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## Effect of water shortage on six potato genotypes in the highlands of Bolivia (II): water relations, physiological parameters

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**Abstract** – Six potato genotypes were grown in containers in the highlands of Bolivia under three water regimes: R0 (well-irrigated controls); R1 (progressive drought after tuberisation and recovery period), and R2 (no recovery). Soil water content ( $\theta_w$ ), leaf relative water deficit (RWD), leaf water potential ( $\Psi_w$ ), stomatal resistance ( $r_s$ ) and chlorophyll fluorescence were evaluated. The objective of this research was to characterise the drought adaptation of the potato genotypes studied, and to identify physiological indicators of drought tolerance. Under drought conditions, cultivar Alpha maintained the highest  $\theta_w$  and the lowest RWD. Cultivar Luky exhibited a high  $r_s$  and cultivar Alpha showed the lowest  $r_s$ , especially at the end of the R2 treatment. The relations RWD– $\Psi_w$ ,  $\theta_w$ –RWD and  $\theta_m$ – $\Psi_w$  were not affected by genotype or treatment. Chlorophyll fluorescence measurements revealed, in all genotypes, a very high drought resistance of the photosynthetic apparatus, which was not affected in a RWD range of 0–50%. No significant correlation was found between tuber yield and the measured physiological parameters.

**drought / relative water content / leaf water potential / chlorophyll fluorescence / Andean Highlands**

**Résumé** – Effet du manque d'eau sur six génotypes de pomme de terre (II) : relations hydriques, résistance stomatique et fluorescence de la chlorophylle. Six génotypes de pomme de terre ont été cultivés en conteneurs dans les Andes Boliviennes, sous trois régimes hydriques : R0 (témoins bien irrigués), R1 (sécheresse suivie de récupération) et R2 (sécheresse sans récupération). La teneur en eau du sol  $\theta_m$ , le déficit relatif en eau des feuilles RWD, le potentiel hydrique foliaire  $\Psi_w$ , la résistance stomatique  $r_s$  et la fluorescence de la chlorophylle ont été mesurés. Notre objectif était de caractériser l'adaptation à la sécheresse des génotypes étudiés et d'identifier des indicateurs de tolérance à la sécheresse parmi les caractères physiologiques examinés. En conditions de sécheresse cultivar Alpha maintient le  $\theta_m$  le plus élevé et le RWD le plus faible, cultivar Luky montre un  $r_s$  élevé et cultivar Alpha présente la  $r_s$  la plus basse particulièrement à la fin du traitement R2. Les relations RWD– $\Psi_w$ ,  $\theta_w$ –RWD and  $\theta_m$ – $\Psi_w$  ne sont pas affectées par les génotypes et traitements. Les mesures de fluorescence de la chlorophylle révèlent chez tous les génotypes une résistance élevée à la sécheresse de l'appareil photosynthétique, qui n'est pas affecté dans une gamme de RWD allant de 0 à 50 %. Aucune corrélation significative entre le rendement en tubercules et les paramètres physiologiques n'a pu être mise en évidence.

**sécheresse / contenu relatif en eau / potentiel hydrique foliaire / fluorescence de la chlorophylle / Andes**

**Abbreviations:** DAP: days after planting; FC: field capacity; Fm, F0, Fs, Fv = maximal, initial, steady-state and variable levels of chlorophyll fluorescence, respectively; PSII: photosystem II;  $r_s$  = stomatal resistance; RWC = relative water content; RWD = relative water deficit; Y = tuber yield;  $\theta_m$  = gravimetric soil water content;  $\Psi_w$  = leaf water potential.

### 1. INTRODUCTION

Potato genotypes subjected to drought may differ, in terms of their yield response and in terms of their morphology and

physiology. An analysis of these responses was carried out on a sample of contrasting genotypes grown in the Andean highlands of Bolivia. This analysis was intended to contribute to a better knowledge of the mechanisms of drought

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adaptation and to a characterisation of the morpho-physiological behaviour of the genotypes. Drought is, indeed, a major constraint in the highlands of Bolivia and little information is available concerning the behaviour of native species and genotypes under drought conditions. A comparison has been made between quinoa and the native genotype cultivar Luky (also known as 'Luki'), which belongs to the species *Solanum juzepczukii* Buk. and a cultivar of *Solanum tuberosum* L. [50]. The study confirmed the relatively high resistance to drought of Luky compared with the cultivar of *Solanum tuberosum* L. Luky maintained lower stomatal resistance and higher rates of photosynthesis than quinoa under conditions of water shortage. However, when drought stress became extreme, there was a massive drop in both these parameters and the water use efficiency of Luky was lower than that of quinoa. Our objective in this study was to characterise drought adaptation and identify morphological and physiological indicators of drought tolerance in potatoes in the Andean Highlands of Bolivia.

A paper previous to this one [48] has already focused upon morphological and agronomic behaviour. In the present paper, therefore, we discuss the effects of water stress on the physiological parameters related to water status, and the relationships between tuber yield and these parameters. According to Levy [32], differences in drought tolerance between potato genotypes are partially due to differences in water relations and stomatal behaviour. It was reported that one of the first effects a period of drought has upon potato is a reduction in the rate of photosynthesis, which is mainly caused by an increase in stomatal resistance [35].

Physiological parameters, such as stomatal resistance and rate of photosynthesis, could explain genotypic variations under drought – when they are related to parameters defining the water status of the plant (such as leaf water potential  $\Psi_w$  and leaf relative water content, RWC). The use of the relationship between  $\Psi_w$  and soil water content has been advocated for screening for drought-tolerant wheat [39]. In other cases, the use of the relationship between RWC and  $\Psi_w$  [24], or between stomatal resistance ( $r_s$ ) and  $\Psi_w$  [28] have also been advocated. We, therefore, studied the correlations between stomatal resistance, leaf water potential and tuber yield.

The measurement of the kinetics of chlorophyll fluorescence [29] has been reported as a sensitive tool for use in quantifying the effects of stress on the photosynthetic apparatus [1] and, therefore, the effects on photosynthesis independently of stomatal behaviour. This technique gives rapid results and can be used in the field [31]. A clear review of the state of the art is given in [33].

Fv/Fm (measured after dark incubation) is an estimate of maximal PSII activity; it correlates with the quantum yield of photosynthesis at low irradiance, and the slow relaxing, long-lasting component of its decrease is considered to be an indication of damage to PSII. Quantum yield in light  $\Delta F/F_m$  can be used to calculate the rate of non-cyclic electron transport during steady-state photosynthesis, and this rate is correlated with photosynthetic rates. This method has been used previously to screen for drought tolerance [21]. It has

been reported that the photosynthetic apparatus is fairly resistant to water stress [20, 47] and that the interest of the method is limited in the context of water stress [16, 17]. However, the technique was used here because of the possibility that it might complement our characterisation of the behaviour of potato genotypes, by examining the effect of leaf dehydration on their photosynthetic apparatus. Recent literature mentions increased fluorescence in potatoes submitted to drought [2, 51]. In wheat the ratio Fv/Fm was unaffected by water stress but quenching (photochemical and non-photochemical) was decreased [44].

## 2. MATERIALS AND METHODS

### 2.1. Experimental conditions

This trial was conducted between 1995 and 1996 at the Toralapa Research Station, Cochabamba, Bolivia (3450 m a.s.l.). A preliminary trial, carried out between 1994 and 1995, corroborated the results presented in this paper.

Plants were cultivated in containers, under a permanent rain shelter. They were either fully irrigated ('R0' treatment), or submitted to one of two drought treatments (treatments 'R1' or 'R2'). In treatment R1, drought was imposed progressively and was followed by a recovery period (progressive decrease in watering for five weeks, starting at tuberisation of cultivar Waycha at 54 days after planting, then suspension for one week, followed by resumption of irrigation). Treatment R2 was similar to R1, but lacked recovery irrigation (it was subjected to a lethal drought).

### 2.2. Genetic material

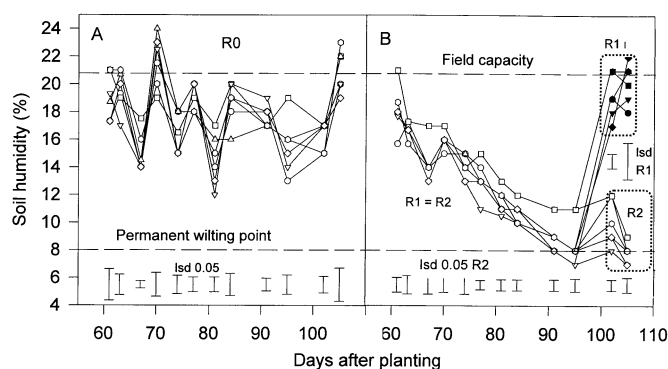
Six genotypes of potato were used. They are the same as those used previously [48]: Alpha, Waycha, Luky, Ajahuri, Janko Choquepito and clone CIP 382.171.10. Alpha belongs to the subspecies *tuberosum*; Waycha and Luky belong to the subspecies *andigena*; Janko Choquepito is a *Solanum curtilobum*, and the clone is the result of crosses (*tuberosum* × *andinum*) × *tuberosum*. The Luky cultivar used in this trial was *S. tuberosum* subsp. *andigena* and not *S. juzepczukii*, which is the type most often referred to as Luky.

### 2.3. Soil water content

Soil samples were collected from each container twice a week, at 17h00, with a borer (volume sampled = 35 to 50 cm<sup>3</sup> per container; depth = 25 cm). Soil samples were weighed, to obtain their fresh weight, then oven-dried (105 °C for 24 h) and weighed again, to obtain their dry weight. Soil water content (soil gravimetric water content  $\theta_m$ ) was calculated as:  $\theta_m$  (%) = (fresh weight – dry weight) / dry weight × 100.

### 2.4. Plant water status

Leaf relative water content (RWC) and leaf water potential ( $\Psi_w$ ) was determined for 10 fully-expanded leaves between



**Figure 1.** Time course of soil water content measured before watering on controls (A) and drought-stressed plants (B). (O) Waycha, (□) Alpha, (▽) Ajahuri, (△) Clone 382171.10, (◇) Luky, (○) Janko Choquepito. Closed symbols indicate the rewatering in treatment R1. Field capacity and permanent wilting point are also indicated. Each point is the mean of three replicates.

6h00 and 7h30 (before sunrise), and between 14h00 and 15h30 (the period of highest evaporation during the day). Two leaf samples were collected per container.

Leaf RWC was measured for six leaf discs (2 cm in diameter), collected at random from each genotype from all treatments (i.e. two leaf discs per container). Leaf discs were weighed immediately, then floated on distilled water for 12 h at 5 °C, in darkness. After removing excess moisture, the samples were weighed (turgid weight), oven-dried at 80 °C for 12 h and then weighed again (dry weight). Leaf RWC (%) was calculated as  $(\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}) \times 100$ . Leaf relative water deficit was calculated as  $\text{RWD} (\%) = 100 - \text{RWC}$ . Leaf samples from the same treatment and the same cultivar were bulked and mixed before weighing, in order to ensure accurate measurements. Therefore, statistical analyses are not available for this parameter.

A pressure chamber was used to measure  $\Psi_w$  [43]. Leaf samples used for the determination of  $\Psi_w$  were collected at the same time as the samples used to obtain RWC measurements, and from the same leaves.  $\Psi_w$  was not evaluated for cultivar Alpha, because of the small size and the limited number of leaves formed. For the same reason, RWC was measured on Alpha only until 91 DAP.

## 2.5. Stomatal resistance

Stomatal resistance to water vapour diffusion ( $r_s$ ) was determined using a steady-state diffusion porometer (LI 1600, Li-Cor Inc., Lincoln, USA) attached to the abaxial side of leaves. The readings were taken weekly (between 8h00 and 9h30 and between 14h00 and 15h30) on two fully-expanded leaves per container, situated at the top of the canopy and of similar age. Leaf and air temperatures, relative air humidity

and incident radiation were also recorded during stomatal resistance measurements.

## 2.6. Chlorophyll fluorescence

Chlorophyll fluorescence emission from the upper surface of leaves selected from the top of the canopy was evaluated using a portable pulse amplitude modulation fluorometer (PAM 2000, Walz, Effeltrich, Germany). Readings were conducted weekly (between 6h00 and 8h00 and between 13h30 and 15h30).

Leaves were dark-adapted by wrapping them in aluminium foil for at least 30 minutes. Then, after quickly removing the aluminium foil, initial chlorophyll-fluorescence ( $F_0$ ) was measured following exposure to a 650 nm non-actinic light, modulated at 1.6 KHz. Maximal chlorophyll-fluorescence ( $F_m$ ) was obtained by submitting the leaf to a saturated pulse of 0.8 s (about  $8000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ). The steady-state level of chlorophyll-fluorescence ( $F_s$ ) was determined by irradiating light-adapted leaves with an actinic light of  $230 \pm 10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ .

The maximal photochemical efficiency of photosystem II (PSII) was calculated as  $F_v/F_m = (F_m - F_0)/F_m$ , where  $F_v$  is the variable fluorescence. The actual quantum yield of PSII photochemistry during steady-state photosynthesis ( $\Phi_{\text{PSII}}$ ) was calculated as  $\Delta F/F_m = (F_m - F_s)/F_m$  according to Genty et al. [15].

## 3. RESULTS AND DISCUSSION

### 3.1. Soil water content

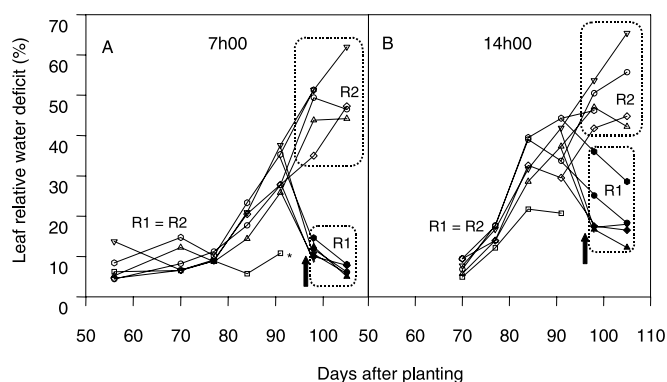
Figure 1 illustrates the time course of gravimetric soil water content ( $\theta_m$ ) evaluated before the watering of controls (Fig. 1A) and of water-stressed plants (Fig. 1B).

Control soil water content ranges from 14% to field capacity ( $\text{FC} = 21\%$ ). Oscillations are due to variations in temperature, air humidity and radiation (data not shown), which influence evaporative demand and, therefore, soil water content.  $\theta_m$  values above field capacity are, perhaps, due to errors in the determination of field capacity or soil water content.

Soil water content decreased with time in response to drought treatments, and reached the permanent wilting point (about 8%) within 91 DAP (37 days after the beginning of drought treatment) in all genotypes, except in cultivar Alpha, which maintained a higher soil water content (13% at 91 DAP).

### 3.2. Plant water status

As shown in Figure 2, leaf relative water deficit (RWD) strongly increased in response to drought stress, particularly after 98 DAP, reaching 66% in Ajahuri 105 DAP (R2 treatment). Before rewatering, cultivar Alpha maintained the

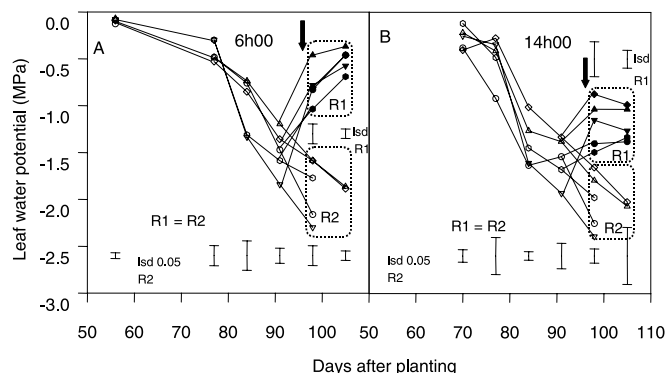


**Figure 2.** Time course of leaf relative water deficit evaluated between 6h00 and 7h00 (A), and between 14h00 and 15h00 (B) on six potato genotypes. \* RWD was measured on cv. Alpha only until 91 DAP because of a lack of leaves. See symbols in Figure 2. The arrows and closed symbols indicate rewatering in treatment R1.

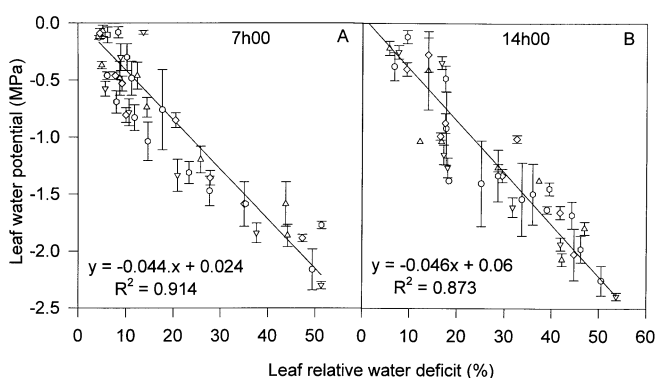
lowest leaf water deficit during the R1 treatment at 6h00 (10% RWD at 97 DAP, 27 to 38% in other genotypes), as well as at 14h00 (21% RWD at 92 DAP, 30 to 43% in other genotypes). At 107 DAP Ajahuri demonstrated the highest levels of RWD (61% at 6h00, 66% at 14h00), while clone 387121.10 and cultivar Luky demonstrated the lowest levels of RWD, especially at 14h00 (42–44%). The recovery of plants in the R1 treatment was much faster at 6h00 (Fig. 2A, closed symbols) than at 14h00 (Fig. 2B, closed symbols), due to the inability of plants to sustain a high leaf water content during the afternoon, when evaporative demand was at a maximum.

As RWD increased,  $\Psi_w$  decreased in response to water stress (Fig. 3), reaching  $-2.4$  MPa in Ajahuri at 98 DAP. During drought treatments,  $\Psi_w$  values were much lower than control values, which ranged from  $-0.06$  to  $-0.43$  MPa at 6h00, and from  $-0.08$  to  $-0.99$  MPa at 14h00 (data not shown). In treatment R1 and at 98 DAP, Ajahuri exhibited the lowest levels of  $\Psi_w$  ( $-2.3$  MPa at 6h00, and  $-2.4$  MPa at 14h00); clone 387121.10 and cultivar Luky showed the highest  $\Psi_w$  levels ( $-1.5$  MPa at 6h00 and  $-1.6$  to  $-1.7$  MPa at 14h00). Using regression analysis, a significant linear relationship was found between  $\Psi_w$  and leaf RWD both at 6h00 ( $R^2 = 0.914$ , Fig. 4A) and 14h00 ( $R^2 = 0.873$ , Fig. 4B). The slope of the  $\Psi_w$ –RWD relation is often used to discriminate the behaviour of varieties or species submitted to drought. A genotype showing a lower  $\Psi_w$  for a given leaf RWD is generally considered to be more drought-tolerant [36] or drought-acclimated [28]. Figure 4, however, shows that the relation between  $\Psi_w$  and leaf RWD is not affected by genotype, time of measurement, or drought treatment and therefore cannot be used for screening potato genotypes. This result agrees with two other studies on potato varieties [52, 53] which reported no effect of genotype on the relation between  $\Psi_w$  and leaf RWD. The absence of genotypic differences could indicate an absence of osmotic adjustment in the six potato genotypes in this study, but osmotic potential measurements would be necessary to corroborate this assertion.

Figure 5 presents the effect of soil water content  $\theta_w$  on leaf RWD (Fig. 5A) and on  $\Psi_w$  (Fig. 5B). No difference was



**Figure 3.** Time course of leaf water potential, evaluated between 6h00 and 7h00 (A), and between 14h00 and 15h00 (B), for five potato genotypes. See symbols in Figure 1.  $\Psi_w$  was measured at the same time and for the same leaves sampled for the measurements of leaf RWD (Fig. 2). Each point is the mean of six replicates. It should be noted that  $\Psi_w$  measurements were not performed on cv. Alpha.



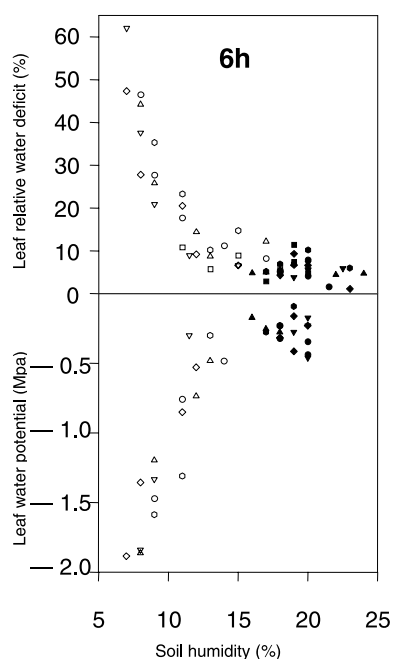
**Figure 4.** Relationship between leaf water potential and leaf relative water content measured between 6h00 and 7h00 (A), and between 14h00 and 15h00 (B) for the same leaves. See symbols in Figure 1. Vertical bars indicate standard deviations of means of six measurements of  $\Psi_w$ .

observed between genotypes for these two relations. When soil water content decreases from FC to about 12%, leaf RWD increases slowly (Fig. 5A). It increases much faster below 12% soil water content. Leaf water potential ( $\Psi_w$ ) shows a much faster decrease below a threshold of about 12% soil water content, without significant difference between genotypes (Fig. 5B).

### 3.3. Stomatal resistance

Figure 6 presents the time course of stomatal resistance ( $r_s$ ) measured at 14h00 in control plants (Fig. 6A), during water stress (Fig. 6B, open symbols) and during the R1 recovery period (Fig. 6B, closed symbols).

Stomatal resistance in controls exhibited strong variation with time (Fig. 6A) and ranged from  $0.3$  to  $5$   $s \cdot cm^{-1}$ , except in the clone (69 and 83 DAP) and cultivar Luky (69 DAP) where higher  $r_s$  were observed. Stomatal conductance is known to be



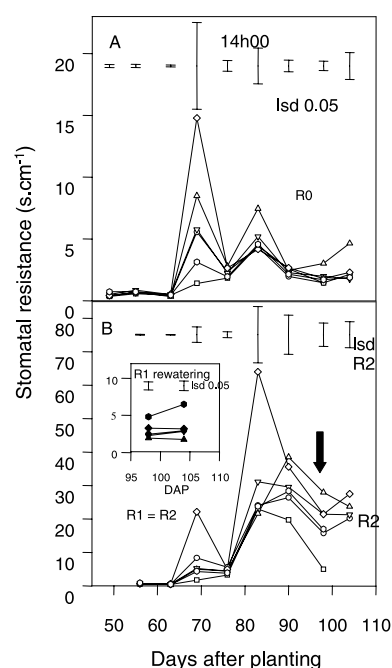
**Figure 5.** Effect of soil water content  $\theta_w$  on leaf water potential  $\Psi_w$  and relative water content deficit RWDF.  $\Psi_w$  and RWDF were measured between 6h00 and 7h00 on the same leaves. See symbols for genotypes in Figure 1. Closed symbols: controls; open symbols: drought treatments.

affected by climatic conditions, such as irradiance [10, 30], temperature [30] and air humidity [18].

Stomatal resistance also showed strong variations during drought treatment (Fig. 6B). A strong increase in  $r_s$  was noted, especially after 63 DAP. Cultivar Luky showed a much higher stomatal resistance than the other genotypes 69 DAP ( $21 \text{ s}\cdot\text{cm}^{-1}$ , but 2 to  $8 \text{ s}\cdot\text{cm}^{-1}$  in other genotypes) and 83 DAP ( $63 \text{ s}\cdot\text{cm}^{-1}$ , but 21 to  $31 \text{ s}\cdot\text{cm}^{-1}$  in other genotypes). These higher values, also observed in the controls, occurred on bright days when evaporative demand was particularly high. Cultivar Alpha exhibited the lowest  $r_s$  levels, especially at the end of the R1 treatment. The recovery of plants in the R1 treatment was very fast for all genotypes studied (Fig. 6B). One day after the rewatering of treatment R1, no significant difference was observed between the control and treatment R1 for stomatal resistance, except in the clone (which showed a significantly lower  $r_s$  in the R1 than in the R0 treatment).

As shown in Figure 7, stomatal resistance was higher in the afternoon than in the morning, especially at the end of the drought period. This demonstrated the capacity of plants to limit water losses when evaporative demand is at its maximum. This effect was also observed in the controls (data not shown) but the variations were smaller. This stomatal response to drought depended on genotype, and was much more accentuated in cultivar Luky and the clone than in cultivars Janko Choquepito and Ajahuiri.

The relationship between  $\Psi_w$  and  $r_s$  measurements between 14h00 and 16h00 is given in Figure 8. Above a threshold value



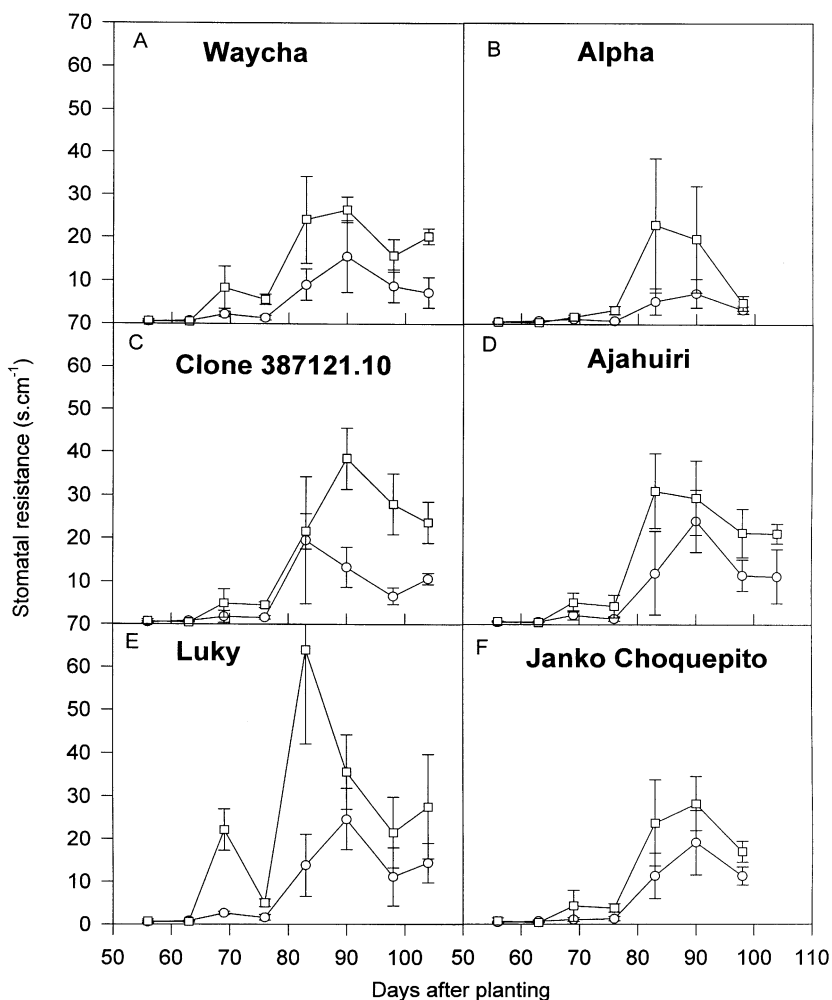
**Figure 6.** Time course of stomatal resistance ( $r_s$ ) on the abaxial leaf surface, measured at 14h00, for six genotypes. See symbols in Figure 1. The arrow indicates rewatering for recuperation in treatment R1. Each point is the mean of six replicates. The two graphs in the figure have different scales.

of  $\Psi_w$  (about  $-1.0 \text{ MPa}$ )  $r_s$  ranged from 1 to  $5 \text{ s}\cdot\text{cm}^{-1}$ , except in cultivar Luky. Below this threshold,  $r_s$  rapidly increased, without significant difference between genotypes. In the range 0 to  $-1.0 \text{ MPa}$ , some of the  $r_s$  values of cultivar Luky were much higher than were seen in other genotypes. It seems that these high  $r_s$  values are due to climatic variations with which  $\Psi_w$  values were not directly associated.

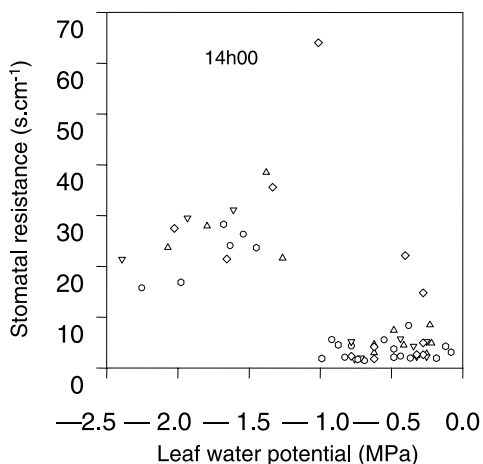
No difference was observed between genotypes in the  $r_s$ – $\Psi_w$  relationship (Fig. 8). The threshold  $\Psi_w$  value for strong stomatal closure was about  $-1.0 \text{ MPa}$  (Fig. 8). This value is high compared with those of other species, which range from  $-0.8 \text{ MPa}$  (in faba bean) to  $-2.8 \text{ MPa}$  (in cotton) according to Turner [49].

### 3.4. Chlorophyll fluorescence parameters

Figure 9 shows the effect of leaf dehydration on maximal PSII activity, as seen by measuring Fv/Fm ratios in dark-adapted leaves at 6h00 (Fig. 9A), and at 13h30 (Fig. 9B). The ratio  $\Delta F/F_m$  was evaluated using light-adapted leaves at 6h00 (Fig. 9C) and at 13h30 (Fig. 9D). In all genotypes studied, no effect of drought treatments was found on the Fv/Fm ratio in the range of 0–40% RWD, at 6h00 or at 13h30. For a RWD above 40%, an inhibition of only 0 to 10% was found. The high dehydration-resistance of PSII has previously been reported both in the potato [20, 23, 47] and in other



**Figure 7.** Time course of  $r_s$  evaluated at 8h00 and 14h00 in the R2 treatment (drought without rewatering).



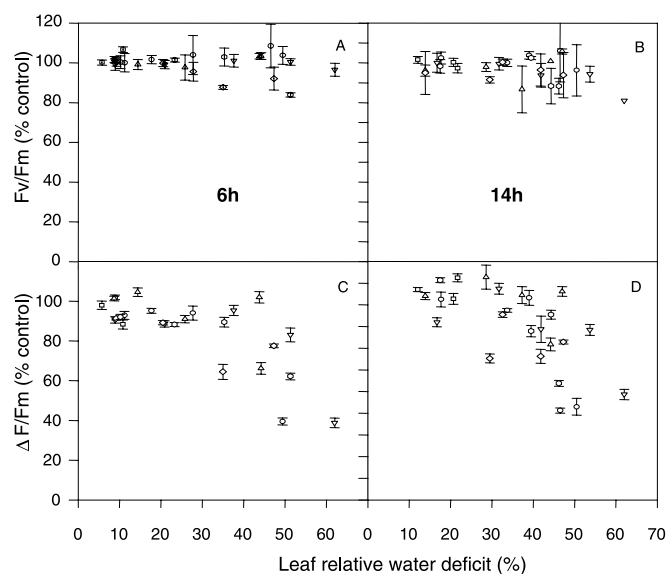
**Figure 8.** Relationship between stomatal resistance ( $r_s$ ) and leaf water potential ( $\Psi_w$ ) measured between 14h00 and 15h00 for five genotypes. See symbols in Figure 1. Each point is the mean of six replicates.

species [11, 14], revealing that drought has little effect on the photochemistry of PSII.

In the range of 0–40% RWD,  $\Delta F/F_m$  inhibition was very weak (0–10%) in all genotypes studied, which shows the drought resistance of the photosynthetic apparatus, as has been reported in previous studies [7, 47]. These results indicate that, for mild water stress (RWD <35%), the decrease observed in the rate of photosynthesis in response to drought [35, 42] is mainly due to stomatal closure and not to a direct effect on the photosynthetic apparatus. For more severe water deficits (>35%),  $\Delta F/F_m$  declined and showed a 40% inhibition for a 50–60% RWD, at both 6h00 and at 13h30. This result is in agreement with another study [27], and suggests that the decrease evident in the rate of photosynthesis is mainly due to a stomatal effect for mild water stress (RWD <35%) and to non-stomatal effects for more severe water deficits.

### 3.5. Relation between physiological parameters and total tuber yield

Cultivars Waycha, Alpha, Janko Choquepito and clone CIP 382171.10 maintained a relatively high tuber yield in drought



**Figure 9.** Effect of leaf relative water deficit (RWD) on parameters of chlorophyll fluorescence measured between 6h00 and 8h00 and between 14h00 and 16h00. Values are expressed in relative values (as a % of controls). Absolute values for controls ranged from 0.760 to 0.825 in the morning, and from 0.720 to 0.790 in the afternoon, in the case of  $F_v/F_m$ . For  $\Delta F/F_m$ , the corresponding values were 0.610 to 0.690 and 0.620 to 0.720. Symbols for genotypes are given in Figure 1.

conditions, although the tuber yields of cultivars Luky and Ajahuiri were drastically affected in response to water stress [48]. Table I shows the correlation coefficients between total tuber yield and physiological parameters (stomatal resistance and leaf water potential), measured either in the morning or afternoon during four drought stress periods. There are only a few significant correlations and their

corresponding  $R^2$  values are small ( $<0.5$ ). No highly significant correlations were obtained, with the exception of that for leaf water potential ( $P < 0.01$ ), which was evaluated at 14h00, 83 DAP in the R1 treatment. Various authors have pointed out the complexity of the processes involved in potato yield development and the lack of strong correlations between tuber yield and physiological parameters [4, 13, 35, 45, 53]. The lack of strong correlations is mainly ascribed to the strong genotype-environment interaction for drought tolerance, and the contrast between rapid physiological responses (like stomatal resistance, leaf water potential, etc.) and slow cumulative responses (such as tuber yield, dry matter production, etc.). The relationship between  $r_s$  and potato yield has been reported to vary greatly from year to year [9]. In sorghum, as in several other species, leaf area is reduced under drought stress before stomatal conductance and this reduction accounts for most of the decrease in canopy photosynthesis [3].

The degree of influence of a character (trait) on yield depends on the time scale and on the level of organisation (molecule, cell, organ, plant, crop) in which the trait is primarily expressed. The closer a trait is to the level of organisation of the crop the more influence it will have on productivity, thus a trait influencing leaf area should be more important than one that affects stomatal response to the onset of drought [41]. Traits that confer drought tolerance are subtle, depend on the type of drought, and often have no direct connection to plant water relations [38].

#### 4. CONCLUSION

This study demonstrates that wide physiological differences exist between the six potato genotypes studied, a finding which was anticipated because of the diversity of the material tested (different species and subspecies of potato). Table Cultivar Alpha maintained the highest soil water

**Table I.** Correlation coefficients between total tuber yield ( $y$ ) and leaf water potential ( $\Psi_w$ ) or stomatal resistance ( $r_s$ ), measured in the morning and in the afternoon during the drought treatments R1 and R2.

DAP	Treatment	$r(y, \Psi_w)$		$r(y, r_s)$	
		6h00	14h00	8h00	14h00
76	R1	0.187	-0.223	-0.276	0.157
	R2	0.282	-0.191	-0.311	-0.359
83	R1	0.014	-0.691 (**)	0.014	0.002
	R2	0.138	-0.142	-0.321	-0.272
90	R1	-0.109	-0.316	-0.189	-0.327
	R2	0.044	0.014	-0.578 (*)	-0.265
97	R1	0.102	-0.563 (*)	-0.264	0.109
	R2	-0.015	-0.152	-0.392	-0.412

\*  $P < 0.05$ , \*\*  $P < 0.01$ .



content, and exhibited the lowest leaf water deficit and the lowest stomatal resistance during the drought period. Its very low leaf area index and canopy cover helped reduce its water losses.

Cultivar Luky also demonstrated capacities for drought adaptation, showing very high stomatal resistance in the drought treatments under conditions of high evaporative demand; under such conditions, its stomatal resistance greatly increased. It has also been shown, previously, that its root system is generally very developed [48]. Despite this, this variety yielded very little, especially under drought-stress conditions.

Cultivar Ajahuri demonstrated a low  $\psi_w$  and a high RWD in response to water stress (it had the highest leaf water deficit during the R2 treatment). It did not yield well under drought stress conditions. Its high foliage development probably accentuated its water losses.

Cultivar Alpha and CIP 382171.10 are early-maturing whereas the other genotypes are late-maturing. Such differences in the length of the growth period may influence their response, in terms of physiological characters, to drought. In a comparison of 12 potato cultivars, which differed in their response to drought and which represented three different growth periods, a clear relationship between chlorophyll fluorescence and drought tolerance was found only in the cultivars with a short growth period [51].

The different behaviours of the genotypes and cultivars studied showed, first, that the material grown in a region may be characterised by quite different patterns of response to water shortage. Second, (by the comparison of genotypes) it was shown that the tuber yield response is not clearly related to the well-defined behaviour of physiological characters.

Little correlation was observed between total tuber yield and physiological parameters. The relationships between yield on one hand, and the water-status parameters on the other, did not differ between the genotypes studied and could not, therefore, be used to discriminate between the genotypes. Physiological characters involve mostly instantaneous processes, measured on particular leaves and at particular times, and which strongly interact with the environment. Their values at specific times do not necessarily have an impact on the entire cycle, or on those parts which are critical for yield determination. Also, these characters may not correspond to the level of organisation at which integrative complex characters such as yield or crop survival are determined. Such issues were discussed by Richards [41] and are further discussed below.

The process of selection (through natural selection under different environmental conditions and human controlled selection) is likely to have differed between the Dutch variety Alpha, or the CIP 382171.10 clone on one hand, and the native varieties on the other. In the case of the native potatoes, selection may have been targeted at stability of yield rather than high yield potential. In the case of the native potatoes, the difference of species and level of ploidy may be another source of discrepancy. Similar objectives, such as plant survival (in the case of the wild relatives or ancestors of the plant), may have been achieved by different means. Recent man-made selection focuses more on high tuber yield in

normal conditions than on survival in a hostile environment. Reduction of growth and reproduction are adaptive measures for plant survival under stress, and potential yield may interact negatively with drought adaptation [3]. The dual system of reproduction of the potato (sexual through true seeds or vegetative through tubers) further complicates the problem. The association between the reproductive structure (fruit, seeds on one hand and tubers on the other) and the vegetative parts of the plant (shoots and roots) is not under the same physiological and genetic control for the two types of reproduction. The linkage between initiation of flower primordia and tuberisation is known to be loose [12].

Sink activity and the diversion of assimilates from the shoot is obviously greater in the case of tuber production (in comparison with seed production). Feedback on shoot and roots is likely to differ between the two modes of reproduction. The physiological characters measured in this case concerned leaves. Such characteristics may, therefore, have been affected differently according to the relative importance of the two types of reproductive structures in the plants used in this study, or throughout their evolution from their wild ancestors to the present selected material.

We are aware, of course, that this study did not take into account all those physiological parameters which describe aspects of plant water status, and which have been previously reported as showing possible relationships with growth and yield. For instance, we did not take into account water use efficiency or carbon isotope discrimination  $\Delta$ , a parameter reported to be related to water use efficiency. However, the poor relationship with yield found in previous work [8] or conflicting results [18, 19, 41] did not encourage the use of carbon isotope discrimination. In addition,  $\Delta$  provides an index for water stress under non-nutrient-limiting conditions but is influenced by many factors and must be used with caution [5, 6].  $\Delta$  does not provide a simple method for selecting for dry matter production in potato under water stress [25]. Neither did we study osmotic adjustment and the accumulation of solutes under conditions of water shortage. It has been reported that potato has a limited capacity for osmotic adjustment [24]. However, recent reports do not confirm this conclusion [22].

Decrease in osmotic potential, leading to osmotic adjustment, is partly a consequence of a reduction of the cell expansion rate rather than an active adaptive process [46]. Osmotic adjustment has been repeatedly reported as an important drought adaptive mechanism through better root growth in dry soil, but there are also cases where no adaptive advantage was linked to it [3].

Measurements of turgor pressure were not made. Correlation between turgor and physiological function has been shown in many studies, but turgor pressure is not always associated with changes in physiological functions which are induced by water stress. It also varies with the type of tissue and the stage of development. The turgor of juvenile tissue undergoes little or no change in reaction to water limitations (cell elongation occurs mostly during the night when cell turgor is less dependent on water stress treatments). More integrative physiological criteria, or a combination of criteria, may be more relevant when screening for drought tolerance of

tuber yield. The absence of a relationship between short-term measurements of physiological characters and more integrative characters, like yield, is a problem. Possibly, it may be alleviated by sequential measurements through time and appropriate integration in physiologically sound growth models and the use of such models to simulate the behaviour of the plant in different drought scenarios.

Increased knowledge of the genetic and physiological regulation of tuberisation will be of help in the future. Use of molecular marker technologies, QTL mapping techniques (comparison of QTL for specific traits and QTL for yield under drought stress or yield stability) may, in the future, increase our understanding of response to drought stress and the efficiency of breeding for drought resistance [40]. A better understanding of the mechanisms of growth and development in leaf, root and reproductive structures at the level of the whole plant remains essential. However, simpler characters, such as morpho-physiological characters, may continue to be of interest.

Control of leaf growth, root growth and carbon transfer in drought-affected plants plays an essential role. Mechanisms at the whole plant level appear to be quite efficient and the transfer of genes for desiccation tolerance may have no appreciable effect on the growth and yields of agronomic plants [46]. In the case of the potato, the understanding of the signification and implications of tuber formation on behaviour in the case of water shortage could benefit from comparison with related species or genus not bearing tubers, such as some wild potatoes and tomato.

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