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Original article

Effects of water shortage on six potato genotypes in the highlands of Bolivia (I): morphological parameters, growth and yield

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Abstract – The objective of this paper is to characterize drought-adaptation, and to identify indicators of drought-tolerance in potato in the Andean Highlands. Six genotypes, representing a range of contrasting morphological and agronomic characters and belonging to three species, were grown in containers. The treatments were R0 (irrigated control), R1 (progressive drought after tuberisation, with a recovery period) and R2 (as R1, but no recovery irrigation). Genotypes differed in plant height, leaf area index (LAI), proportion of ground covered by green foliage and root expansion. Drought did not significantly affect stem number, and slightly decreased plant height and leaf number. It reduced leaf area index and canopy cover in all genotypes. Dry matter production was greatly affected in cultivars Ajahuiri and Luky, but very little in the other genotypes. Under drought, Alpha and CIP 382171.10 gave the highest yields and Luky the lowest. Depending on genotype and degree of yield reduction, yield losses were associated with a decrease either in radiation intercepted, the efficiency of its conversion into dry matter, or harvest index. Harvest index and root biomass correlated well with tuber yield. Other parameters, such as leaf number, plant height and canopy cover, correlated with tuber yield only in the R2 treatment.

drought / intercepted radiation / light conversion / morphology / Andean Highlands

Résumé – **Effets d'un manque d'eau sur six génotypes de pomme de terre (I) : caractères morphologiques, croissance et facteurs du rendement.** Notre but était de caractériser l'adaptation à la sécheresse de génotypes de pomme de terre en altitude dans les Andes et d'identifier des indicateurs de tolérance. Six génotypes ont été cultivés en conteneurs. Les traitements étaient : R0 (témoin), R1 (sécheresse progressive à partir de la tubérisation et récupération) et R2 (sécheresse sans récupération). Des différences de morphologie entre génotypes ont été observées pour la hauteur, l'indice foliaire, la couverture du sol et le développement des racines. La sécheresse n'a pas affecté significativement le nombre de tiges et a diminué légèrement la hauteur des plantes et le nombre de feuilles. Elle a réduit l'indice foliaire et la couverture du sol chez tous les génotypes. La production de matière sèche a été fortement affectée chez Ajahuiri et Luky et très peu chez les autres génotypes. En conditions de sécheresse Alpha et CIP 382171.10 ont présenté les rendements les plus élevés et Luky le plus faible. Suivant le génotype, les pertes de rendement ont été associées, soit à une diminution de la radiation interceptée par le feuillage, soit à l'efficacité de sa conversion en matière sèche, soit à l'indice de récolte. Il y a une bonne corrélation entre indice de récolte et biomasse racinaire d'une part et rendement en tubercules de l'autre. Dans le cas de R2, les autres paramètres tels que le nombre de feuilles, la hauteur des plantes et la couverture du sol par le couvert sont bien liés au rendement en tubercules, et pourraient donc servir d'indicateurs de tolérance à la sécheresse.

sécheresse / radiation interceptée / conversion de la lumière / morphologie / Andes

Abbreviations: CC: canopy cover; C_{dm}: tuber dry matter content; DAP: days after planting, E: efficiency of conversion of Ri into dry matter; HI: harvest index; LAI: leaf area index; Ri: radiation intercepted by green foliage; Wp, Wt, Wr: whole plant (total), tuber and root dry weight, respectively; Y: total tuber yield.

1. INTRODUCTION

Potato is a traditional staple crop produced by more than 200000 families in Bolivia (total production was estimated to be 677000 tons in 1993-94 [32]). It is cultivated mainly in the highlands, above 3000 meters. Around 228 potato cultivars are cultivated in Bolivia [1]. These belong to eight different species and subspecies (*Solanum ajanhuiri, S. goniocalyx,*

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Table I. Characteristics of the six potato genotypes studied.

Variety/clone	Species background*	Chromosome number	Origin	Maturity
Alpha	*Solanum tub* subsp. *tub*	2n = 48	Netherlands	Early
Waycha	*Solanum tub* subsp. *and*	2n = 48	Bolivia	Late
Luky	*Solanum tub* subsp. *and*	2n = 48	Peru	Late
Ajahuiri	Solanum ajanhuiri	2n = 24	Bolivia	Late
Janko Choquepito	Solanum curtilobum	2n = 60	Bolivia	Late
Clone CIP 382171.10	(*tub* × *and*) × *tub*	2n = 48	CIP, Peru.	Early

*Species background: *tub* = *tuberosum; and* = *andigena.*
It should be noted that the Luky used in this trial is a *Solanum tub* subsp. *and,* and not a *Solanum juzepczukii* as is normally the case for Luky potatoes.

S. stenotonum, S. chaucha, S. juzepczukii, S. curtilobum and *S. tuberosum* subspp. *tuberosum* and *andigena*).

Agroeconomic biotic factors, such as pests and diseases, and also abiotic factors, such as frost and low soil fertility, limit potato production in Bolivia. Drought is one of the major constraints in the Andean Highlands of Bolivia, limiting tuber yield and affecting tuber quality [14]. The highest potato yields in Bolivia are between 5 and 7 $t \cdot ha^{-1}$ [10] whereas yields reach 20–35 $t \cdot ha^{-1}$ in Europe and North America. This crop has the potential to yield more than 90 $t \cdot ha^{-1}$ under optimum conditions [3]. The potato is known to be very sensitive to a shortage of water [30, 31] and genotypic differences in drought tolerance have been observed [11, 20]. The wide variations in morphological and physiological characters found among the numerous genotypes of potato grown in Bolivia make these a precious material which can be used to study the relationships between drought tolerance and these characters.

Drought adaptation of plants relies, mainly, on four groups of mechanisms: escape, avoidance, tolerance and recovery [19] (with each mechanism implying specific processes). Many physiological characters of the potato plant (such as stomatal resistance, photosynthesis, leaf water content and leaf water potential), and morphological or agronomic characters (such as leaf area index, leaf senescence, canopy cover, dry matter production, partitioning of assimilates into tubers and tuber yield components) are affected by lack of water, and could be used as indicators of the effects of drought on potato yield. Potato yield also depends upon the timing of water stress within the growing period [27], and upon climatic and soil conditions. Therefore, due to the many processes involved, and the interaction of these with environmental factors, potato response to drought is a very complex issue. Little information is available concerning the morpho-physiological behavior of the native cultivated potato genotypes of Bolivia under drought stress conditions. The objectives of this study were, therefore: (1) to obtain information on the differential response of a subset of native genotypes, with different growing cycles, to early and terminal drought; (2) to identify parameters associated with, or responsible for, tuber yield-response to stress treatments. The information obtained in relation to the first objective should be of direct interest to those using these genotypes in agronomic and plant breeding programs. The information obtained by addressing the second objective should increase our knowledge of the mechanisms involved in drought tolerance. It could also help to determine indirect ways of differentiating between potato genotypes on the basis of their tolerance to water stress, using parameters other than tuber yield.

This paper presents the results of a study on the effects of drought on morphological parameters (canopy cover, plant height, leaf area index, stem and leaf number), growth variables (tuber, root and whole plant dry biomass production), and yield components of the potato crop (total and marketable tuber yield, harvest index, tuber dry matter content and tuber number). The effects of drought on physiological parameters will be presented in a companion paper (Tourneux et al., to be published).

2. MATERIALS AND METHODS

The trial was conducted during the 1995/1996 growing season at Toralapa Research Station, Cochabamba, Bolivia (3450 m asl). Preliminary trials, carried out during the 1994/1995 season, under the same conditions, corroborate the results presented in this paper (Mamani et al., personal communication).

2.1. Plant material

Table I presents the characteristics of the six potato genotypes evaluated. They include an early-maturing cultivar (Alpha), a medium-early genotype (CIP-382171.10) and four late-maturing cultivars (Waycha, Ajahuiri, Luky and Janko Choquepito). The cultivars Alpha and Waycha (commercially grown in Bolivia) were used as controls.

Potato plantlets were cultivated in vitro for four weeks, from stem axillary buds, on a Murashige and Skoog [25] medium supplemented with a 25 $g \cdot l^{-1}$ sucrose solution. Plantlets were cultivated at radiation levels of 40–60 μmol(photons) $m^{-2} \cdot s^{-1}$, under a 16 h/8 h photoperiod and at a temperature of 22 ± 1 °C.

2.2. Experimental conditions

Having reached a height of 4 to 5 cm, the plantlets were transplanted first to greenhouse conditions for four weeks (the adaptation phase), and then outdoors and into large containers (90 × 70 × 40 cm). The containers were placed in a permanent rain shelter. The substrate used was a mixture of soil and sand in a ratio of 80:20.

A randomized complete block design with three irrigation treatments and six potato genotypes was used. There were six plants of the same genotype per container and per treatment, with three replications. Three water regimes (R0, R1, R2) were applied. In the R0 treatment (well-watered control) plants were irrigated twice per week up to field capacity throughout the growing period.

Irrigation volume (V) was calculated as:

$$V\ (m^3) = (FC - H)/100 \times Da \times D \times A \qquad (1)$$

where FC (%) is the field capacity (FC = 21%); H (%) is the actual soil humidity; Da the apparent soil density (Da = 1.23 $g \cdot cm^{-3}$); D the soil depth (D = 35 cm), and A the irrigated area (A = 0.63 m^2).

The plants in the R1 treatment (drought followed by a recovery period) were irrigated normally (in containers) until tuberisation (tuber formation) of cv. Waycha (the reference cultivar) at 54 days after planting (DAP). Watering was then decreased progressively for five weeks, and then stopped for a week (89 to 97 DAP). At 97 DAP, irrigation was reestablished (recovery irrigation).

In the R2 treatment (lethal drought) plantlets were irrigated normally until tuberisation of the cultivar Waycha. Watering was then decreased, progressively, for five weeks, and was suspended at 97 DAP until plant death (there was no recovery irrigation). The R1 and R2 treatments were thus identical until 97 DAP.

Drought stress risks are high in the potato growing areas of the highlands of Bolivia. The type of drought stress observed in Bolivia is relatively erratic. The R1 treatment was applied to simulate a drought stress during the growing period, which is normally followed by a period of rain. The R2 treatment simulates the situation where there is a decrease in rain at the end of the growing season, and which usually leads to plant death.

2.3. Morphological parameters

Secondary stem number, leaf number and plant height were evaluated (two measurements were made for each container on two plants selected at random). A visual estimation of canopy cover or the fraction of soil covered by green leaves (CC) was obtained using a grid system [4, 24]. The grid used had 100 rectangles within a 0.7 × 0.9 m area. The number of rectangles with more than 50% of green leaf coverage were counted. The percentage of canopy cover was calculated as CC = number of rectangles counted × 100/total number of rectangles.

CC was evaluated weekly. Stem number, main stem leaf number and plant height were evaluated twice: at 77 DAP, or five weeks after the initiation of the drought treatment, and at 98 DAP, one day after rewatering in the R1 treatment and 44 days after the initiation of the R2 treatment.

2.4. Leaf area index

Leaf Area Index (LAI) was evaluated before the water shortage at 54 DAP, at the end of the water shortage period at 97 DAP, and at the final harvest. Destructive measurements were necessary for measuring LAI, so a fourth replication was grown for the sole purpose of evaluating LAI before each harvest. No leaf area meter was available to measure leaf area. Consequently we collected, at random, a sample of six leaf discs of 2 cm in diameter. These leaf discs were immediately oven-dried at 80 °C for 24 hours, and then weighed. Specific leaf dry weight was calculated as SLDW ($g \cdot cm^{-2}$) = dry weight (g)/leaf area (cm^2). All the plant leaves in each container evaluated were harvested, oven-dried and weighed. Total leaf area (cm^2) was calculated as total leaf dry weight (g)/SLDW. The LAI ($m^{-2} \cdot m^{-2}$) was calculated as leaf area / soil total area.

2.5. Tuber yield and dry biomass

All the plants in each container were harvested 120 DAP in the R2 treatment, and 133 DAP in R0 and R1 treatments.

Fresh tuber weight was measured for each container, and the total number of tubers was counted. Ware tubers (>30 mm in diameter) were counted and weighed.

Root, tuber, leaf, stem and fruit dry biomass (including dead material) were measured. All roots, stems and fruits were oven-dried at 80 °C for 72 hours, and then weighed. To measure tuber dry weight (Wt), a 250 g-fresh tuber sample was collected. The tubers were sliced, oven-dried for 72 hours at 80 °C and weighed, in order to obtain a tuber dry matter percentage. Wt was calculated as total tuber fresh weight × tuber dry matter content. Harvest index was calculated as HI (%) = tuber dry weight/total dry biomass ×100.

2.6. Partitioning of total tuber yield

Total tuber yield can be divided into four components as indicated in the following equation [22, 27]:

$$Y = Ri \times E \times HI / C_{dm} \qquad (2)$$

where Y = total tuber yield; Ri = cumulative solar radiation intercepted by the foliage; E = efficiency of conversion of Ri into dry biomass; HI = harvest index and C_{dm} = tuber dry matter content.

Canopy cover provides a good estimate of the fraction of radiation intercepted by the foliage [4, 12]. Therefore we assumed the following equation: radiation intercepted = canopy cover × incident radiation (incident radiation (Rad) being measured daily in the adjacent Meteorological Station at the Toralapa Research Station). Cumulative Ri, throughout the cycle, was calculated as Σ (CC × Rad) from planting day to harvest time [26] – daily canopy cover CC was obtained from the CC curves (Fig. 2). E was calculated as Wp/Ri.

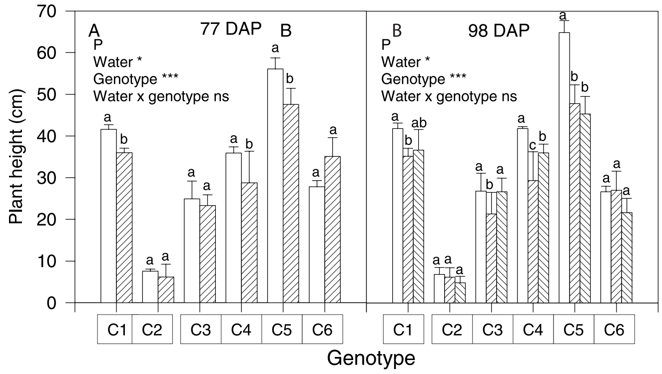

Figure 1. Height in cm of six potato genotypes in three treatments: well-irrigated (□), drought stress R1 (▨) and drought stress R2 (▨). A. Plant height at 77 DAP (five weeks after the beginning of drought treatments) and B. at 98 DAP (one day after the R1 recovery treatment). C1 = Waycha; C2 = Alpha; C3 = clone CIP 382171.10; C4 = Ajahuiri; C5 = Luky; C6 = Janko Choquepito. Bars indicate standard error of the mean of six measurements. P = probability level of statistical significance *** $P < 0.001$; * $P < 0.05$; ns non-significant. For each genotype separately, different letters (a, b) indicate significant differences between treatments when Duncan's Multiple Range Test ($P < 0.05$) was conducted within cultivars.

3. RESULTS AND DISCUSSION

3.1. Morphological parameters

Highly significant genotypic differences were observed in morphological parameters ($P < 0.001$ in plant height, main stem leaf number and stem number). For example, cv. Alpha was very short with less than 10 cm height (Fig. 1), and presented less stems and leaves than the other varieties (Tab. II). Alpha had a rosette type growth due to the fact that in vitro plantlets were used as planting material since it was the only disease free material available at the time. Its canopy cover did not exceed 0.35 (Fig. 2), and its LAI was lower than 1 (Fig. 3). In comparison, cv. Luky was very high with 63 cm at 98 DAP (Fig. 1), had many leaves (Tab. II), and consequently a high LAI with a value of 5.8 in the control treatment at 97 DAP. Cv. Ajahuiri had also many stems and leaves (Tab. II), and a high LAI with a value of 5.2 in the control at 97 DAP (Fig. 3).

Although statistically significant differences were observed between treatment ($P < 0.001$) in leaf number per main stem (Tab. II) and in plant height (Fig. 1), the effect of drought treatments on these parameters was slight. Effects on plant height have been reported in the literature on this subject, but they depend on cultivar characters, such as time to maturity (earliness), and also on the timing of the drought [7]. The drought treatments did not have any significant effect on stem number (Tab. II). This fact agrees with Lynch and Tai [21], who did not observe any effect of drought on stem number in eight potato genotypes. Treatment-by-genotype interaction was not significant for stem number, main stem leaf number, or plant height, indicating that observations of drought effects on these parameters did not allow discrimination among cultivars.

Figure 2 shows that, in the control, full canopy cover (CC = 1.0) was reached during no less than 42 days, from 58 to 100 DAP for each genotype except in the case of cultivar

Table II. Number of stems and number of leaves of the main stem of six potato genotypes at 77 days after planting in containers (DAP) and at 98 DAP. P = probability level of statistical significance *** $P < 0.001$; ns non-significant. For each genotype, means followed by different letters (a, b) indicate significant differences between treatments using Duncan's Multiple Range Test ($P < 0.05$). Values in brackets indicate standard error of the mean of six measurements.

Genotype	Number of stems per plant 77 DAP		Main stem leaf number 77 DAP		Main stem leaf number 98 DAP		
	R0	R1 = R2	R0	R1 = R2	R0	R1	R2
Waycha	7.2 a	9.0 a	11.7 a	10.7 a	10.5 a	9.0 a	10.0 a
	(2.3)	(1.4)	(2.1)	(0.7)	(1.3)	(1.0)	(1.4)
Luky	4.7 a	3.8 a	16.5 a	13.5 b	16.0 a	13.0 b	13.3 b
	(0.7)	(1.3)	(1.6)	(1.5)	(1.0)	(1.3)	(1.5)
Janko Choquepito	8.3 a	9.5 a	13.2 a	11.8 b	10.5 a	9.2 a	8.7 b
	(2.2)	(1.9)	(0.9)	(0.9)	(1.6)	(1.3)	(0.5)
Clone	4.0 a	2.8 a	15.7 a	14.2 a	13.7 a	11.2 b	10.7 b
CIP 382171.10	(1.6)	(1.1)	(2.1)	(1.1)	(1.2)	(1.5)	(1.1)
Alpha	2.5 a	2.8 a	8.5 a	7.5 a	7.2 a	5.0 b	5.7 b
	(1.0)	(1.8)	(1.0)	(1.7)	(1.3)	(0.8)	(0.9)
Ajahuiri	8.0 a	11.0 a	17.5 a	14.8 a	16.5 a	13.5 b	13.0 b
	(0.8)	(2.9)	(2.1)	(2.4)	(1.5)	(0.8)	(1.3)
	P		*P*		*P*		
Water	ns		***		***		
Genotype	***		***		***		
W × G	ns		ns		ns		

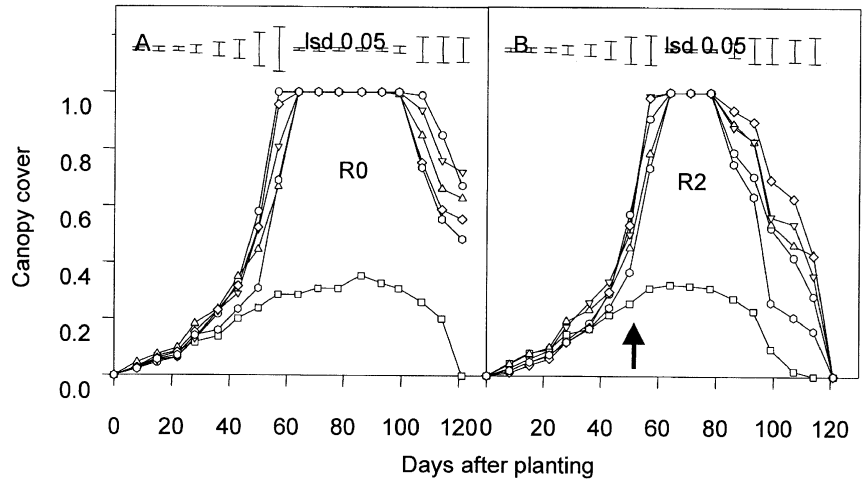

Figure 2. Time course of canopy cover development of six potato genotypes when well-irrigated (A) or subjected to drought (B). R0 denotes the irrigated control and R2 denotes the treatment of water stress without recuperation. (O) Waycha, (□) Alpha, (∇) Ajahuiri, (△) Clone CIP 382171.10, (◇) Luky, (⬡) Janko Choquepito. The arrow indicates the beginning of the drought treatment.

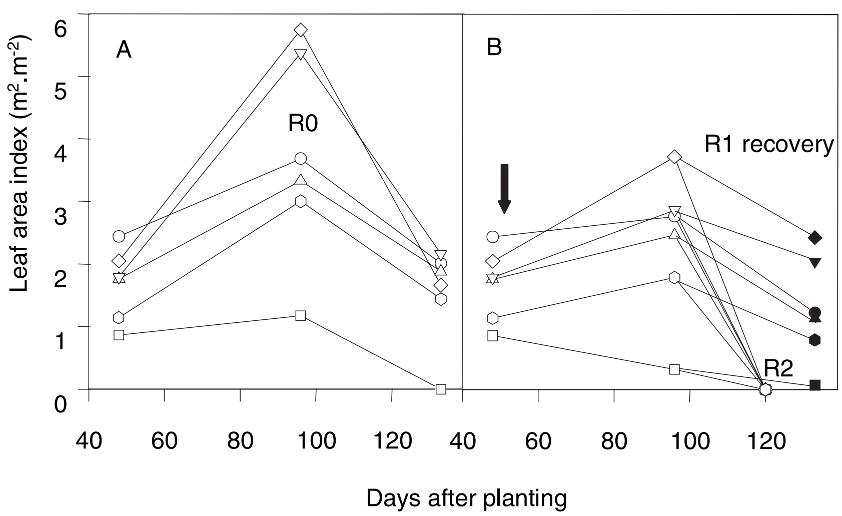

Figure 3. Time course of leaf area index (LAI) development of six potato genotypes. See Figure 2 for definition of symbols; R1 denotes the treatment of water stress followed by rewatering to allow recovery.

Alpha. CC then decreased to 0.50–0.75 at 120 DAP, which was harvest time. In the R2 treatment, a full canopy was reached in all cultivars, except Alpha, for at least 22 days, until 80 DAP. CC then decreased faster, due to leaf wilting and early senescence. During the period of decrease and, essentially, after 100 DAP, cultivars Alpha and Janko Choquepito showed the smallest CC values.

Leaf area index (LAI) decreased in response to drought in each cultivar. Cultivar Luky maintained the highest LAI during the drought period (3.8 at 97 DAP), whereas cultivar Alpha exhibited the lowest LAI (0.3). LAI and CC were strongly correlated, with an r^2 of 0.916 (Fig. 4). The relation between these two parameters was given by CC = LAI/3.3, until LAI reached the value of 3.3. For higher values of LAI, CC became equal to 1. This relation is close to that obtained by Mackerron and Waister [23] and Haverkort et al. [13]. Canopy cover, evaluated using the grid method, provided a good estimate of LAI for LAI < 3.3. This method has the advantage of being easy, fast and non destructive.

3.2. Total dry biomass production and roots

Total dry matter (Wp) differed between genotypes in the control treatment (Tab. III). Cultivars Alpha and clone CIP 382171.10 presented the lowest Wp, and cultivars Luky and Ajahuiri the highest. However, these differences were not statistically different. Nevertheless, significant differences for Wp production were observed among genotypes in the R1 and R2 treatment. A highly significant treatment-to-genotype interaction ($P < 0.01$) was observed. The Wp of cultivars

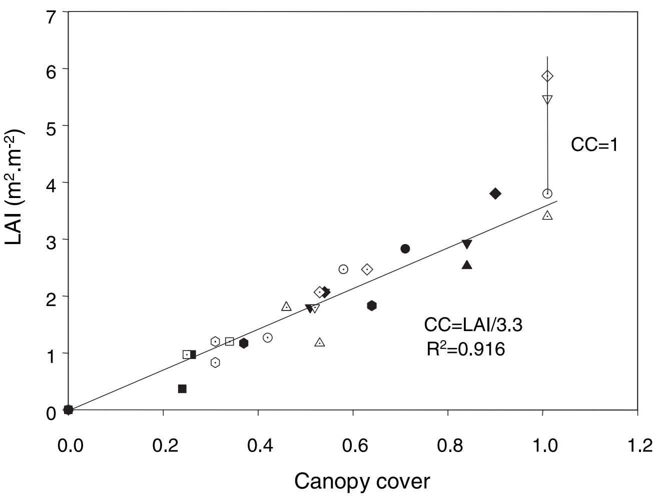

Figure 4. Relationship between canopy cover and LAI evaluated at 54 DAP, 97 DAP and at harvest time in the R0 irrigated control treatment (open symbols) and in the drought treatments (closed symbols). (O) Waycha, (□) Alpha, (∇) Ajahuiri, (Δ) Clone CIP 382171.10, (◇) Luky, (⬡) Janko Choquepito.

Waycha, Alpha and clone CIP 382171.10 did not decrease significantly in response to drought, while the Wp of the cultivars Luky and Ajahuiri strongly decreased.

A large root system is thought to be one of the plant's drought adaptation mechanisms [19]. Table III shows highly significant differences in root dry biomass (Wr) between genotypes (P < 0.001). Cultivar Luky presented the highest Wr (Tab. III), and Alpha the lowest. Root dry biomass of cultivar Waycha increased significantly in response to drought. A good indicator of drought-adaptation is root-to-shoot ratio, which was shown to increase in response to drought [2, 11, 15]. Root-to-shoot ratio was very high in cultivar Luky, and very low in cultivar Alpha. It increased significantly in response to drought only in cultivar Waycha and clone CIP 382171.10, indicating that root growth was maintained to a greater extent than shoot growth during drought treatments in these potato genotypes (Fig. 5). Despite this differential behavior among the genotypes, the overall treatment-by-genotype interaction was non-significant for this character.

3.3. Tuber yield, harvest index and yield components

The production of tuber dry matter decreased in response to drought (Tab. III), with differences apparent between genotypes. The tuber dry matter of cultivars Luky and Ajahuiri strongly decreased in the R2 treatment, when compared with controls R0 (from 601.4 to 89.0 $g \cdot m^{-2}$ and from 866.5 to 290.6 $g \cdot m^{-2}$, respectively). However, clone CIP 382171.10 and cultivar Alpha did not demonstrate much change in tuber dry matter production, which remained high during water stress. The early maturation of these genotypes may have allowed them to partly escape the drought period, by early tuber initiation and bulking. In a study by Deblonde et al. [8], in which the effect of early drought and late drought were compared with a control, the relation between speed of maturation, timing of water shortage and effect on tuber yield was not as marked as expected. However, later cultivars were shown to tolerate water shortage occurring in the early part of the season.

Table III. Tuber, root and total dry biomass of six potato genotypes: well-irrigated (R0) or under drought stress (R1, R2). P = probability level of statistical significance *** P < 0.001; ** P < 0.01; ns non-significant. For each genotype, means followed by different letters (a, b) indicate significant differences between treatments using Duncan's Multiple Range Test (P < 0.05). Values in brackets indicate standard error of the mean of three measurements.

Genotype	Tuber dry biomass (Wt) ($g \cdot m^{-2}$)			Root dry biomass (Wr) ($g \cdot m^{-2}$)			Total dry biomass (Wp) ($g \cdot m^{-2}$)		
	R0	R1	R2	R0	R1	R2	R0	R1	R2
Waycha	622.2 a (172.4)	628.3 a (90.2)	511.6 a (60.3)	18.4 a (3.7)	26.7 ab (7.1)	41.9 b (5.9)	824.1 a (187.9)	836.3 a (103.7)	689.5 a (74.1)
Alpha	628.4 a (129.0)	583.3 a (45.9)	565.4 a (83.7)	1.6 a (0.7)	1.8 a (0.8)	1.5 a (0.8)	720.3 a (150.3)	650.2 a (51.4)	614.3 a (88.4)
Clone CIP 382171.10	487.3 a (29.7)	455.1 a (27.3)	476.7 a (138.9)	15.1 a (3.7)	25.7 a (14.0)	36.3 a (10.3)	712.2 a (17.0)	689.5 a (41.7)	697.0 a (146.3)
Ajahuiri	866.5 a (270.6)	753.3 ab (171.1)	290.6 b (117.6)	58.4 a (5.4)	50.2 a (10.5)	41.6 a (6.8)	1307.8 a (244.9)	1112.7 ab (163.0)	648.1 b (113.7)
Luky	601.4 a (153.8)	288.1 b (77.1)	89.0 b (21.7)	141.3 a (26.0)	151.7 a (34.9)	127.5 a (14.8)	1191.3 a (91.4)	888.3 b (99.7)	551.9 c (41.3)
Janko Choquepito	707.1 a (80.6)	404.1 a (84.3)	576.3 ab (161.9)	16.9 a (1.6)	21.0 a (19.0)	17.8 a (8.1)	918.4 a (90.0)	606.3 b (94.1)	694.9 ab (101.6)
		P			P			P	
Water		***			ns			***	
Genotype		**			***			***	
W × G		**			ns			**	

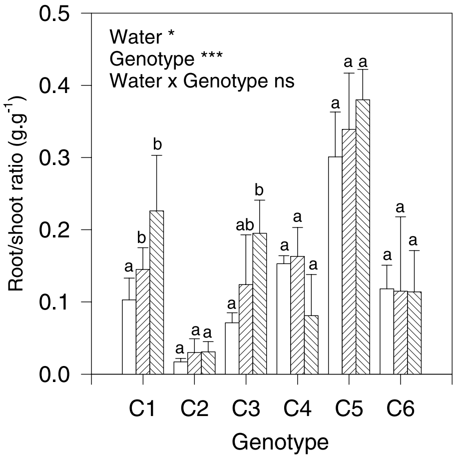

Figure 5. Root-to-shoot ratio (shoot dry matter/root dry matter) of six potato genotypes under three treatments: well-irrigated ( ) or under drought stress (, R1; , R2). C1 = Waycha; C2 = Alpha; C3 = clone CIP 382171.10; C4 = Ajahuiri; C5 = Luky; C6 = Janko Choquepito. Bars indicate standard error of the mean of three replicates. *P* = probability level of statistical significance *** $P < 0.001$; * $P < 0.05$; ns non-significant. For each genotype, different letters (a, b) indicate significant differences between treatments when Duncan's Multiple Range Test ($P < 0.05$) was conducted within cultivars.

Cultivars Waycha and Janko Choquepito also maintained a high level of tuber dry matter production under the R2 treatment. The R1 treatment did not affect tuber dry matter production significantly, except in cultivars Luky and Janko Choquepito. The same trend was observed for the fresh total and marketable yield (tubers > 30 mm in diameter). Cultivar Alpha and clone CIP 382171.10 gave the highest yield, and cultivar Luky the lowest one (Figs. 6 A and B). Despite the differences observed, the overall treatment-by-genotype interaction for total and marketable tuber yields remained non-significant.

The very low tuber production observed in cultivar Luky in the drought treatments (Fig. 6 and Tab. III) was due mainly to a low partitioning of dry matter into tubers as showed by the harvest index (HI), which declined strongly, from 49.8 in R0 to 15.9 in R2 (Tab. IV). However, total dry matter production was similar to that of the other genotypes (Tab. III).

Significant change ($P < 0.001$), as well as a highly significant treatment-by-genotype interaction ($P < 0.001$), was observed in HI in response to drought. Cultivars Luky and Ajahuiri demonstrated a decrease of HI in response to water stress, and cultivar Alpha showed a slight increase (Tab. IV). Moreover, highly significant differences were observed between genotypes ($P < 0.001$) for HI. In the controls, the early-maturing cultivar Alpha had a very high HI, whereas the late-maturing cultivar Luky had a low HI (values were 87.3 and 49.8, respectively). These results are in agreement with those of Jefferies [15] who observed a relationship between HI and cultivar precocity, early-maturing cultivars showing the highest HI values.

Cultivar Alpha and clone CIP 382171.10 had few tubers per plant (Tab. IV), but the percentage of marketable tubers was higher than 50%. Cultivar Janko Choquepito had many tubers, but only less than 15% were marketable. The number of tubers per plant decreased in response to drought stress, except in cultivar Alpha and clone CIP 382171.10. This decrease was more marked in cultivar Luky. Mackerron and Jefferies [22] showed that drought stress reduced tuber number when it was applied during tuber initiation. This could explain why no change was observed in the tuber number of the early-maturing genotypes Alpha and clone 382171.10 (Tab. IV), tuber initiation of these genotypes having occurred before the onset of water stress.

Total tuber yield can be divided into four components, corresponding to four factors or processes by which tuber yield is affected, as indicated in equation (1). Table V presents, in relative values (drought divided by controls), each of these components. The cause of yield losses appears to depend on genotype. Decrease in total tuber yield is likely to

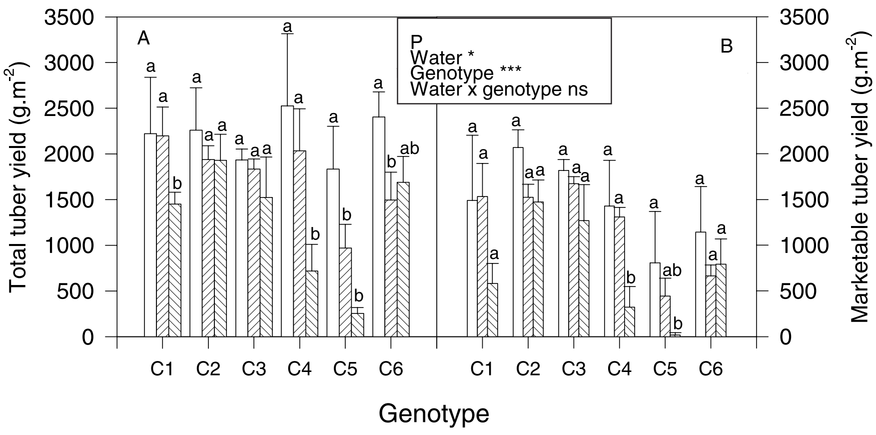

Figure 6. Total tuber yield (A) and marketable tuber yield (tuber diameter > 30 mm) (B) of six potato genotypes under three experimental treatments: well-irrigated ( ) or subjected to drought stress (, R1; , R2). C1 = Waycha; C2 = Alpha; C3 = clone CIP 382171.10; C4 = Ajahuiri; C5 = Luky; C6 = Janko Choquepito. Bars indicate standard error of the mean of three replicates. *P* = probability level of statistical significance *** $P < 0.001$; ns non-significant. For each genotype, different letters (a, b) indicate significant differences between treatments with Duncan's Multiple Range Test ($P < 0.05$).

Table IV. Yield components of six potato genotypes: well-irrigated (R0) or under drought stress (R1, R2). *P* = probability level of statistical significance *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns non-significant. For each genotype, means followed by different letters (a, b) indicate significant differences between treatments using Duncan's Multiple Range Test ($P < 0.05$). Values in brackets indicate standard error of the mean of three measurements.

Genotype	Tuber dry matter content (%)			Harvest index (%)			Number of tubers per plant (m^{-2})			% marketable tubers (>30 mm)		
	R0	R1	R2	R0	R1	R2	R0	R1	R2	R0	R1	R2
Waycha	28.0	28.6	30.5 (1.1)	74.5 a (4.8)	74.9 a (1.8)	64.3 a (4.3)	34.1 a (1.4)	29.1 a (1.7)	31.2 a (5.8)	19.3 a (9.2)	23.9 a (6.9)	9.9 a (5.2)
Alpha	27.8	30.1	29.3 (0.8)	87.3 a (0.9)	89.7 b (1.2)	92.0 c (0.8)	15.6 a (4.4)	16.1 a (2.7)	15.0 a (2.2)	55.1 a (7.7)	44.1 a (6.8)	43.8 a (7.0)
Clone CIP 382171.10	25.2	24.8	31.3 (3.0)	68.4 a (2.8)	66.0 a (0.5)	67.0 a (7.2)	9.5 ab (0.2)	8.6 b (1.4)	11.3 a (1.8)	64.9 a (6.3)	66.3 a (13.9)	49.6 a (0.5)
Ajahuiri	34.3	37.1	40.4 (2.1)	64.7 a (8.1)	67.0 a (5.1)	43.2 a (11.3)	58.6 a (11.8)	50.9a (18.2)	28.8 a (5.7)	10.1 a (6.3)	13.3 a (3.8)	5.8 a (4.9)
Luky	32.8	29.7	34.8 (1.0)	49.8 a (8.7)	31.9 b (6.0)	15.9 c (2.8)	35.1 a (2.0)	27.8 a (1.1)	13.0 b (5.2)	13.2 a (3.3)	7.7 b (3.5)	0.6 c (0.09)
Janko Choquepito	29.4	26.9	31.0 (0.7)	76.9 a (3.7)	65.9 b (3.8)	75.1 ab (1.8)	46.4 a (3.6)	35.2 b (0.8)	36.0 b (1.6)	15.4 a (2.7)	9.0 a (1.7)	10.6 a (3.1)
					P			*P*			*P*	
Water					***			**			*	
Genotype					***			***			***	
W × G					***			ns			*	

Table V. Relative values of yield components of drought-stress (R1, R2) treatments (values divided by those of R0 (irrigated control) treatment. Y = total tuber yield; Ri = intercepted radiation assuming that Ri = canopy cover × incident radiation; E = efficiency of conversion of intercepted radiation into dry biomass, estimated as the ratio of total dry matter by cumulated canopy cover; HI = harvest index; C_{dm} = tuber dry matter content.

Genotype	Treatment	Y =	Ri ×	E ×	HI ×	$1/C_{dm}$
Waycha	R1	0.98	0.79	1.27	1.00	0.98
	R2	0.65	0.73	1.13	0.86	0.92
Alpha	R1	0.85	0.71	1.26	1.03	0.92
	R2	0.85	0.81	1.04	1.06	0.95
Clone	R1	0.95	0.88	1.10	0.96	1.02
CIP 382171.10	R2	0.79	0.82	1.22	0.98	0.81
Ajahuiri	R1	0.81	0.88	0.96	1.04	0.92
	R2	0.28	0.82	0.61	0.67	0.85
Luky	R1	0.53	0.97	0.77	0.64	1.10
	R2	0.14	0.87	0.53	0.32	0.94
Janko Choquepito	R1	0.62	0.78	0.85	0.86	1.09
	R2	0.70	0.72	1.05	0.98	0.95

be due to a decrease in intercepted radiation (R_i), especially in cultivars Janko Choquepito (–21.8% and –28% in the R1 and R2 treatments), Waycha (–20.8% and –27.3%) and Alpha (–28.7% and –18.5%). A decrease in E (efficiency of conversion of R_i into biomass) affected tuber yield of cultivars Ajahuiri (–38.6% in the R2 treatment) and Luky (–23.1% and –46.6% in the R1 and R2 treatments). An increase in E was identified in cultivars Waycha, Alpha and clone CIP 382171.10. Cultivar Luky showed a strong decrease in E, with a slight decrease in Ri. By contrast, genotypes that suffered strong decreases in Ri (such as Waycha, Alpha, Janko Choquepito) exhibited a slight decrease (or increase) in E, an

Table VI. Correlation coefficients between total tuber yield and morphological, growth and agronomic parameters in R1 and R2 drought treatments (df = 16).

Treatment	Stem number 77 DAP	Leaf number 77 DAP	Leaf number 98 DAP	Plant eight 98 DAP	Cumulative[a] canopy cover	Leaf dry biomass at harvest	Root dry biomass at harvest	Total dry biomass at harvest	Harvest index	% Tuber dry matter
R1	0.299	–0.231	–0.271	–0.467 (*)	–0.225	–0.375	–0.619 (**)	0.364	0.763 (**)	0.170
R2	–0.08	–0.549 (*)	–0.748 (**)	–0.666 (**)	–0.635 (**)	–0.695 (**)	–0.776 (**)	0.629 (**)	0.938 (***)	–0.689 (**)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
[a] Cumulative canopy cover is calculated as the integration of the curve of Figure 2 from planting day to harvest time.

observation in accordance with Harris [11]. Nevertheless, clone CIP 382171.10, in the R1 and R2 treatments, and cultivar Ajahuiri, in the R2 treatment, both showed a slight decrease in Ri and little change in E.

Yield loss was partly due to a decrease in harvest index in cultivars Luky, in the R1 and R2 treatments, and Ajahuiri, in the R2 treatment. Genotypes suffering a strong decrease in HI also exhibited a strong decrease in E (Tab. V). Tuber dry matter content was not affected by drought, except in the case of clone CIP 382171.10 (which exhibited an increase of 19.5% in the R2 treatment) and, to a lesser extent, in cultivar Ajahuiri (which exhibited an increase of 15.1% in the R1 treatment).

Several authors stated that drought had strong effects on intercepted radiation [9, 12, 17, 29]. A decrease in radiation intercepted by the foliage has been reported [12, 17] to be a main cause of yield losses in four potato cultivars subjected to drought. When comparing cultivars which mature at different rates and with different drought tolerances, it was found that a ranking of tuber yields was consistent with a ranking based on intercepted radiation and ground cover duration [6]. Effects on E [9, 17, 29] and on harvest index HI [15, 18] have also been reported. Moreover, an increase in tuber dry matter content has also been found to be an important factor influencing tuber yield variations in response to drought stress [17, 18], although in this trial it played a minor role.

Tuber dry matter content of cultivar Luky and clone CIP 382171.10 increased in response to drought (+15% and +20% in the R2 drought treatment, respectively). The effect of water stress on tuber dry matter content was much lower in other genotypes. The high dry matter content observed in the R0 treatment (higher than, or at the higher limit of, the range of 18–26% reported for most cultivars [11]) might also be due to growing conditions in the containers. Dry matter content of tubers has been reported to be influenced by a wide range of factors, mainly radiation, soil temperature and cropping techniques. Low application of N and K can increase the percentage of dry matter, as can a higher temperature and soil with a high sand, gravel or light loam content [5, 11].

In the present trial, tuber dry matter content was only slightly affected by drought, whereas Ri, HI and E could better explain yield losses due to water stress (but only to an extent which depends on the genotype). Cultivars Luky and Ajahuiri showed a strong decrease in E in response to treatment.

3.4. Correlation between total tuber yield and morphological and agronomic parameters

Table VI gives correlation coefficients between total tuber yield and morphological parameters (such as stem number, leaf number, plant height, and canopy cover), growth parameters (such as leaf, root, and total biomass), and agronomic parameters (such as harvest index and tuber dry matter content). Correlation was found between yield and several of the agro-morphological characters studied, especially in the R2 treatment (Tab. VI). Both agronomic and morphological parameters are determined on a long term basis and by complex effects involving cumulative processes. This may explain why yield is better associated with morphological characters than with instantaneous or short term measurements of physiological processes, as pointed out by Spitters and Schapendonk [27] .

HI is the parameter that exhibits the highest correlation with total tuber yield (Y), in both R1 ($P < 0.01$) and R2 ($P < 0.01$) treatments. Final total dry biomass was less strongly correlated with Y, indicating that, in the genotypes studied, yield elaboration was more affected by the variation of assimilates' distribution in tubers (HI) than by the variation of the total amount of dry biomass produced.

Root dry biomass exhibited a high negative correlation with total yield ($P < 0.01$), indicating that genotypes exhibiting a strong root expansion (for example, cultivar Luky) produced a high amount of root dry biomass at the expense of tuber yield. Moreover, a high significant negative correlation ($P < 0.01$) was found to exist between root biomass production and harvest index (data not shown) in the R1 and R2 treatments, also indicating a negative relationship between root production and yield elaboration.

The other parameters studied were not correlated with total yield (Tab. VI) in the R1 treatment. A highly significant correlation with yield in the R2 treatment was noted only for leaf number at 98 DAP, cumulative CC, final leaf dry biomass and tuber dry matter content ($P < 0.01$). These parameters could serve as indicators of drought-tolerance in potato. The stem number at 77 DAP was not correlated with total yield, in neither the R1 nor in the R2 treatments.

3.5. Adaptation to drought and low tuber yield: the case of cv. Luky

Cultivar Luky exhibited great drought-adaptation capacities, however, its tuber yield was very low in drought-conditions. As for the other species studied, it seems that morphological and physiological adaptive criteria are not always an effective means of identifying drought-tolerant potato genotypes. Genotypes tolerant to abiotic stresses, such as frost and drought, may expend most of their energy resisting the stress, to the detriment of tuber yield. For a screening process for superior genotypes, it is important to look for the right balance between abiotic stress resistance and yield ability. Obviously, characters that determine high potential tuber yield are not necessarily similar to those which determine survival or tuber yield under stress conditions. This fact clearly also applies to marketable yield. The strategies developed by the potato for drought survival, either as individual plants or as successive generations, are likely to differ as a result of the different difficulties the plant encountered in its environment through evolutionary time.

The possibility exists that the plant's two alternative methods of reproduction played an important role in that regard. It has been hypothesized that asexual reproduction through tubers (that method related to agricultural tuber yield) is an asset under favorable, stable conditions and with low competition with other species [11]. By contrast, if the environment is changing, or if competition is more intense, vegetatively propagated plants are disadvantaged, and tend to disappear and be replaced by new plants developed from true seeds [11]. Both methods of reproduction have definite advantages and disadvantages, according to environmental conditions.

Clonal reproduction enables the survival of individuals with low fertility, as frequently found in the case of interspecific crossing. Sexual reproduction, however, has a higher multiplication rate and also greatly limits the transmission of diseases through generations, such as those caused by viruses [5, 11]. Longevity of seed tubers is much less than that of true seeds. In short term adverse conditions, however, plants developing from tubers are less dependent on the environment during their establishment, due to their larger reserves [5]. The length of the necessary growing season is also shorter in the case of vegetative reproduction. This is an advantage in the case of adverse conditions at the end of the growing season [5]. However, the larger diversity (lower uniformity) of seedlings grown from seeds may be an advantage in fluctuating conditions. Thus, the way different species, or varieties, of potato have evolved and adapted to the environment may differ greatly according to the conditions encountered, and does not necessarily favor tuber yield. Moreover, flowering and berry development do not necessarily respond to the environment in the same way as tuberisation and tuber growth. Special treatments may be needed when crops are cultivated to obtain true seed [28], removal of young tubers being a method often used to favor flowering and true seed production [5]. Optimum temperatures and the effects of water shortages may differ for the two modes of reproduction, but the effects of a water shortage on true seed production has been much less studied than its effect on tubers. However the hypothesis that there exists a conflict between tubers and shoots has been considered as not supported experimentally [11]. In the specific case of a water shortage, the limited ability of the potato's root system to conduct water has been associated with its limited length and density in the soil, as well as with its shallow depth. Nevertheless desert and wild coastal species of potato are able to withstand considerable drought and heat, but this point may be less applicable to cultivated potato species, because they are reported to have evolved in cool temperate regions [11]. The cultivated potato responds markedly to irrigation, and is considered very sensitive to water [5].

The production of high root biomass at the expense of tuber yield by cultivar Luky, and the highly significant negative association found between root biomass production and harvest index (data not shown) in the R1 and R2 treatments, suggest that survival through investment in more root tissue (possibly ensuring the survival of the individual plant in conditions of water limitation) is not necessarily associated with survival through tuber production (survival through a next generation obtained vegetatively). We are aware that this discussion, based mainly on the relevant literature, may seem rather speculative. To what extent the behavior of cultivar Luky (which has a high drought adaptation capability and high root-to-shoot ratio, but a low tuber yield) may be explained in terms of this discussion remains an open question.

4. CONCLUSIONS

The present study revealed wide morphological and physiological differences between the six potato genotypes studied.

Cultivar Alpha yielded well under water stress conditions, and its total tuber yield was not affected by drought treatments. This may be due to the fact that it matures early, which allowed it to escape to drought stress. Moreover, foliage expansion was very weak, as shown by its very low leaf area index and canopy cover (Figs. 2 and 3); this would have contributed to reduced water loss.

Cultivar Luky also showed capacities for drought adaptation; its root system was very developed (Tab. III). Nevertheless, this variety yielded very little, especially under drought stress conditions. This lack of a relationship between tuber yield and adaptive criteria had already been observed by Carrasco et al. (personal communication) in field studies, in which six potato genotypes were submitted to frost stress. Varieties with leaves presenting a very good frost-resistance were not always those which yielded well. Clone 382171.10 and cultivar Alpha were early-maturing and yielded well under drought stress conditions, with no effect of drought treatments on tuber yield (Fig. 6). In cultivar Waycha and clone 382171.10, root dry biomass and root-to-shoot ratio increased significantly in response to water stress (Fig. 5). These factors are considered to be mechanisms of plant drought-adaptation [3, 11, 16]. However, cultivar Ajahuiri did not show particular drought-adaptation characteristics and did not yield well under drought stress conditions. This is perhaps due to its high foliage development (Tab. I and Fig. 3), which probably accentuated its water losses.

We observed wide genotypic differences for the effects of drought stress on tuber yield (Tab. V). Early-maturing genotypes clone CIP 382171.10 and Alpha did not show a significant tuber yield decrease in response to drought, but cultivar Luky showed drastic losses of yield in response to both the R1 and the R2 drought treatments. Strong decreases were observed in: intercepted radiation in cultivars Waycha, Alpha, and Janko Choquepito; conversion efficiency of Ri into dry matter, in cultivars Ajahuiri and Luky; and in harvest index, in cultivars Ajahuiri and Luky. Nevertheless, the cultivars exhibited little change in tuber dry matter content, except in clone CIP 382171.10 (which demonstrated an increase of 19.5% in comparison with the control), and in cultivar Ajahuiri (which exhibited an increase of 15%, but only in the R2 treatment).

Harvest index showed the highest correlation with tuber yield, while total dry matter showed only a weak correlation with total tuber yield. This could indicate that genotypic variations in tuber yield were due more to differences in the distribution of assimilates into tubers, than to variations in production of dry matter. Morphological parameters such as plant height, main stem leaf number and cumulative canopy cover also appeared to be significantly correlated with tuber yield, but only in the R2 treatment. These rapidly- and easily-measured parameters could be good indicators of drought-tolerance in the potato. Nevertheless, additional data should be obtained to take into account spatio-temporal variability in environmental conditions.

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