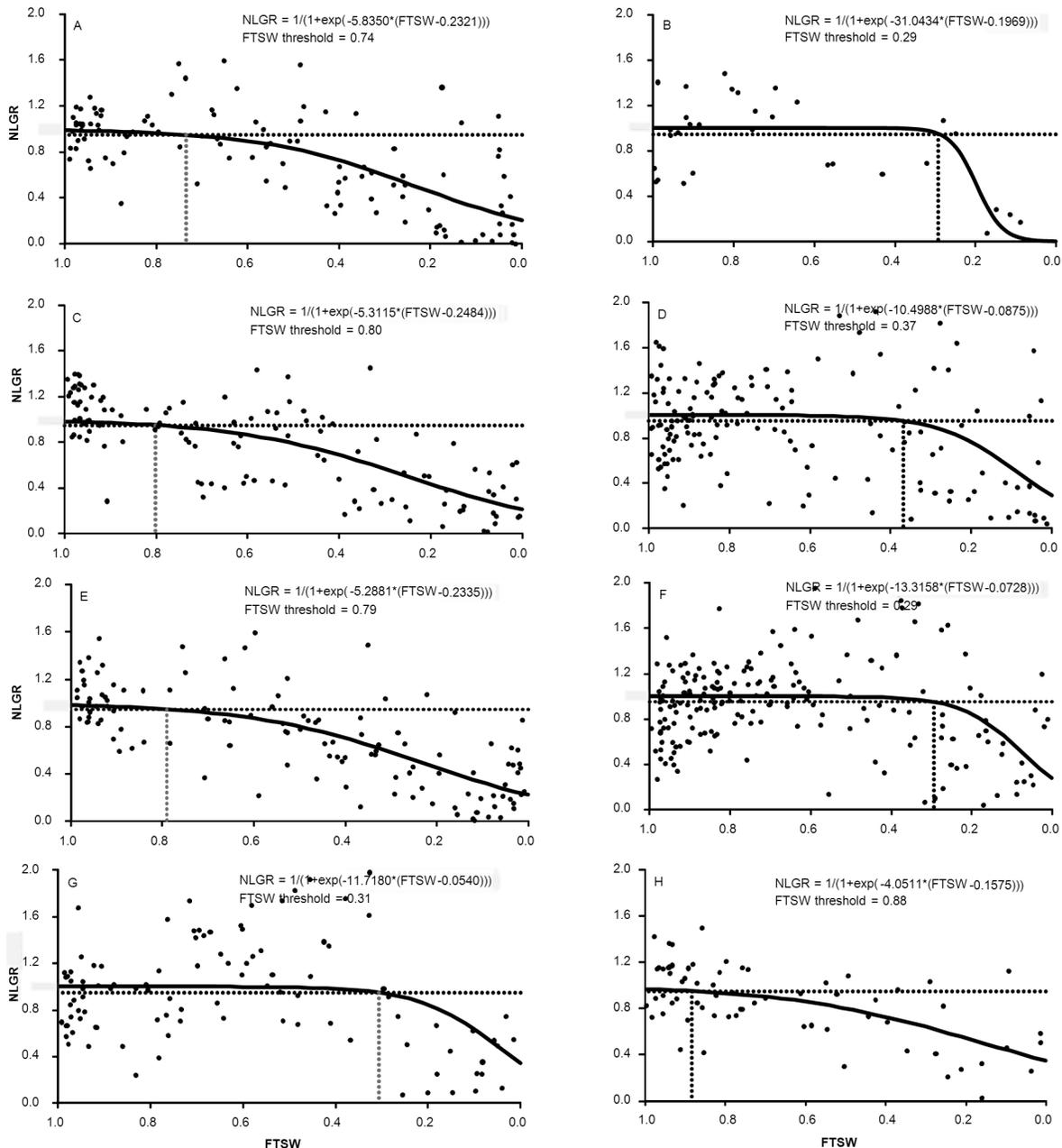


Figure 3 – Normalized relative leaf growth (NLGR) as a function of fraction of transpirable soil water (FTSW) for potato clones SMINIA 02106-11 (A, B), SMINIA 00017-6 (C, D), SMINIA 793101-3 (E, F) and cultivar Asterix (G, H) grown in a greenhouse in two experiments: E1 = water deficit started on 05 Oct 2010 (A, C, E, G), E2 = water deficit started on 03 May 2011 (B, D, F, H). Santa Maria, RS, Brazil, 2010-2011. Threshold FTSW: fraction of transpirable soil water when NLGR starts to decrease due to water deficit.

group allowed transpiration at a maximum rate until the soil dried to a lower FTSW threshold. In order for the second group to conserve water and have some tolerance to low soil water contents, these genotypes must have low transpiration rates while soil is still in the well-watered phase, mainly early in the season (Gholipoor et al., 2012). In our study, the cultivar Asterix (which had the lowest FTSW threshold) had one of the highest transpi-

ration rates in well-watered plants during experiment E1 (Table 1), indicating that this cultivar has lower tolerance in a drying soil as compared with the other three clones. This cultivar is currently widely used by potato growers in the State of Rio Grande do Sul.

The clones SMINIA 02106-11 and SMINIA 00017-6 consistently had a higher FTSW threshold (Figure 3A, 3B, 3C, 3D) as compared with cultivar Asterix (Figure

3G, 3H) in both experiments. These results indicate that these two clones that are adapted to subtropical environments have good quality chips are resistant to major diseases (Bisognin et al., 2008), and also have tolerance to water deficit in the soil.

The trait tolerance to water shortage of the three clones is particularly important if the trend of years with rainfall below normal observed in Rio Grande do Sul during the first decade of this century continues in the coming years (Streck et al., 2009). Thus, the first step which is to identify from the already developed potato clones those with a difference in FTSW threshold in drying soil, has been addressed.

We used the FTSW approach (Sinclair and Ludlow, 1986) to identify differences in tolerance to water deficit in potato genotypes. This approach assumes that the water content in the soil used by the plant for transpiration varies between field capacity (when transpiration is at the maximum rate) and the water content in the soil when transpiration of plants under stress equals 10 % of maximum transpiration (Sinclair and Ludlow, 1986). Compared to other approaches such as the total extractable soil water (Ritchie, 1973, 1981), the FTSW is a better indicator of the actual amount of soil water that can be extracted by plants for transpiration (Ludlow and Sinclair, 1986).

The response of plant transpiration to FTSW has two phases (Ludlow and Sinclair, 1986): (i) phase I, in which transpiration takes place at the maximum rate in the range of FTSW from one (field capacity) to the onset of transpiration reduction due to stomatal closure (threshold FTSW), and (ii) phase II, in which transpiration decreases almost linearly to a minimum value as soil water decreases from an FTSW threshold down to zero. The greater the FTSW threshold the earlier stomata close in a drying soil, which allows for conservation of water in the soil and, therefore, more time is available for the plant to activate long-term strategies for accessing more or conserving the available soil water so as to increase the growth of roots and to reduce the transpiring leaf area.

In addition to helping in identifying water-deficit tolerant genotypes, the response curves of transpiration and leaf growth *versus* FTSW (Figures 2 and 3) also have a direct application in potato simulation models. Fagundes et al. (2010) calibrated such models for the Rio Grande do Sul conditions, but the effect of water deficit was not taken into account, that is, it was considered that the crop was irrigated (near optimum conditions). The next step, now possible, is to take into account the effect of water deficit on transpiration and incorporate this effect into models of the potato cultivars Asterix and Macaca and the new clones.

Conclusions

The fraction of transpirable soil water (FTSW) approach is an efficient method to separate potato clones differing in their responses to water deficit. The ad-

vanced clones SMINIA 02106-11 and SMINIA 00017-6 are more tolerant to soil water deficit than the cultivar Asterix under both high and low solar radiation. The clone SMINIA 793101-3 is more tolerant to soil water deficit than the cultivar Asterix under high solar radiation.

References

- Amir, J.; Sinclair, T.R. 1991. A model of water limitation on spring wheat growth and yield. *Field Crops Research* 29: 59-96.
- Bindi, M.; Bellesi, S.; Orlandini, S.; Fibbi, F.; Moriondo, M.; Sinclair, T.R. 2005. Influence of water deficit stress on leaf area development and transpiration of Sangiovese grapevines grown in pots. *American Journal of Enology and Viticulture* 56: 68-72.
- Bisognin, D.A.; Müller, D.R.; Streck, N.A.; Andriolo, J.L.; Sausen, D. 2008. Development and yield of potato clones during spring and autumn. *Pesquisa Agropecuária Brasileira* 43: 699-705 (in Portuguese, with abstract in English).
- Davatgar, N.; Neishabouri, M.R.; Sepaskhah, A.R.; Soltani, A. 2009. Physiological and morphological responses of rice (*Oryza sativa* L.) to varying water stress management strategies. *International Journal of Plant Production* 3: 19-32.
- Devi, M.J.; Sinclair, T.R.; Vadez, V.; Krishnamurthy, L. 2009. Peanut genotypic variation in transpiration efficiency and decreased transpiration during progressive soil drying. *Field Crops Research* 114: 280-285.
- Fagundes, J.D.; Streck, N.A.; Bisognin, D.A.; Schwantes, A.P.; Alberto, C.M. 2010. Potato tuber simulated yield in climate change scenarios. *Pesquisa Agropecuária Brasileira* 45: 351-360 (in Portuguese, with abstract in English).
- Gholipoor, M.; Sinclair, T.R.; Prasad, P.V.V. 2012. Genotypic variation within sorghum for transpiration response to drying soil. *Plant Soil* 357: 35-40.
- Hsiao, T.C.; Acevedo, E. 1974. Plant responses to water deficits, water-use efficiency, and drought resistance. *Agricultural Meteorology* 14: 59-84.
- Hufstetler, E.V.; Boerma, H.R.; Carter, T.E. Jr.; Earl, H.J. 2007. Genotypic variation for three physiological traits affecting drought tolerance in soybean. *Crop Science* 47: 25-35
- Kholova, J.; Hash, C.T.; Kakkera, A.; Kocova, M.; Vadez, V. 2010. Constitutive water-conserving mechanisms are correlated with the terminal drought tolerance of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Journal of Experimental Botany* 6: 369-377.
- Kiniry, J.R.; Landivar, J.A.; Witt, M.; Gerik, T.J.; Cavero, J.; Wade, L.J. 1998. Radiation-use efficiency response to vapor pressure deficit for maize and sorghum. *Field Crops Research* 56: 265-270.
- Lago, I.; Streck, N.A.; Bisognin, D.A.; Souza, A.T.; da Silva, M.R. 2011. Transpiration and leaf growth of cassava plants as a response to soil water deficit. *Pesquisa Agropecuária Brasileira* 46: 1415-1423 (in Portuguese, with abstract in English).
- Lago, I.; Streck, N.A.; Zanon, A.J.; Hanauer, J.G.; Bisognin, D.A.; Silva, M.R. 2012. Transpiration and leaf growth of potato clones as a function of fraction of transpirable soil water. *Revista Brasileira de Ciência do Solo* 36: 745-754 (in Portuguese, with abstract in English).

- Lecoeur, J.; Sinclair, R.T. 1996. Field pea transpiration and leaf growth in response to soil water deficits. *Crop Science* 36: 331-335.
- Marengo, R.A.; Lopes, N.F. 2005. *Plant Physiology: Photosynthesis, Respiration, Water Relations and Mineral Nutrition = Fisiologia Vegetal: Fotossíntese, Respiração, Relações Hídricas e Nutrição Mineral*. 3ed. Universidade Federal de Viçosa, Viçosa, MG, Brazil (in Portuguese).
- Martins, F.B.; Streck, N.A.; Silva, J.C.; Morais, W.W.; Susin, F.; Navroski, M.C.; Vivian, M.A. 2008. Soil water deficit affecting transpiration, growth and development of seedlings of two eucalyptus species. *Revista Brasileira de Ciência do Solo* 32: 1297-1306 (in Portuguese, with abstract in English).
- Muchow, R.C.; Sinclair, T.R. 1991. Water deficits effects on maize yields modeled under current and "greenhouse" climates. *Agronomy Journal* 83: 1052-1059.
- Oliveira, S.L.; Macedo, M.M.C.; Porto, M.C.M. 1982. Effects of water stress on cassava root production. *Pesquisa Agropecuária Brasileira* 17: 121-124 (in Portuguese, with abstract in English).
- Ray, J.D.; Sinclair, T.R. 1997. Stomatal conductance of maize hybrids in response to drying soil. *Crop Science* 37: 803-807.
- Ritchie, J.T. 1973. Influence of soil water status and meteorological conditions on evaporation from a corn canopy. *Agronomy Journal* 65: 893-897.
- Ritchie, J.T. 1981. Soil water availability. *Plant Soil* 58: 327-338.
- Shao, H.; Chu, L.; Jaleel, C.A.; Zhao, C. 2008. Water-deficit stress induced anatomical changes in higherplants. *Comptes Rendus Biologies* 331: 215-225.
- Sinclair, T.R.; Ludlow, M.M. 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. *Australian Journal Plant Physiology* 13: 319-340.
- Streck, N.A.; Paula, F.L.M.; Bisognin, D.A.; Heldwein, A.B.; Dellai, J. 2007. Simulating the development of field grown potato (*Solanum tuberosum* L.). *Agricultural and Forest Meteorology* 142: 1-11.
- Streck, N.A.; Buriol, G.A.; Heldwein, A.B.; Gabriel, L.F.; Paula, G.M. 2009. Linking rainfall variability in Santa Maria with the Pacific Decadal Oscillation. *Pesquisa Agropecuária Brasileira* 44: 1553-1561 (in Portuguese, with abstract in English).
- Taiz, L.; Zeiger, E. 2006. *Plant Physiology*. 4ed. Sinauer, Sunderland, MA, EUA.
- Wahbi, A.; Sinclair, T.R. 2007. Transpiration response of Arabidopsis, maize, and soybean to drying of artificial and mineral soil. *Environmental and Experimental Botany* 59: 188-192.
- Weisz, R.; Kaminski, J.; Smilowitz, Z. 1994. Water deficit effects on potato leaf growth and transpiration: utilizing fraction extractable soil water for comparison with other crops. *American Potato Journal* 71: 829-840.