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Physiological responses of quinoa (*Chenopodium quinoa* Willd.) to drought and waterlogging stresses: dry matter partitioning

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ABSTRACT. Quinoa (*Chenopodium quinoa* Willd.) plants responded differently to drought and waterlogging. Plant and root dry weights (DW) were lower in both drought and waterlogging conditions than in well-watered conditions, but the lowest values were obtained under waterlogging. However, the root weight ratio (RWR: root dry weight per unit of plant dry weight) did not show significant changes in any treatments. Leaf area (LA) and specific leaf area (SLA) were higher in drought than in waterlogging, but drought and control treatments showed no significant differences. Conversely, specific leaf weight (SLW) and relative water content (RWC) were higher under waterlogging than drought. However, between control and waterlogging conditions, no a significant difference in RWC values emerged. In addition, the number of leaves and height of plants remained unchanged in all treatments. The lowest content of total chlorophyll, chlorophyll *a* and chlorophyll *b* was observed in waterlogging conditions while between control and drought treatments there were no significant differences. Chlorophyll *a*/*b* ratio remained unchanged in all treatments. Leaf nitrogen content, expressed per unit of leaf dry weight (N_m), was lower in control plants and remained unchanged under drought and waterlogging conditions. However, when it was expressed per unit of leaf area (N_a), waterlogging produced the highest value. In addition, soluble protein content was also higher in waterlogging than in control and drought conditions. Proline content was higher under drought than in control and waterlogging conditions; however, there was no a significant difference between control and waterlogging treatments. Between control and drought treatments there were no differences in starch, sucrose or fructose contents. Glucose and total soluble sugar contents were higher under drought than in well-watered conditions. However, the highest amounts of soluble sugars and starch were found in waterlogging. Relationships between soil water surplus and quinoa growth are discussed.

Keywords: *Chenopodium quinoa*; Chlorophyll; Drought; Dry matter partitioning; Nitrogen; Protein; Soluble carbohydrates; Waterlogging.

Abbreviations: LA, leaf area; **N_a,** leaf nitrogen content per unit of leaf area; **N_m,** leaf nitrogen content per unit of leaf dry weight; **RWC,** relative water content; **RWR,** root weight ratio; **SLA,** specific leaf area; **SLW,** specific leaf weight.

INTRODUCTION

Drought and waterlogging are common adverse environmental factors that affect the growth of plants and are considered as the main factors determining the global geographic distribution of vegetation and restriction of crop yields in agriculture (Schulze et al., 2005; Lin et al., 2006). Symptoms of drought or waterlogging stresses include photosynthesis decline, protein degradation, slower leaf expansion, decreases in respiration and biomass production, and stomatal closure, among others (Kozlowski, 1997; Chai et al., 2001; Li and Li, 2005; Henriques, 2008). However, under drought many species respond by increasing the proportion of assimilates diverted to root growth with the concomitant root/shoot ratio increase (Sharp and Davies, 1989). In this condition soil nutrients can be available to plants (McDonald and Davis, 1996). Also, drought has been associated with cell osmotic adjustment, which is accomplished by accumulation of different compounds such as soluble sugars, proline, glycine betaine, polyols, and other organic compounds (Thomas, 1997; Chai et al., 2001). Soluble sugars (sucrose, glucose and fructose) play a key role in

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osmotic adjustment in many species; however, proline only plays an important role in a few species, such as potato and tomato (Escobar-Gutiérrez et al., 1998; Büssis and Heineke, 1998; Li and Li, 2005). Nevertheless, in tomato proline represents only a small fraction of the total osmotic solutes (Claussen, 2005). Additionally, proline is very labile and accumulates in growing cells only after a few weeks of drought while in mature tissues it appears to be a symptom of imminent cell death.

Under waterlogging or flooding conditions plant responses also include anatomical, morphological, and metabolic alterations (Huang, 1997; Subbaiah and Sachs, 2003). During waterlogging the low oxygen concentration in the rooting medium produces an inadequate oxygen supply to the plant roots (Huang, 1997). Carbohydrate metabolism and respiratory activity decreases, as well as reductions of root and shoot growth, are common symptoms of waterlogging stress (Zeng et al., 1999; Subbaiah and Sachs, 2003). In this sense, we can say that plants respond and adapt to different stresses through various biochemical and physiological processes, thereby acquiring stress tolerance. Thus, responses of plants to combined stresses are neither independent nor specific and so they can result in increases and/or overlapping of stress effects. Consequently, to know plant responses to combined stresses can be useful in understanding the mechanisms allowing them to survive in adverse conditions. Drought and waterlogging conditions normally occur in several of the worlds' regions, including the South America Andean region (Schulze et al., 2005). In fact, global climate change and the El Niño and La Niña events have severely altered rainfall distribution and intensity (Nuñez et al., 1999, Minetti and González, 2006) in Andean arid regions of Argentina, Bolivia, Chile, Peru, and Ecuador, during the last 20 years. Thus, heavy rains followed by long drought periods are more and more frequent in these regions, which alter the normal growth of both wild and cultivated species (Grimm et al., 2000). On the other hand, due to an increasing demand for foods with high nutritional values in many countries, cultivation of quinoa (*Chenopodium quinoa* Willd.), the ancestral Inca crop, has surged.

Quinoa is a species that can tolerate different stresses such as salinity, cold air, high solar radiation, night sub-freezing temperatures, and different soil pHs (Risi and Galwey, 1984; González and Prado, 1992; Jacobsen et al., 1998). It can also grow in arid and semiarid regions, lowlands, brackish lands, and salt-water marshes (Jacobsen et al., 1994). However, Gallardo and González (1992) have demonstrated that soil moisture plays an important role in determining the time and rate of quinoa seed germination and seedling growth. Nevertheless, studies of the quinoa plant's ability to survive drought conditions and waterlogging stresses are scarce. Thus, the aim of the present work was to answer the following questions: 1) How does quinoa respond physiologically to drought and waterlogging? 2) Is the dry matter partitioning affected by drought and waterlogging conditions? 3) Is quinoa well adapted to growth under drought and waterlogging?

MATERIALS AND METHODS

Plant material and growth conditions

Seeds of *Chenopodium quinoa* Willd. cv. Sajama were surface sterilized with 2% (v/v) sodium hypochlorite solution for 10 min and washed thoroughly with distilled water. After this treatment seeds were germinated during 3 days in plastic boxes (28 × 20 × 5 cm) containing moistened vermiculite as substrate. After this process boxes were transferred to a greenhouse for 13 days. Seedlings were supplied with a fourth-strength Hoagland solution every 3 days. After this period intact plants were transferred to 1000-mL plastic pots (one plant per pot) containing a dry mixture of sandy clay soil (50% sand and 50% clay). Pots were kept in a controlled growth chamber under a 12-h photoperiod, 25/20°C (light/dark) temperature regime, 60% relative humidity, and 430 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR) provided by Philips TLD 36 W/83 white fluorescent tubes (Philips Lighting, Buenos Aires, Argentina) for 50 days. Three treatment sets with two replicates of 20 plants each in a randomised block were designed: set one, drought (watering every 12 days, equivalent to near -0.20 MPa of soil water potential), set two, waterlogging (pots were flooded with distilled water to 1 cm above soil surface), and set three, control (watering every 2 days, equivalent to near -0.05 MPa of soil water potential). Control and drought stressed plants were watered with distilled water in the morning on the correspondent day by using 170 mL for each pot. At the 50^{th} day, plants (control, drought, and waterlogging pots) were harvested and divided into leaves, stems, and roots prior to use in growth and chemical analyses.

Growth and dry matter partitioning

Dry weight (DW) was determined after drying plant material for 48 h at 84°C. Leaf relative water content (RWC) was determined as follows: discs (3.0 cm^2) of different leaves were taken from the middle of the lamina (excluding major veins) and weighed to obtain fresh weight (FW). After this process leaf discs were floated on distilled water for 24 h at 15°C in the dark. Fully hydrated leaf discs were removed and weighed to obtain the turgid weight (TW). RWC was calculated as RWC (%) = (FW-DW) / (TW-DW) × 100. Leaf area (LA) corresponding to the second pair of leaves was estimated using digitised images obtained with a 200E charged-coupled device video camera (Videoscope International, Washington, DC, USA) coupled to a Macintosh Quadra 700 computer. Image analysis was performed with NIH Image 1.45 software (Rasband W, National Institute of Health, Bethesda, MD, USA). Root weight ratio (RWR: root dry weight per unit of plant dry weight) was determined as the ratio of root dry weight to total plant dry weight (g

g^{-1}). Specific leaf area (SLA) was determined as the ratio of leaf area to leaf dry weight of individual leaves (cm^2 g^{-1}) while the specific leaf weight (SLW) corresponding to 1/SLA was expressed as (mg cm^{-2}). Plant height was measured using a 100 cm rule.

Chemical analysis

Chlorophyll extraction (50 mg leaf FW) was performed using 2 mL of dimethyl sulfoxide (12 h in the dark at 45 °C) according to the method of Chapelle and Kim (1992). Chlorophyll content was calculated from absorbance values at 665 and 649 nm according to equations of Wellburn (1994). Soluble sugars (glucose, fructose, and sucrose), starch, and proline were extracted from 0.5 g leaf FW with 4 mL of 80% ethanol at 75°C according to the procedure of Rosa et al. (2004). Total soluble sugars were determined by the phenol-sulphuric acid method (Dubois et al., 1956); glucose was estimated by using a glucose oxidase-peroxidase coupled assay according to Jorgensen and Andersen (1973); fructose was measured by the method of Roe and Papadopoulos (1954) and sucrose by the procedure of Cardini et al. (1955). For starch measurement the insoluble fraction remaining after ethanolic extraction of soluble sugars was resuspended in 2 mL of 2.5 M NaOH and boiled for 5 min. After cooling the solution pH was adjusted to pH 4.5 with 2 M HCl, and the resulting gelatinised starch was hydrolysed 10 min at 50°C with buffered *Rhizopus* mold amyglucosidase (15 IU mL^{-1} in 0.1 M sodium acetate buffer, pH 4.5). After this process, starch was measured as reducing sugars by Nelson's method (Nelson, 1944) and expressed in maltose equivalents. Soluble protein was extracted from 0.5 g leaf FW with 2 mL of 50 mM sodium phosphate buffer (pH 7.4), containing 5 μM $MnSO_4$ and 1 mM β-mercapethanol. Soluble protein content was determined by the method of Lowry et al. (1951) using bovine serum albumin (BSA) as a standard. Total nitrogen content was determined in a Kjeltec-auto 1030 analyser (Tecator, Höganäs, Sweden) after digestion in sulphuric acid with potassium sulphate by the Kjeldahl procedure using selenium sulphate as catalyst. Proline was determined according to the Bates et al. (1973) procedure.

Statistical analysis

Values shown in tables are means of two independent replicates. Comparisons between means were analyzed by one-way ANOVA, along with Tukey's test at a $p \leq 0.05$ significance level (Zar, 1984).

RESULTS

Plant growth and dry matter partitioning

Dry weight of the whole plant as well as of individual parts was higher in control than under drought and waterlogging conditions, but the lowest values were observed under waterlogging. However, RWR (an indicator of dry matter partitioning) did not show changes in any treatments (Table 1). Plant height showed no great differences across treatments, but waterlogging conditions produced the lowest values (data not shown). Leaf area and SLA were decreased under waterlogging stress (36.2% and 26.2%, respectively), but they were not affected by drought. By contrast, SLW (organic matter spent to produce one cm^2 of leaf) was found to be higher under waterlogging (4.2 mg cm^{-2}) than in drought and control treatments (2.4 mg cm^{-2} and 2.7 mg cm^{-2}, respectively) (Table 2).

Table 1. Total plant DW, root DW, stem DW, leaf DW, inflorescence DW, and RWR (root dry weight per unit of plant dry weight) of *Ch. quinoa* plants subjected during 50 days to 3 different watering regimes. Data are means of two independent replicates. Means ± standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level (n = 6, for each replicate).

Treatment	Total plant DW (mg)	Root DW (mg)	Stem DW (mg)	Leaf DW (mg)	Inflorescence DW (mg)	RWR (mg)
Control	400.2±16.3^a	84.1±5.7^a	147.4±5.2^a	149.5±10.5^a	17.6±1.2^a	0.21±0.03^a
Drought	347.6±14.0^b	74.8±6.4^b	126.5±5.0^b	130.7±11.8^b	15.6±1.6^a	0.21±0.05^a
Waterlogging	269.8±25.4^c	60.5±7.0^c	86.8±8.9^c	112.9± 6.7^c	9.6±2.3^b	0.22±0.02^a

Table 2. Relative water content (RWC), leaf area (LA), specific leaf area (SLA), specific leaf weight (SLW) and number of leaves of *Ch. quinoa* plants subjected during 50 days to 3 different watering regimes. Data are means of two independent replicates. Means ± standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level (n = 6, for each replicate).

Treatment	RWC (%)	LA (cm^2)	SLA (cm^2 g^{-1})	SLW (mg cm^{-2})	Number of leaves
Control	97.5±1.4^a	56.3±2.4^a	405.7±28.5^a	2.7±0.2^a	11.0±0.4^a
Drought	70.3±1.4^b	53.8±4.1^a	411.6±31.2^a	2.4±0.1^a	11.3±0.5^a
Waterlogging	98.8±1.8^a	34.3±2.6^b	303.8±55.1^b	3.3±0.2^b	11.0±0.2^a

Table 3. Chlorophyll (total, *a*, *b* and *a/b* ratio) and leaf nitrogen (N_m and N_a) content in leaves of *Ch. quinoa* plants subjected during 50 days to three different watering regimes. Data are means of two independent replicates. Means ± standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level (n = 10, for each replicate).

Treatment	Total Chl (mg g^{-1} DW)	Chl *a* (mg g^{-1} DW)	Chl *b* (mg g^{-1} DW)	Chl *a/b*	N_m (mmol g^{-1} DW)	N_a (mmol m^{-2})
Control	21.3 ± 1.8[a]	15.2 ± 0.5[a]	5.0 ± 0.2[a]	3.0 ± 0.1[a]	1.26 ± 0.2[a]	31.1 ± 3.4[a]
Drought	20.1 ± 1.7[a]	15.0 ± 0.8[a]	5.1 ± 0.3[a]	2.9 ± 0.1[a]	1.33 ± 0.1[b]	32.3 ± 4.2[a]
Waterlogging	17.3 ± 0.4[b]	13.0 ± 0.3[b]	4.3 ± 0.2[b]	3.0 ± 0.1[a]	1.30 ± 0.4[b]	42.8 ± 3.6[b]

Chlorophyll and leaf nitrogen content

Total chlorophyll and chlorophyll *a* and *b* content was lower in plants under waterlogging than in drought and control, and contents of the latter two showed no significant differences. Chlorophyll *a*/*b* ratios remained unchanged across all treatments (Table 3). Total chlorophyll to N_m molar ratio for control, drought, and waterlogging treatments were 0.0178, 0.0169 and 0.0149, respectively (data not shown). Leaf nitrogen content expressed per unit of leaf DW (N_m) did not show significant differences between drought and waterlogging stresses (1.33 mmol g^{-1} DW and 1.30 mmol g^{-1} DW, respectively) while in control plants it was lower (1.26 mmol g^{-1} DW). However, when the nitrogen content was expressed per unit of LA (N_a), obtained dividing N_m by SLA, the highest value was observed under waterlogging (42.8 mmol m^{-2}). Drought and control conditions showed no significant differences (Table 3).

Carbohydrate, soluble protein, and proline content

Leaf total soluble sugars, sucrose, glucose, fructose, and starch contents were higher in waterlogging conditions than in drought or control treatments. However, drought showed higher values of total soluble sugars and glucose than control while fructose, sucrose and starch contents showed no significant differences. Leaf soluble protein content was also higher under waterlogging than in drought or control conditions. In addition, the lowest value (70.6 mg g^{-1} DW) was observed in control leaves. With respect to proline content the highest value (0.47 mg g^{-1} DW) was observed under drought while waterlogging and control treatments revealed no significant differences (Table 4).

DISCUSSION

Plants under drought and waterlogging stresses exhibit growth reduction, low SLA, photosynthesis declination, protein degradation, decrease in respiration and biomass production, and stomatal closure when compared to their well-watered counterparts (Kozlowski, 1997; Chai et al., 2001; Li and Li, 2005). However, our results showed higher values of SLA and chlorophyll content in drought treatment than in waterlogging conditions while there was no a significant difference between control and drought treatments (Tables 2 and 3). According to Walter et al. (1993) high values of SLA and chlorophyll represent a lower metabolic cost to maintain a cm^2 of leaf area and, consequently, higher productivity. Thus, the productivity of quinoa plants appears to be more affected by waterlogging conditions. On the other hand, leaf nitrogen content has been recognised as a determinant of net photosynthetic capacity, and a positive correlation is usually observed between CO_2 assimilation rate and leaf nitrogen content (Niinemets, 1997). In quinoa plants the leaf nitrogen content, expressed as N_m (nitrogen per unit of leaf DW), did not differ between drought and waterlogging treatments, but it was lower in the control treatment. However, when it was expressed as N_a (nitrogen per unit of LA) the highest value was observed under waterlogging, and there was no a significant difference between drought and control treatments (Table 3). The lowest N_a values

Table 4. Total soluble sugars, glucose, fructose, sucrose, starch, soluble protein, and proline content in leaves of *Ch. quinoa* plants subjected during 50 days to three watering regimes. Data are means of two independent replicates. Means ± standard deviations (SD) within each column followed by different letters are significantly different at 0.05 probability level (n =10, for each replicate).

Treatment	Total sol. sugars	Glucose	Fructose	Sucrose	Starch*	Soluble protein	Proline
	(mg g^{-1} DW)						
Control	4.6±0.1[a]	1.2±0.08[a]	0.93±0.10[a]	0.79±0.06[a]	39.9±3.6[a]	70.6±3.1[a]	0.37±0.05[a]
Drought	5.2±0.2[b]	1.5±0.10[b]	0.94±0.08[a]	0.78±0.05[a]	42.0±4.8[a]	80.5±2.9[b]	0.47±0.03[b]
Waterlogging	7.2±0.2[c]	2.1±0.10[c]	1.74±0.12[b]	1.21±0.06[b]	75.7±5.3[b]	122.4±3.5[c]	0.35±0.04[a]

*Starch is expressed as mg maltose g^{-1} DW.

being observed under drought and control conditions signifies that a larger surface area can be constructed with the same plant nitrogen investment, and then plants have a more extensive foliar display for interception and light capture (Mendes et al., 2001). Consequently, we can conclude that under drought or well-watered treatments the leaves of quinoa are metabolically more efficient than in waterlogging conditions. In this context, we also analysed the effects of both stresses on growth parameters and dry matter partitioning. Thus, in the waterlogging treatment significant decreases in LA and DW accumulation in root, stem, leaf, and inflorescence were observed when they were compared with those under well-watered conditions. By contrast, under drought a smaller decrease in DW values was observed (Tables 1 and 2). Although decreases in LA have been reported as a common effect of drought stress (Lawlor and Leach, 1985), quinoa plants under similar conditions do not exhibit a significant reduction in LA (Table 2). Thus, our results could be in agreement with the assumption of Zeng et al. (1999), who considered that sacrifice of non-essential sinks such as root and stem may be advantageous to survival under the extreme conditions imposed by waterlogging or flooding, and with the finding of Kozlowski (1997) who demonstrated that an excess of soil water affects root and shoot growth as well as leaf expansion. Also under prolonged drought stress many plants develop a profuse radicular system in order to help the water absorption, while under waterlogging or flooding conditions some species develop a system of adventitious roots in order to contribute to plant oxygenation (Visser et al., 1996; Thomas, 1997; Li and Li, 2005). In this context, increases in root weight ratio (RWR), an indicator of dry matter allocation (van den Boogaard et al., 1997), have been reported as a response of plants to drought stress (Frensch, 1997; Munns, 2002). However, in our study neither drought nor waterlogging conditions brought about any changes in this parameter (Table 1). Consequently, we suppose that in quinoa plants other physiological adaptation mechanisms could be acting in response to drought and waterlogging treatments. In addition, several authors have proposed that leaf number can be used to characterise plant assimilation capacity (Hoogenboom et al., 1987). In the present study, however, no difference in this parameter was observed.

Although accumulation of soluble sugars is particularly significant in plants undergoing drought stress (Escobar-Gutiérrez et al., 1998; Chai et al., 2001; Munns, 2002; Li and Li, 2005), high soluble sugar levels have also been demonstrated in roots under flooding and waterlogging conditions (Barta, 1988; Huang and Johnson, 1995, Zeng et al., 1999). Nevertheless, unlike what occurs in drought stress, sugar accumulation under waterlogging has been attributed to the need to have an appropriate carbohydrate supply for survival of plant tissues at the low oxygen concentration found in waterlogged soils (Barta, 1988; Guglielminetti et al., 1995; Subbaiah and Sachs, 2003). Nevertheless, the possibility that this is due to the decrease in enzyme activities related to sucrose cleavage cannot be dismissed. Inhibition of root invertase and sucrose synthase activities at low oxygen levels has been reported (Drew, 1997; Zeng et al., 1999). Thus, the high soluble sugars and starch content observed in leaves of quinoa plants under waterlogging (Table 4) could be related to a reduction in carbohydrate sink strength imposed by lower root respiration. In addition, the higher soluble protein contents observed under these conditions could be attributed to anaerobic stress protein (ASPs) synthesis induced by root hypoxia (Blom and Voesenek, 1996; Subbaiah and Sachs, 2003). However, the higher values in soluble sugars and proline observed in plants under drought stress, when compared with their well-watered counterparts, probably correspond to an osmotic adjustment more than to a metabolic decrease. In this context, our results could be in agreement with the findings of Vacher et al. (1994), who demonstrated that quinoa plants exhibit a high assimilation rate under drought stress. Consequently, we can conclude that the soil water surplus constitutes the main limiting factor in quinoa growth and dry matter partitioning. Our results may have great significance for farming done in frequently waterlogged areas or dry lands. Our findings should also be of use in further agricultural studies on quinoa waterlogging or drought-tolerance.

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Quinoa 對乾旱及淹水之反應：乾物之分配

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Quinoa (*Chenopodium quinoa* Willd.) 植株對乾旱及淹水有不同之反應。植株及根之乾重在乾燥及淹水兩種逆境下都比正常供水者低 ； 但最低者為受淹水者。但根重比率（根之　重 / 單位植株乾重）在所有處理組都沒有顯著差異。葉面積及比葉面積受旱者比淹水者高，但受旱者和正常供水者之間並無顯著差異。相反地，比葉重及相對水含量以淹水者比受旱者高。但是，正常供水者和淹水者之間，其相對水含量並無顯著差異。再者，葉之數目及植株高度在各處理組是一樣的。最低量之總葉綠素，葉綠素 *a* 及葉綠素 *b* 是受淹水者，但是正常供水者及受旱者之間並無差異。葉綠素 *a/b* 之比率在所有供試者是一樣的。葉之氮含量（以單位乾物量為比較基準），*Nm* 以正常供水者較低，而在受旱者及淹水者則不變。不過，當表示方式不同時（以單位葉面積為比較基準），*Na* 淹水者具最高值。此外，水溶蛋白量淹水者也比受旱者及正常供水者高。Proline 量受旱者比正常供水及淹水者高 ； 但是正常供水者及淹水者之間並無顯著差異。在正常供水者及受旱者之間，澱粉，蔗糖，及果糖含量並無顯著差異。葡萄糖及總可溶糖含量受旱者高於正常供水者。但是，最高量之總可溶糖及澱粉則存於淹水者。本文討論土壤水超量及 quinoa 生長兩者之相關。

關鍵詞 ：*Chenopodium quinoa*； 葉綠素 ； 乾旱 ； 乾物分配 ； 氮 ； 蛋白質 ； 可溶糖 ； 淹水。