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## Leaf gas exchange and water relation characteristics of field quinoa (*Chenopodium quinoa* Willd.) during soil drying

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### Abstract

The effects of soil drying on leaf water relations and gas exchange were studied in quinoa grown in pots with sandy soil and in lysimeter plots with sandy loam in the field. Midday values of leaf water potential ( $\psi_l$ ), leaf osmotic potential ( $\psi_\pi$ ), relative water content (RWC), leaf conductance ( $g_l$ ), light saturated net photosynthesis ( $A_{sat}$ ), and specific leaf area (SLA) were determined in fully watered and droughted plants. At branching, flowering and grain filling  $g_l$  in leaves of fully watered plants varied from 0.3 to 1.0, 0.3 to 0.6 and 0.2 to 0.7 mol m<sup>2</sup> s<sup>-1</sup> and  $A_{sat}$  varied from 18 to 34, 14 to 24 and 8 to 26  $\mu$ mol m<sup>2</sup> s<sup>-1</sup>. In droughted plants stomatal closure began when leaf water potential ( $\psi_l$ ) decreased below  $-1.2$  to  $-1.6$  MPa and  $A_{sat}$  was reduced to 5–10  $\mu$ mol m<sup>2</sup> s<sup>-1</sup> as a result of stomatal closure, when  $\psi_l$  decreased to  $-1.5$  to  $-2.0$  MPa. The osmotic potential at full turgor ( $\psi_\pi^{100}$ ) decreased by age from  $-1.0$  to  $-1.4$  MPa. During severe water stress quinoa maintained positive turgor down to a zero turgor leaf water potential value ( $\psi_l^0$ ) of  $-1.8$  MPa. Quinoa had a limited osmotic adjustment  $\psi_\pi^{100}$  between fully watered and droughted plants being 0.3–0.4 MPa at the most. During branching the turgid weight/dry weight (TW/DW) ratio decreased from 9 to 5. At flowering and grain filling the TW/DW ratio was low (4–6). The bulk elastic modulus ( $\epsilon_{max}$ ) determined at the beginning of the grain filling period was medium to high (18–22 MPa). SLA was high (23–21 m<sup>2</sup> kg<sup>-1</sup>) during branching and decreased during the later growth stages. Conclusively, both high net photosynthesis rates and SLA values during early vegetative growth probably result in early vigour of quinoa supporting early water uptake and thus tolerance to a following drought. The stomatal response of quinoa was insensitive to drought induced decrease of leaf water status. The leaf water relations were characterised by low osmotic potentials and low TW/DW ratios during later growth stages sustaining a potential gradient for water uptake and turgor maintenance during soil drying. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Leaf gas exchange; Water relation characteristics; *Chenopodium quinoa*

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## 1. Introduction

In recent years there has been a growing interest for introducing so-called alternative crops in Europe. One such crop is quinoa (*Chenopodium quinoa* Willd) originating from the South American highlands, where it has been cultivated by local farmers for several millennia. The Andes region is characterised by a harsh climate, with frequent periods of drought, imposing great demands on the local flora, and quinoa is therefore considered a hardy plant with good drought tolerance (Galwey, 1989; Jacobsen, 1993; Jacobsen et al., 1997a,b, 1998). Previously, several investigations have shown that quinoa is drought tolerant which has been attributed to morphological characteristics such as an extensive ramified root system and hygroscopic papillae on the leaf cuticula (Canahua, 1977; Espindola, 1986) but data on physiological response to drought are scarce (Vacher, 1998). However, until now few investigations have been undertaken in order to study the leaf water relations of quinoa in the field and during the season.

Turgor maintenance during reduction in leaf water status due to drought was thought to be the means by which a plant maintains its metabolic processes and sustains its growth and survival (e.g. Hsiao et al., 1986; McCree, 1986). Turgor maintenance may be obtained by a sensitive stomata closure response induced by phytohormones generated in the roots (Jensen et al., 1998; Ali et al., 1999), osmotic adjustment (Ali et al., 1999) or facilitated by changes in cell wall properties (Cutler et al., 1977). Under limited water conditions, higher yield was obtained by wheat genotypes having high osmotic adjustment than low osmotic adjustment (Morgan et al., 1986). Furthermore, inherent low osmotic potentials will be a mean by which the plants can sustain a potential gradient for water uptake when the soil water potential is decreased during soil drying (Jensen et al., 1993; Shalhevet, 1993). Finally, high photosynthetic rates and specific leaf area (SLA) support early vigour important to drought resistance to a following long lasting drought period in Mediterranean-type climate by reducing the amount of water lost by soil evaporation (Turner, 1997).

As gas exchange and water relations have not been studied in field quinoa as far as we know, the purpose of the present investigation was to study the effects of drought on leaf conductance, net photosynthesis and leaf water relations characteristics during drought at different stages of growth in field grown plants. Gas exchange and water relations characteristics of quinoa were compared with various cultivated crop species.

## 2. Materials and methods

A pot and a lysimeter experiment was conducted in the field at the experimental station Højbakkegaard of the Agricultural University, KVL, 20 km west of Copenhagen (55°40' N; 12°18' E; 28 m above MSL). A mobile glass roof automatically protected pots and lysimeter plots against rain. When rain ceased the roof was removed automatically.

### 2.1. Pot experiment

The quinoa variety *Chenopodium quinoa* Willd. cv. Kankolla was sown on 20 May 1997, in pots and germinated 1 June 1997. Kankolla is a traditionally grown variety of the Peruvian altiplano with a high level of drought and frost tolerance. The pots were fertilised with 3 g N, 1 g P and 3 g K per pot mixed into the soil. The pots contained a sandy soil (a coarse textured melt-water top sand from the Danish Governmental Research Station, Jyndevad) with a water content of 19 vol.% at field capacity ( $-0.01$  MPa) and 5 vol.% at permanent wilting ( $-1.5$  MPa). The soil water retention curve is shown in Fig. 1. Forty pots were used and each contained 21.6 kg of dry soil comprising 3.4% organic matter, 4.2% clay (0–2  $\mu\text{m}$ ), 3.8% silt (2–20  $\mu\text{m}$ ), 10% fine sand (20–200  $\mu\text{m}$ ) and 78.7% coarse sand (200–2000  $\mu\text{m}$ ). The pots had a diameter of 20 cm and a height of 40 cm. Two plants were grown in each pot. Four pots per treatment was used for final yield determination after drying at 80°C for 24 h. Drought was imposed during branching (eight true leaves) (stage 0), flowering (stage 8–12) and grain filling (stage 14–18; according to Jacobsen and Stølen,

1993) by withholding watering. The drought treatment was undertaken under moderate evaporative demands (Fig. 2).

## 2.2. Lysimeter experiment

Quinoa (*Chenopodium quinoa* Willd. cv. KVL 205) sown on 20 May 1994 and emerged on 3 June 1994, was grown under temperate climatic conditions (Fig. 2). Seeds were sown at a density of 30 grains  $m^{-2}$  with a row spacing of 12.5 cm, i.e. 400 seeds  $m^{-2}$ . Prior to sowing 120, 30, 90 and 9 kg  $ha^{-1}$  of N, P, K and Mg, respectively, was applied. The experiment was established in 12 lysimeter plots (each  $2 \times 2 m^2$  area) on sandy loam (Kristensen and Aslyng, 1971). At the border of each lysimeter plot the protection areas were treated the same as the lysimeter plots. The sandy loam contained 3% organic matter, 16% clay (0–2  $\mu m$ ), 17% silt (2–20  $\mu m$ ), 40% fine sand (20–200  $\mu m$ ) and 24% coarse sand (200–2000  $\mu m$ ) in the top soil (0–30 cm depth) and 20% clay,

17% silt, 43% fine sand and 20% coarse sand in the bottom layer (30–100 cm depth). The water content in this soil is 260 mm at field capacity ( $-0.01$  MPa) and 115 mm at permanent wilting ( $-1.5$  MPa), giving the plant available soil water of 145 mm. The soil water retention curve is seen in Fig. 1.

Each lysimeter plot was supplied with an individually operated trickle irrigation system. Six plots were well-watered and six were equally treated with a single drought treatment and subjected to increasing soil water deficits at the late anthesis/early grain filling (stage 12–14 according to Jacobsen and Stølen, 1993). The drought treatment was undertaken under moderate evaporative demands (Fig. 2).

## 2.3. Plant water relations

Leaf water relation measurements were made during 4 h centred around solar noon. The leaf was enclosed in a polyethylene bag after gas exchange measurement in the field, and immediately detached for measurement of its water potential ( $\psi_l$ ) using a pressure chamber (Soil Moisture Equipment, Santa Barbara, CA). After taking the water potential measurement, the leaf was divided into two parts, one of which was immediately plunged into liquid nitrogen and then transferred to a freezer of  $-20^\circ C$  for later osmotic potential determination. The second half of the leaf was used for relative water content determination [ $RWC = (FW - DW)/(TW - DW)$ ]. To this end the leaf sample was weighted (FW) and then floated on distilled water for 4 h at  $22^\circ C$  under dim light. The turgid weight (TW) was determined after blotting, and the dry weight (DW) was measured after the samples had been dried for 24 h at  $80^\circ C$ . The one-sided area was measured by a leaf area meter (model 3050A, LiCor Inc. Lincoln NE). Specific leaf area (SLA) was calculated as leaf area per unit of dry mass.

To determine the osmotic potential, the frozen leaf was allowed to thaw for about 20 min before being pressed. Then the press sap was removed with a filter paper disc and sealed in a C-52 chamber (Wescor Inc. Logan, UT) and incubated at  $22^\circ C$  for 10–15 min before osmotic potential

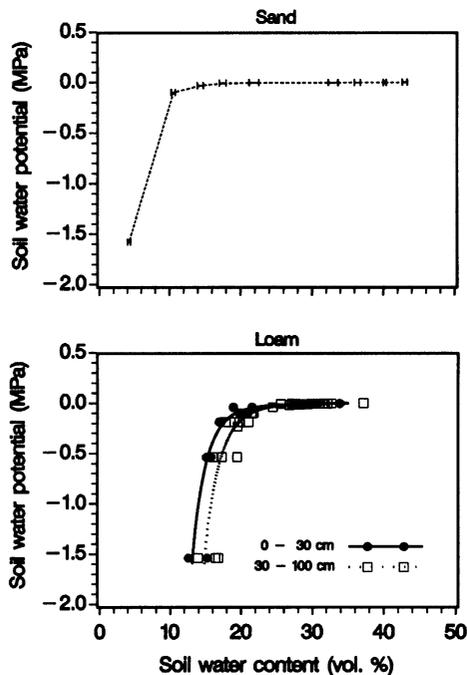


Fig. 1. Soil–water characteristic curve in sand (Hansen and Jensen, 1986) (pot experiment) and loam (lysimeter experiment). In sand bars indicate  $\pm$  S.E.M. ( $n = 24$ ).

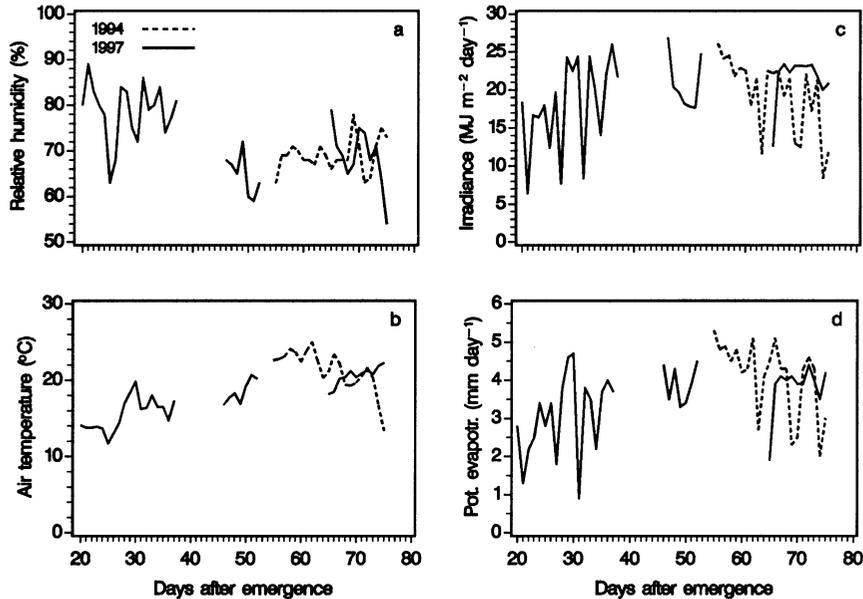


Fig. 2. Mean daily values of relative humidity (a), air temperature (b), irradiance (c), and potential evapotranspiration as calculated by the equation of Penman (1956). ····· 1994 (lysimeter experiment). ---- 1997 (pot experiment).

was read with a dew point microvoltmeter (HR–33T, Wescor Inc., Logan, UT, USA). Leaf turgor potential ( $\psi_p$ ) was obtained as:  $\psi_p = \psi_1 - \psi_\pi$ . The osmotic potential at full hydration ( $\psi_\pi^{100}$ ) was calculated as:  $\psi_\pi^{100} = \psi_\pi \times \text{RWC}$ .

Water retention characteristics of leaves were assessed using pressure–volume (PV) curves obtained with a pressure chamber at the end of the drying period of the lysimeter experiment. Fully expanded upper leaves selected from the gross boundary layer of the crop were excised in distilled water at dawn and rehydrated for 3–4 h in sealed glass in the dark. Drying of the leaves between  $\psi_1$  measurements took place on the bench, and changes in leaf water contents were determined by weighing immediately after the  $\psi_1$  determination with six replicates for every treatment. Each leaf was partially wrapped in a plastic sheet in order to decrease the rate of drying. Data for one PV-curve of each single leaf were obtained within 12 h.

By plotting  $1/\psi_1$  versus RWC (type II transformation) a curve was obtained with an initially non-linear portion followed by an approximately linear section. The beginning of the linear portion

indicates the leaf water potential at the turgor loss point ( $\psi_{\text{leaf}}^0$ ) and the RWC value at zero turgor ( $\text{RWC}^0$ ). Data points belonging to the turgor and zero turgor region were discriminated by eye. The bulk elastic volumetric modulus ( $\epsilon$ ) was defined as:

$$\epsilon = \frac{V d\psi_p}{dV}$$

which is the change in turgor pressure ( $d\psi_p$ ) for an infinitesimal change in symplastic water content ( $V$ ) (Andersen et al., 1991). When  $\text{RWC} = 1$  then  $\epsilon = \epsilon_{\text{max}}$ . It was assumed that the relationship between  $\psi_p$  and  $1/\text{RWC}_s$ , where  $\text{RWC}_s$  is relative symplastic water content, can be described by an exponential function. Hereby, at  $\text{RWC}_s = 1 - \text{RWC}_a$ , where  $\text{RWC}_a$  is the relative apoplastic water content, the maximum turgor ( $\psi_{p(\text{max})}$ ) is reached. The derivation of  $\text{RWC}_a$  is given by Andersen et al. (1991). Turgor in the turgid region was described as:

$$\psi_p = \psi_{p(\text{max})} e^{\beta[\text{RWC}_s^{-1} - (1 - \text{RWC}_a)^{-1}]}$$

where  $\beta$ , the sensitivity factor of elasticity, relates exponential changes in turgor to changes in  $\text{RWC}_s$  (Andersen et al., 1991).

## 2.4. Gas exchange measurement

Leaf conductance ( $g_l$ ) and photosynthesis ( $A$ ) were measured in 10–15 days old fully expanded upper leaves on attached leaves using the LI-6200 portable photosynthesis system (LiCor, Lincoln, NE) and a 250 ml cuvette. The leaves were positioned within the gross boundary layer of the crop. Inside the cuvette the photosynthetic active radiation (PAR, 400–700 nm) was 87% of that outside. Only light saturated photosynthesis at PAR > 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was used. Leaf temperature varied between 27 and 33°C. Relative humidity in the cuvette was 35–45%. [CO<sub>2</sub>] in the cuvette was between 320 and 340 ppm. The gas exchange measurement was undertaken about 0.5 min after the leaf had been inserted into the cuvette. The standard calibration check was performed by the manufacturer before and after the growing season. No drift had occurred in the water vapour and CO<sub>2</sub> calibration curves. As a daily routine a CO<sub>2</sub> calibration check was performed on the instrument. The boundary layer conductance in the cuvette as measured on leaf-shaped humidified filter paper was 3.0 mol m<sup>-2</sup> s<sup>-1</sup>.

## 2.5. Nitrogen

The total nitrogen content in the dry matter was measured by the Kjeldahl method (Bremner and Mulvaney, 1982).

## 2.6. Statistics

The experiment was arranged in a systematic block design with four to six replicates of each treatment. Student *t*-test was used to determine if the means of the two treatments were different (SAS, 1988).

# 3. Results

## 3.1. Pot experiment

After onset of soil drying by withholding irrigation of the pots gas exchange and leaf water

relations of quinoa were measured during branching (Fig. 3), flowering (Fig. 4) and grain filling (Fig. 5). Pot water use depended on plant size and evaporative demands (Fig. 2d). The periods of soil drying from field capacity until all plant available water had been used were 16, 6 and 10 days for the drying cycles at branching, flowering and grain filling, respectively (Figs. 3a, 4a and 5a).

### 3.1.1. Leaf responses in fully irrigated plants

At branching, flowering and grain filling under fully watered conditions in young fully developed leaves positioned in the gross boundary layer of the atmosphere, leaf conductance ( $g_l$ ) varied from 0.3 to 1.0, 0.3 to 0.6 and 0.2 to 0.7 mol m<sup>-2</sup> s<sup>-1</sup> (Figs. 3b, 4b and 5b) while saturated net photosynthesis of CO<sub>2</sub> ( $A_{\text{sat}}$ ) varied from 18 to 34, 14 to 24 and 8 to 26  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Figs. 3c, 4c and 5c). Due to a spell with high evaporative demands (Fig. 2)  $g_l$  closed at midday 24–26 days after emergence (DAE).

Leaf water potential ( $\psi_l$ ) was high (–0.4 MPa) during branching (Fig. 3d) as compared with –0.8 to –1.0 MPa during flowering and grain filling (Figs. 4d and 5d). Resistance to water transport in the young plants was probably less than at flowering and grain filling (reflected in high stomatal conductance, Fig. 3b), thus causing a lower potential gradient. The RWC was high (0.9) at all three growth stages (Figs. 3g, 4g and 5g). Despite similar levels of RWC leaf osmotic potential ( $\psi_{\pi}$ ) was high (–1.2 to –1.4 MPa) at branching and flowering (Figs. 3e and 4e) as compared with  $\psi_{\pi}$  at grain filling (–1.2 to –1.8 MPa) (Fig. 5e) resulting in a leaf turgor pressure ( $\psi_p$ ) of similar size at the three growth stages (in most cases 0.4–1.0 MPa) (Figs. 3f, 4f and 5f). The solute content of the leaves was built up during the season. Thus, the osmotic potential at full turgor ( $\psi_{\pi}^{100}$ ) varied between –1.0 and –1.4 in fully watered plants during branching and grain filling (Fig. 6). In accord herewith the turgid weight/dry weight ratio (TW/DW) decreased from 9 during early branching to 6–4 during later growth stages (Figs. 3h, 4h and 5h) reflecting the building up of solutes in the cells. Similarly, the specific leaf area (SLA) was 23–21 m<sup>2</sup> kg<sup>-1</sup> at

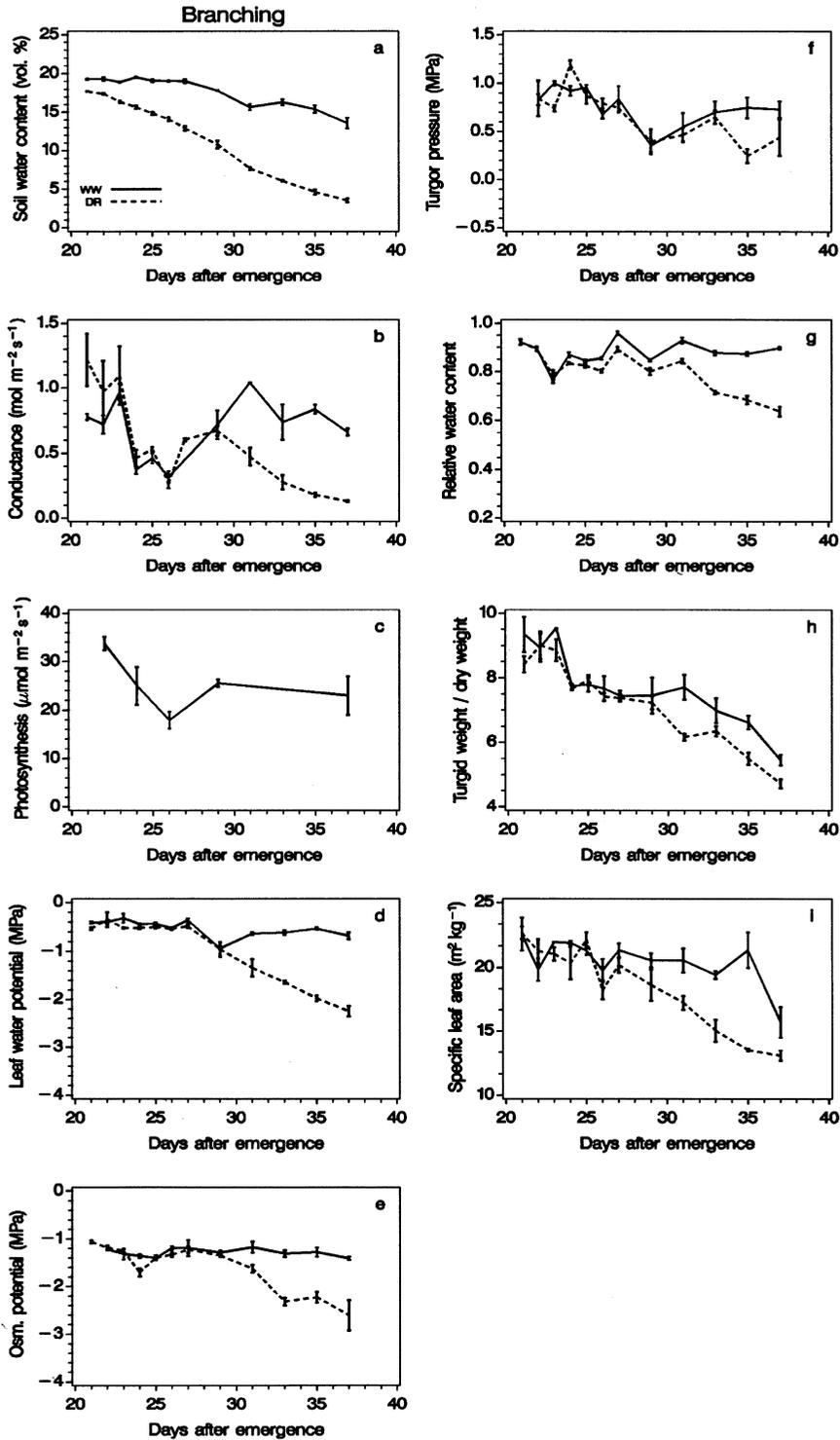


Fig. 3. Changes of soil water content (a), leaf conductance (b), light saturated net photosynthesis (c), leaf water potential (d), leaf osmotic potential (e), leaf turgor pressure (f), leaf relative water content (g), turgid weight/dry weight ratio (h), and specific leaf area (i) during soil drying. WW (—) and DR (---) indicate well watered and droughted plants, respectively. Bars indicate  $\pm$  S.E.M. ( $n = 3-5$ ).

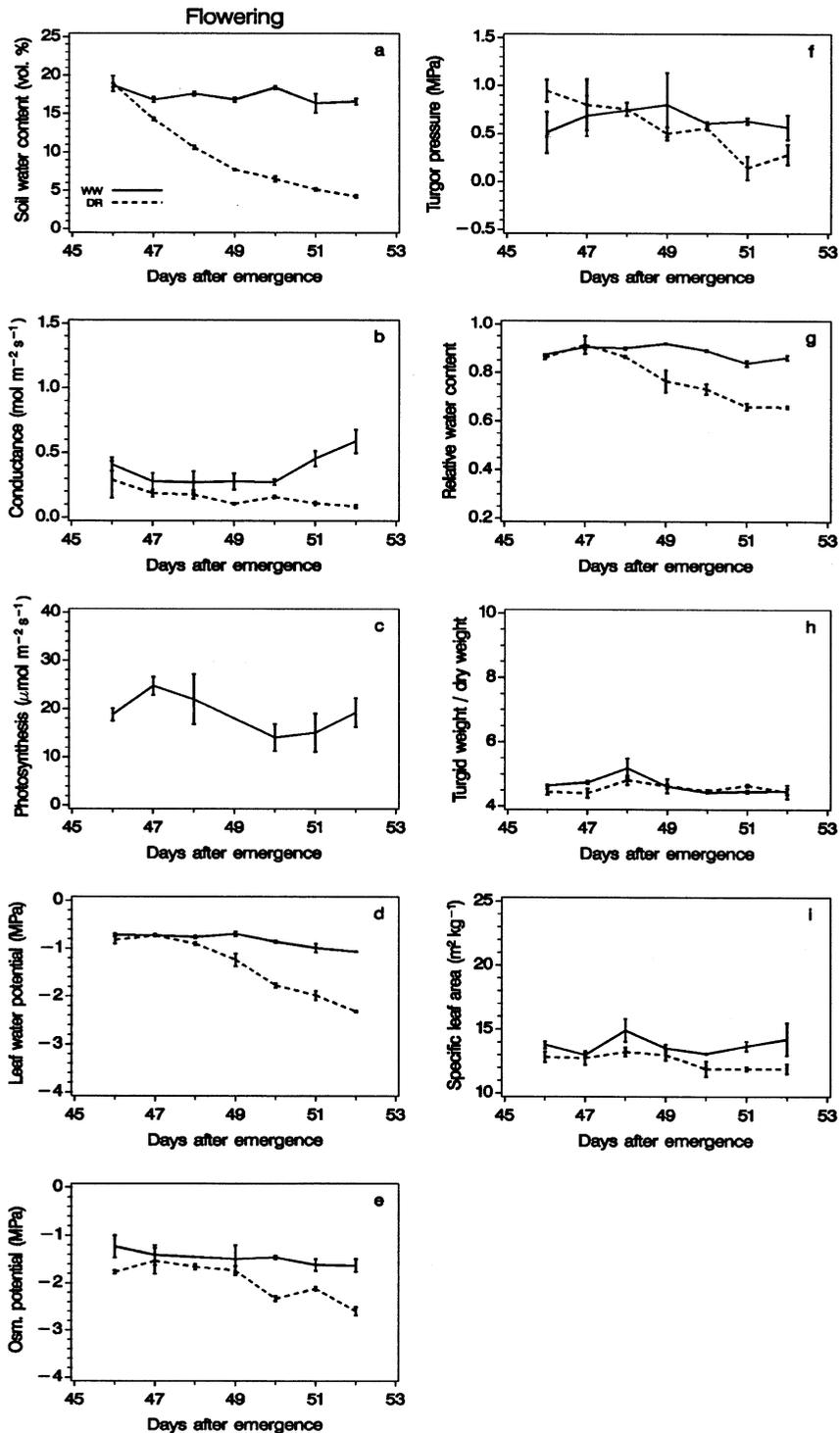


Fig. 4. Changes of soil water content (a), leaf conductance (b), light saturated net photosynthesis (c), leaf water potential (d), leaf osmotic potential (e), leaf turgor pressure (f), leaf relative water content (g), turgid weight/dry weight ratio (h), and specific leaf area (i) during soil drying. WW (—) and DR (---) indicate well watered and droughted plants, respectively. Bars indicate  $\pm$  S.E.M. ( $n = 3-5$ ).

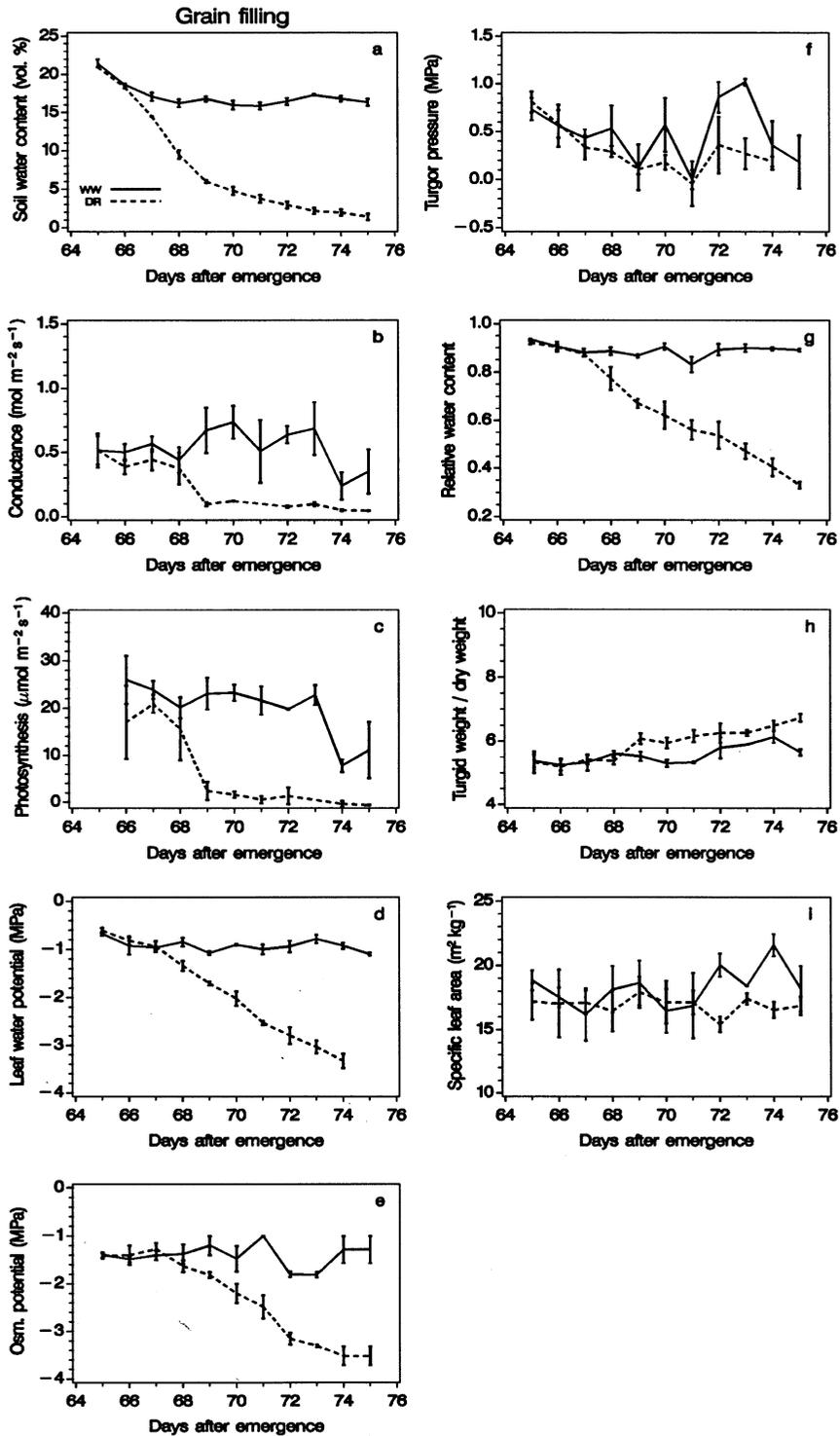


Fig. 5. Changes of soil water content (a), leaf conductance (b), light saturated net photosynthesis (c), leaf water potential (d), leaf osmotic potential (e), leaf turgor pressure (f), leaf relative water content (g), turgid weight/dry weight ratio (h), and specific leaf area (i) during soil drying. WW (—) and DR (---) indicate well watered and droughted plants, respectively. Bars indicate  $\pm$  S.E.M. ( $n = 3-5$ ).

branching (Fig. 3i), while SLA was 20 to 14  $\text{m}^2 \text{kg}^{-1}$  at flowering and grain filling (Figs. 4i and 5i).

### 3.1.2. Stomatal response during soil drying

At branching (at slow soil drying due to small plant size) beginning of stomatal closure occurred 31 DAE (Fig. 3b) when  $\psi_1$  was about  $-1.2$  MPa (Fig. 3d). At flowering beginning of stomatal closure occurred 49 DAE (Fig. 4b) at a similar  $\psi_1$  value. At grain filling beginning of stomatal closure occurred 69 DAE when  $\psi_1$  was about  $-1.6$  MPa (Fig. 5d). Due to scatter these  $\psi_1$ -thresholds for droughted plants were less clear when relating  $g_1$  to  $\psi_1$  during the three growth stages (Fig. 7). The initially high level of stomatal conductance at branching resulted in the highest stomatal con-

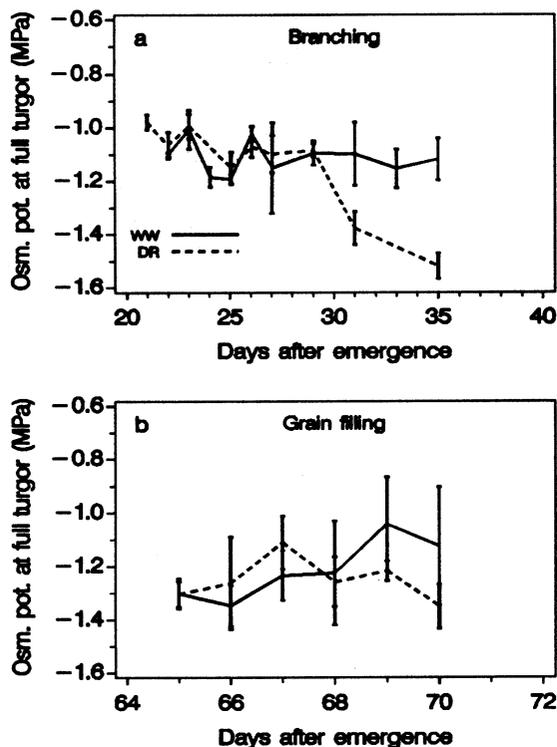


Fig. 6. Leaf osmotic potential at full turgor during soil drying at branching and grain filling. WW (—) and DR (---) indicate well watered and droughted plants, respectively. Bars indicate  $\pm$  S.E.M. ( $n = 3-5$ ).

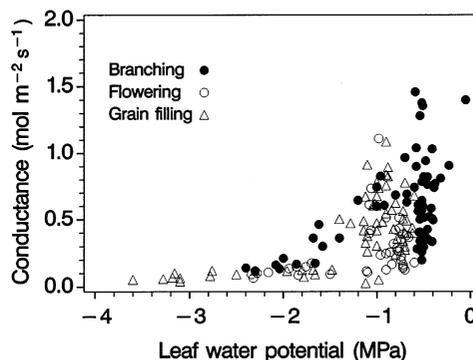


Fig. 7. Single observations of leaf conductance as a function of leaf water potential during soil drying at branching, flowering and grain filling.

ductance at low leaf water potential of the three growth stages (Fig. 7).

### 3.1.3. Leaf water relations during soil drying

During soil drying  $\psi_1$  decreased from about  $-0.7$  to  $-2.4$ –( $-3.2$ ) MPa (Figs. 3d, 4d and 5d).  $\psi_\pi$  decreased from  $-1.1$  to  $-2.7$  MPa during branching (Fig. 3e), from  $-1.4$  to  $-2.7$  MPa during flowering (Fig. 4e) and from  $-1.4$  to  $-3.5$  MPa during grain filling (Fig. 5e).  $\psi_p$  was maintained positive during the main part of the drying cycles (Figs. 3f, 4f and 5f). During branching and grain filling  $\psi_\pi^{100}$  decreased to  $-1.4$ –( $-1.5$ ) MPa indicating a moderate non-significant level of osmotic adjustment of about 0.3 MPa (Fig. 6).

RWC was about 0.9 under fully watered conditions and decreased below 0.65 during branching and flowering (Figs. 3g and 4g). During grain filling severe soil drying was prolonged and RWC decreased below 0.3 (Fig. 5g). Under severe drought TW/DW was only slightly influenced (Figs. 3h, 4h and 5h), while SLA was decreased significantly at branching during the long drying cycle where new leaves might have developed during drought (Fig. 3i).

### 3.1.4. Final grain yield response

Final grain yield was  $12.2 \text{ g plant}^{-1}$  in control plants and it was significantly ( $P < 0.05$ ) increased to  $14.1 \text{ g plant}^{-1}$  when exposed to soil drying during branching, and it was significantly de-

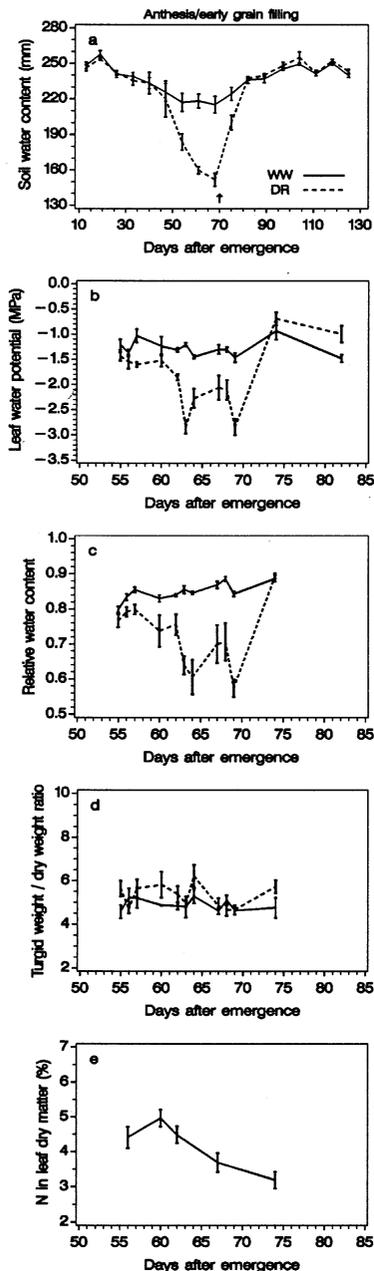


Fig. 8. Changes of soil water content (a), leaf water potential (b), leaf relative water content (c), turgid weight/dry weight ratio (d), and leaf nitrogen content (%) (e) during soil drying. WW (—) and DR (---) indicate well watered and droughted plants, respectively. Bars indicate  $\pm$  S.E.M. ( $n = 3-5$ ).

creased to 9.7 and 4.1 g plant<sup>-1</sup> when exposed to soil drying during flowering and grain filling, respectively. The latter low grain yield is probably due to the long lasting soil drying period (Fig. 5a). Stimulation of grain yield when crops have been exposed to drought during the vegetative stage of growth has earlier been found in several species (Turner, 1990).

### 3.2. Lysimeter experiment

The experiment was conducted during the late anthesis/early grain filling stage.

#### 3.2.1. Photosynthetic characteristics in fully irrigated plants

During the investigated period N% in leaf dry matter decreased from 5 to 3% (Fig. 8e). In order to further investigate gas exchange in quinoa  $A_{\text{sat}}$ ,  $g_1$ , SLA and N% were measured in fully watered plants during early grain filling (growth stage 14) (Table 1). The level of  $A_{\text{sat}}$  was similar to that at similar growth stage in pot experiment (Fig. 5c) while  $g_1$  tended to be higher than in the pot experiment (Fig. 5b). Photosynthetic WUE ( $A_{\text{sat}}/g_1$ ) was  $15 \pm 2.8$  (S.E.M.) [ $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}(\text{H}_2\text{O})$ ] and photosynthetic nitrogen use efficiency (NUE) was  $8.5 \pm 0.99$  (S.E.M.) [ $\mu\text{mol}(\text{CO}_2)\text{g}^{-1}(\text{N})\text{s}^{-1}$ ].

### 3.3. Water relations during soil drying

In fully watered plants midday values of  $\psi_1$  varied between  $-1.0$  and  $-1.3$  MPa (Fig. 8b) and the relative water content (RWC) was 0.85–0.90 (Fig. 8c). The leaf turgor pressure ( $\psi_p$ ) was 0.1–0.6 MPa and the osmotic potential ( $\psi_\pi$ ) was  $-1.3$  to  $-1.6$  MPa. Leaf water relations were clearly affected by drought from about 61 to 63 DAE, where  $\psi_1$  and RWC in stressed plants dropped to  $-2.8$  and 0.64 MPa, respectively (Fig. 8b and c).

At the end of the drying period pressure–volume (PV) analysis (Table 2) was undertaken in well-watered plants and in severely droughted plants just before rewatering. The droughted plants had low midday  $\psi_1$  ( $-2.9$  MPa) and RWC (0.59) values and were close to wilting. The analy-

Table 1

Photosynthesis ( $A_{\text{sat}}$ ), conductance ( $g_1$ ), photosynthetic WUE ( $A_{\text{sat}}/g_1$ ), leaf nitrogen content (leaf N), photosynthetic nitrogen use efficiency (NUE), % N in dry matter, specific leaf area (SLA) and photon flux density ( $Q$ , 400–700 nm) during measurement of irrigated plants<sup>a</sup>

Time of measurement	$A_{\text{sat}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$g_1$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	WUE ( $\mu\text{mol (CO}_2\text{)}\text{ mol}^{-1} \text{(H}_2\text{O)}$ )	Leaf N ( $\text{g m}^{-2}$ )	NUE ( $\mu\text{mol (CO}_2\text{)}\text{ g}^{-1} \text{(N) s}^{-1}$ )	[N] (% in DM)	SLA ( $\text{m}^2 \text{kg}^{-1}$ )	$Q$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
DAE 60–62	$22.0 \pm 1.89$	$1.5 \pm 0.246$	$15 \pm 2.8$	$2.6 \pm 0.20$	$8.5 \pm 0.99$	$4.7 \pm 0.24$	$18.4 \pm 1.09$	$1168 \pm 114$
Sunflower leaves <sup>b</sup>	35 <sup>c</sup>	1.2 <sup>c</sup>	29.2	2.3	15.2	4.3	18.9	1300–1600

<sup>a</sup> Data are means  $\pm$  S.E.M. of five leaves.

<sup>b</sup> After Fredeen et al. (1991) (field grown sunflower).

<sup>c</sup> Measured with LiCor 6200.

Table 2

Water relation characteristics of fully expanded quinoa leaves at early grain filling stage grown in sandy loam in the field as determined by expressed sap (ES) or pressure–volume (PV) technique from well watered and droughted treatments when nearly all plant available soil water had been used.  $\psi_{\text{leaf}}$ , leaf water potential;  $\psi_{\pi}^{100}$ , osmotic potential at full hydration;  $\psi_1^0$ , leaf water potential at the turgor loss point; RWC, leaf relative water content;  $\text{RWC}_a$ , leaf relative apoplastic water content;  $\text{RWC}^0$ , relative water content at the turgor loss point;  $\beta$ , sensitivity factor of elasticity;  $\epsilon_{\text{max}}$ , maximum bulk modulus of elasticity; TW/DW, turgid weight/dry weight ratio<sup>a</sup>

11 August 1994 (70 DAE)			
	Well watered	Droughted	Difference
RWC <sub>midday</sub>	0.84	0.59	0.25**
$\psi_1$ midday (MPa)	−1.47	−2.85	1.38**
ES. $\psi_{\pi}^{100}$ (MPa)	−1.34	−1.64	0.30*
PV. $\psi_{\pi}^{100}$ (MPa)	−1.27	−1.43	0.16*
PV. $\psi_1^0$ (MPa)	−1.57	−1.83	0.25*
PV.RWC <sup>0</sup>	0.85	0.82	0.03 <sup>ns</sup>
PV. $\beta$	−14.2	−10.7	3.5 <sup>ns</sup>
PV. $\epsilon_{\text{max}}$ (MPa)	21.9	18.4	3.5 <sup>ns</sup>
PV.TW/DW	6.7	7.6	0.9 <sup>ns</sup>
PV.RWC <sub>a</sub>	18.7	13.5	5.2*

<sup>a</sup> The values are means based on data of six leaves from each treatment. \*, \*\* differences significantly different from zero at the 0.05, 0.01 probability levels, respectively, using *t*-test to determine the significance levels (SAS, 1988).

sis showed an osmotic adjustment ( $\psi_{\pi}^{100}$ ) of 0.16 MPa by the PV method which was supported by the extraction of sap (ES) method (0.30 MPa). Also, the level of osmotic adjustment was in agreement with the seasonal adjustment at the end of drying period of the pot experiment (Fig. 6). The water potential at zero turgor ( $\psi_1^0$ ) in droughted plants decreased significantly by 0.25 MPa in sand relative to well-watered plants (Table 2). When  $\psi_1$  decreased below the  $\psi_1^0$  value, the leaves turned flaccid. There was no significant difference in the TW/DW ratio and in  $\epsilon_{\text{max}}$  between well-watered and droughted plants during the drying period. The relative apoplastic water content ( $\text{RWC}_a$ ) was significantly decreased in droughted plants from 19 to 14 (Table 2).

## 4. Discussion

### 4.1. Photosynthesis and SLA

This study exhibited features which probably support drought tolerance in quinoa. When compared with photosynthetic characteristics of other dicots at early grain filling the photosynthetic characteristics of quinoa including photosynthetic WUE and NUE (Table 1) were within the range of other dicots (Jensen et al., 1996) but lower than found in the most efficient cultivated plants rape (Jensen et al., 1996) and sunflower (Freeden et al., 1991). However, during early branching in well watered plants the high rate of net photosynthesis ( $A_{\text{sat}}$  18–34  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; Fig. 3c) together with high SLA values (23–21  $\text{m}^2 \text{kg}^{-1}$ ; Fig. 3i) might secure assimilates for rapid leaf expansion and root growth. Poorter and Remkes (1990) found that SLA was highly correlated with relative growth rate in 24 herbaceous species. As plants in drought prone areas often are planted after winter rain at high soil moisture content, features securing rapid root and top growth after germination (early vigour) will cause that available moisture can be utilised ahead of loss due to deep drainage and soil evaporation. Such features of drought resistance have earlier been recognised in wheat. Biomass production at the five- to six-leaf stage was positively correlated with grain yield on deep sandy soils with poor water holding capacity (Turner and Nicolas 1987).

### 4.2. Stomatal response during soil drying

The stomatal response to soil drying indicated that quinoa had an insensitive stomatal response as stomatal closure did not occur before  $\psi_1$  was below −1.2 to −1.6 MPa. This midday- $\psi_1$ -threshold for stomatal closure during soil drying is similar to that in semidwarf-wheat genotypes as measured under glass-house conditions during the vegetative stage of growth (Shimshi et al., 1982; Henson et al., 1989) and to that in vegetative field sorghum predominantly grown under semi-arid conditions (Girma and Krieg 1992a,b). Thus, quinoa can be characterised as a crop tolerating dehydration as compared with other dicots, e.g.

rape (Jensen et al., 1996) and lupins (Henson et al., 1989; Jensen et al., 1998). This makes it less likely that chemical signalling causes a first order of response to drought in quinoa as found lately in lupin (Jensen et al., 1998) and in temperate wheat (Ali et al., 1998).

#### 4.3. Leaf water characteristics during soil drying

The levels of leaf water potential obtained here were in accordance with the results of García et al. (1991), who showed that under irrigation predawn  $\psi_1$  was from  $-0.5$  to  $-1.0$  MPa and in stressed conditions down to  $-1.5$  MPa.  $\psi_\pi$  often decreases as plant age and is lower in field plants than in glass house and climate chamber plants (Turner and Begg, 1981). This was also the case in the present experiment as  $\psi_\pi^{100}$  decreased from  $-1.0$  MPa at early branching to  $-1.4$  MPa during grain filling (Fig. 6; Table 2). The level of osmotic adjustment was  $0.3$ – $0.4$  MPa at the most (Fig. 6; Table 2); thus, the ability of osmotic adjustment of quinoa seems to be moderate. Neither could Delatorre et al. (1997) demonstrate a significant osmotic adjustment in quinoa.

As determined by the PV-method the level of  $\psi_\pi^{100}$  found in quinoa is comparable to that found in monocotyledonous species grown in the field under temperate conditions, e.g. in barley, where  $\psi_\pi^{100}$  was also between  $-1.0$  and  $-1.3$  MPa (Andersen et al., 1991; Jensen et al., 1992), and in wheat flag leaves of fully watered plants  $\psi_\pi^{100}$  was  $-1.2$  MPa (Ali et al., 1999) and under semi-arid conditions  $\psi_\pi^{100}$  was  $-1.1$  MPa in wheat (Rascio et al. 1988) and  $-0.8$  MPa in field sorghum (Girma and Krieg 1992a). In other cultivated C3 dicotyledonous plants such as lupin and rape  $\psi_\pi^{100}$  was only  $-0.7$  and  $-0.9$  MPa, respectively (Jensen and Henson, 1990; Jensen et al., 1996). The low osmotic potential in itself will support the maintenance of the potential gradient for water uptake at low soil water potential under high evaporative demands causing deficits in the plant (Shalhevet, 1993; Ali et al., 1999) as also envisaged in modelling work (Jensen et al., 1993). Field studies have shown that wheat lines with a high degree of osmotic adjustment yielded up to 60% more than genotypes without this characteristic

under drought prone conditions (Morgan et al., 1986). Thus the inherent low osmotic potential in quinoa probably causes drought tolerance as in the case of lowering the osmotic potential by osmotic adjustment in wheat. However this depend partly on the bulk elastic modulus. The bulk elastic modulus ( $\epsilon_{\max}$ ) was higher (Table 2) than values found in the dicot rape ( $15$ – $17$  MPa) (Jensen et al., 1996) and similar to values found in lupin (Jensen and Henson, 1990). However, in droughted plants  $\epsilon_{\max}$  tended to decrease non-significantly from  $22$  to  $18$  MPa (Table 2), which may have sustained turgor maintenance in the droughted plants, as the water potential at zero turgor ( $\psi_1^0$ ) in droughted plants decreased significantly. This way of turgor maintenance has also been described in other species (Jane and Green, 1983). Similarly, the low TW/DW ratio of  $4$ – $6$  at flowering and grain filling (Figs. 4h and 5h) (but not at branching, Fig. 3h) is comparable with the ratio of  $4.0$  in field wheat flag leaves (Ali et al., 1999). This suggests drought resistance, as small thick walled cells may be adapted to large losses of water without loss of turgor (Cutler et al., 1977). The low TW/DW ratio of  $4$ – $6$  probably has caused the relatively high RWC<sub>a</sub> value of  $14$ – $19\%$  (Table 2) as much of the apoplastic water is stored in the cell walls (Andersen et al., 1991).

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