

RESEARCH NOTE

Effect of water availability on physiological performance and lettuce crop yield (*Lactuca sativa*)

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Abstract

M.A. Molina-Montenegro, A. Zurita-Silva, and R. Oses. 2011. Effect of water availability on physiological performance and lettuce crop yield (*Lactuca sativa*). Cien. Inv. Agr. 38(1): 65-74. Water is essential for plants, affecting the majority of the physiological processes related to growth and productivity. Water shortage is one of the most common factors that limit crop productivity worldwide. Many cultivars have elevated water requirements, nevertheless in some countries due to global climate change effects, the availability of water for irrigation is becoming limited. In fact, current models of climate changes predict that central Chile will be a sensitive zone where precipitation will drastically decrease. In this study, the variation of gas exchange and production of fresh biomass in a lettuce cultivar, grown under different water availability regimes, was evaluated. Additionally, the concentration of total soluble sugar and water use efficiency (WUE) as mechanisms related to water shortage responses were also evaluated. Overall, individuals with the lowest water availability (50%) showed lower gas exchange and fresh biomass values than their conspecifics grown in optimal irrigated conditions. On the other hand, those individuals with moderate water shortage showed the highest concentration of total soluble sugars and WUE. Our results suggested that cultures exposed to extensive or intense drought events, could be negatively affected in both physiological performance and productivity. Nevertheless, slight decreases in water availability can enable lettuce plants to exhibit a high WUE, maintaining high levels of physiological performance and productivity.

Key words: Soluble sugars, water use efficiency, water shortage, lettuce, photosynthetic rate.

Introduction

Physiological responses to environmental fluctuations are one of the principal determinants of the distribution and productivity of most plant species worldwide (Bazzaz, 1996; Gurevitch *et al.*, 2002). Water is an essential element for

plants, affecting most physiological processes involved in growth and productivity (Nakayama and Bucks, 1986; Nobel, 2005). Water shortage is one of the most common factors of stress that may affect and limit agricultural productivity at world level (Gallardo *et al.*, 1996; Sánchez, 2000; Hamdy *et al.*, 2003; Pessaraki, 2007; Acar *et al.*, 2008). Several crops have high water demands that must be supplemented with additional irrigation; however, available water for irrigation becomes restricted in many countries

as a result of global climate changes (Hamdy *et al.*, 2003; Flexas *et al.*, 2006). In fact, the current models of global climate changes identify Central Chile as one of the zones where there will be a clear evidence of decreased precipitations (IPCC, 2007), exposing the species inhabiting this zone to the negative effects of water shortage (Dirven and Rodríguez, 2008).

Several efforts have been made to evaluate responses from different crops in the presence of water stress, as they ultimately limit the system productivity (Matthews and Anderson 1988; Jackson *et al.*, 1994; Wheeler *et al.*, 1994; Gallardo *et al.*, 1996; Karam *et al.*, 2002; Acar *et al.*, 2008). For example, Sánchez (2000) showed that water availability in lettuce crops results in larger individuals and fresh biomass. On the other hand, small variations in irrigation regimes affect significantly photosynthesis in cocoa seedlings (Deng *et al.*, 1990), pepper (De Grazia *et al.*, 2007) and lettuce plants (He *et al.*, 2001), which indicate a strong dependence on water for physiological processes in several crops. The negative effects of water shortages may depend on other factors such as ontogeny status, type of root system, presence of other concomitant stress factors, and the presence of protection mechanisms induced by water deficit (Björkman and Powles, 1984; Du and Tachibana, 1994; Morison, 1996; He and Le, 1998; Boroujerdnia *et al.*, 2007; Pelah *et al.*, 2008).

Several morphological and physiological strategies that enable different crops to reduce the negative effects of water shortage have been well documented, where the physiological strategies are the most studied (Deng *et al.*, 1990; Sánchez *et al.*, 1998; Nobel 2005; Flexas *et al.*, 2006). Sugar accumulation has been one of the most documented physiological mechanisms in crops under drought stress (Ingram and Bartels, 1996; Lambers *et al.*, 1998; Stikic *et al.*, 2003). To date, there is abundant literature suggesting the importance of sugars in order to mitigate the negative effects of water stress, as they are involved in osmotic cell adjustment, maintaining turgor and allowing cell expansion even under prolonged

drought (Sánchez *et al.*, 1998; Davies *et al.*, 2000; Pelah *et al.*, 2008).

Likewise, the increase of water use efficiency has been described as another strategy to reduce the negative effects of water stress in crops (Werk and Ehleringer, 1984; Jackson *et al.*, 1994; Tennakoon and Milroy 2003). There is a *trade-off* between the carbon entering through the stomata to be fixed and the water eliminated through the same opening (Lambers *et al.*, 1998). Therefore, in the presence of water shortage, the plant would tend to reduce the stoma opening, minimizing the water loss, with the subsequent decrease of carbon gain and therefore, of biomass accumulation (Jackson *et al.*, 1994; Flexas *et al.*, 2006). Nevertheless, some species can maintain normal photosynthetic rates, after slight decreases of water availability, through a good stomatal regulation, maximizing the available water and thus maintaining higher water use efficiency (Deng *et al.*, 1990; Lambers *et al.*, 1998).

Lettuce is one of the crops most susceptible to water deficit (*Lactuca sativa* L.) (Sánchez, 2000; Karam *et al.*, 2002; Boroujerdnia *et al.*, 2007). This crop has been described to be highly dependent on water at all developmental stages, both for germination and to maintain high photosynthetic rates and a fresh biomass of high commercial value (Wallace and Wallace, 1986; Gallardo *et al.*, 1996; Sánchez, 2000; Nissen and San Martín, 2004). Although lettuce is one of the most important horticultural crops at national level, there is still no fully understanding of the physiological responses and production levels to maximize the use of increasingly limited water for irrigation, often used in inefficient ways.

In order to know how water availability affects the physiological responses and lettuce production, gas exchange parameters and fresh biomass of individuals subjected to three levels of irrigation were measured. Additionally, total soluble sugar concentrations and water use efficiency as potential compensatory mechanisms in response to water deficit, were determined.

Materials and methods

Study site and experimental design

The present work was performed at the agricultural experimental station at Universidad Santo Tomás, 6 km from the city of Los Ángeles (37°27'S; 72°15'W), Chile. The study site corresponds to a Mediterranean climate zone, with slight continentally traces (di Castri and Hajek, 1976). The average annual temperature reaches 13.7 °C, with maximum and minimum averages of 20.1 and 8.1 °C, respectively (di Castri and Hajek, 1976). Additionally, an annual average precipitation of 1,302 mm has been estimated for this site (di Castri and Hajek, 1976).

The plant material was obtained from seedlings generated from lettuce (*Lactuca sativa*), which were germinated in growth chambers, under controlled humidity (75% ± 5) and temperature (22°C ± 2) conditions. For treatments setup, the seedlings were transplanted when each individual presented at least four true leaves and 2 cm-emerged roots. A 20 x 30 cm plantation framework was used inside a 1,500 m²-parabolic roof greenhouse, with polyethylene walls and lateral ventilation. Seedlings were divided into three treatments: (1) 100% of the water irrigation that each seedling receives typically for that region (40 ml/ day), (2) 75% of normal water irrigation (30 ml/ day) and (3) 50 % of normal water irrigation (20 ml/ day). The amount of water that is normally added to reach marketable size in lettuce crops at the experimental station of the Universidad Santo Tomás was considered as 100% of water used to irrigate each plantlet (Molina-Montenegro, unpublished data). The seedlings (n = 20 for each treatment) were planted in rows at 0.5 m-distance, and each seedling was separated from the other by 0.2 m. The water was added by means of a drip irrigation system with plastic ribbons (T-tape brand). Each individual was supplemented with 0.2 g L⁻¹ of Phostrogen® (Solaris, NPK, 14:10:27) each 15 days. The experiment was extended for 80 days, and the measurements were made simultaneously in the three treatments.

Gas exchange

The net photosynthesis rate (A), the stomatal conductance (g), the foliar temperature (T_f), the transpiration rate (E) and the incident photosynthetically active radiation (PAR) were measured in visually healthy leaves from 12 individuals corresponding to each treatment. The measurements were made on the same individual at 10, 40 and 70 days, using an infrared gas analyzer (IRGA, Infra Red Gas Analyser, CIRAS-1, PP-Systems Haverhill, USA).

Total fresh biomass

All the individuals sampled in each treatment were extracted from the soil, without damaging the root system, at the end of the experimental period (80 days). Subsequently, the roots were washed without removing them from the stem and left to dry in shade for a 6-h period. Finally, each individual was weighed with a digital electronic balance (Boeco BBL-52; 0.01 g-precision) indicating the total fresh biomass.

Total soluble sugars

Three leaves from 10 individuals from each treatment were collected at 80 days in order to measure the total soluble sugar concentration. Each sample (three leaves/ individual) was cut into small pieces and kept in ethanol (86%) for a period of 24 H, and then centrifuged at 1200 g for 10 min. The supernatant was depigmented in a mixture of 1:3 (v/ v) with chloroform and the aqueous fraction was dried in cold for 12 H. Subsequently, the dry residue was resuspended in 500 ml of methanol. The total soluble sugar content was determined by spectrophotometry using the resorcinol method (Roe, 1934) with a reading at 520 nm, using sucrose as standard.

Water use efficiency

From the values obtained from gas exchange measurements, the instantaneous water use efficiency (WUE) for photosynthesis was estimated as the ratio between the values of photosynthetic rate and transpiration (A/E). This parameter was used as an indicator of the presence of plant water stress in a microsite or condition, as the incremented WUE would be induced by a decrease in water availability (Lambers *et al.*, 1998).

Statistical analysis

Gas exchange parameters and water use efficiency were analyzed by an analysis of variance (ANOVA) of repeated measurements. Differences between treatments were evaluated by a *posteriori* Tukey test. The production of fresh biomass and total soluble sugar concentrations were compared between treatments using a one-way ANOVA. Similarly, data normality and variance homogeneity were calculated using the Shapiro-Wilks test and Bartlett, respectively (Sokal and Rohlf, 1995).

Results

Gas exchange

The photosynthetic rate (A_{max}) was significantly higher in the treatments with 100% and 75% of water availability ($F_{33,2} = 177.12$; $P < 0.001$), in comparison with the individuals that only received 50% of irrigation (Figure 1A). Additionally, a significant decrease on the photosynthetic rate through time was observed ($F_{66,2} = 80.23$; $P < 0.001$). Similarly, the Time x Treatment interaction was significant ($F_{66,4} = 60.56$; $P < 0.001$), because with increasing exposure time in the treatment, the photosynthetic rate only decreased in plants that received 50% of irrigation (Figure 1A).

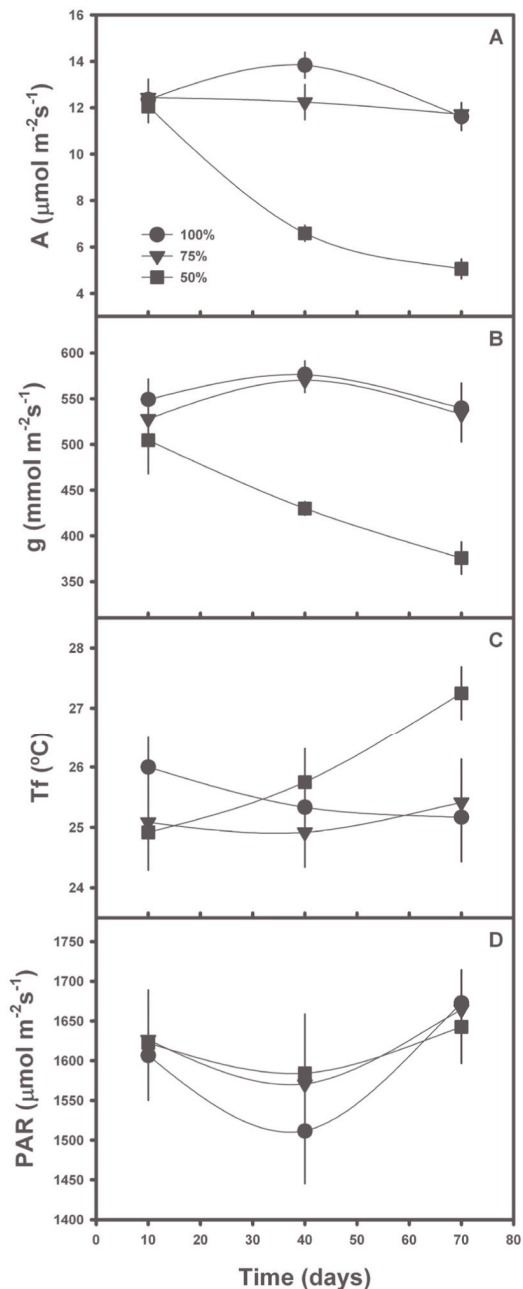


Figure 1. Net photosynthesis rate (A), stomatal conductance (B), foliar temperature (C) and photosynthetically active radiation (D), measured in *Lactuca sativa* individuals, under 100%, 75% and 50% of water availability. Mean values (± 1 SD) are shown at 10, 40 and 70 days of exposition to water treatments.

The stomatal conductance (g) was significantly higher ($F_{33,2} = 90.60$; $P < 0.001$) in the individuals with 100% and 75% irrigation, followed by the con-generic individuals with only 50% irrigation (Figure 1B). Although the stomatal conductance was significantly lower ($F_{66,2} = 13.32$; $P < 0.001$) at the end of the experiment, this trend was only evident in the treatment with the lowest water availability ($F_{66,4} = 11.15$; $P < 0.001$; Figure 1B).

The foliar temperature (Tf) varied significantly among treatments ($F_{33,2} = 4.66$; $P = 0.016$); it was higher in the individuals only with 50% irrigation (Figure 1C). The Time x Treatment Interaction factor was significant ($F_{66,4} = 10.43$; $P < 0.0001$), because while leaf temperature decreased in the treatment of 100% and 75%, the treatment of 50% irrigation increased as the time went by (Figure 1C).

The photosynthetically active radiation (PAR) was not different among the water treatments ($F_{33,2} = 0.77$; $P = 0.47$) nor for the Time x Treatment interaction ($F_{66,4} = 0.95$; $P < 0.44$; Figure 1D).

Fresh biomass

The analysis showed significant differences among the water treatments ($F_{57,2} = 104.07$; $P < 0.0001$). Only the individuals receiving 50% irrigation had a significant decrease in fresh biomass, while there were no differences among the treatments with higher water availability (Figure 2).

Total soluble sugars

The concentration of total soluble sugars was significantly different in the three treatments ($F_{27,2} = 180.52$; $P < 0.0001$). The individuals treated with 75% irrigation significantly displayed the highest soluble sugar concentration, followed by the individuals receiving 100 and 50% irrigation (Tukey test, Figure 3).

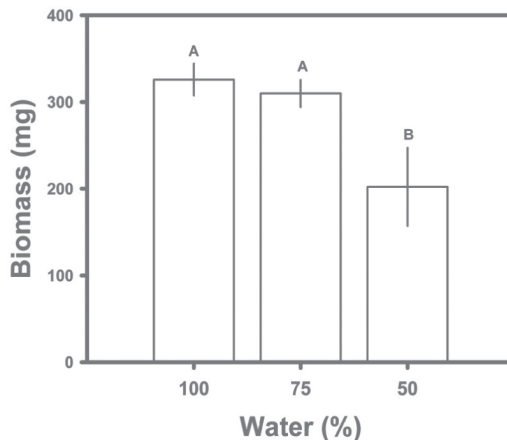


Figure 2. Total fresh biomass (± 1 SD) in *Lactuca sativa* individuals measured at 80 days under 100%, 75% and 50% of water availability treatments. (Different letters indicate significant differences; Tukey test, $\alpha < 0.05$).

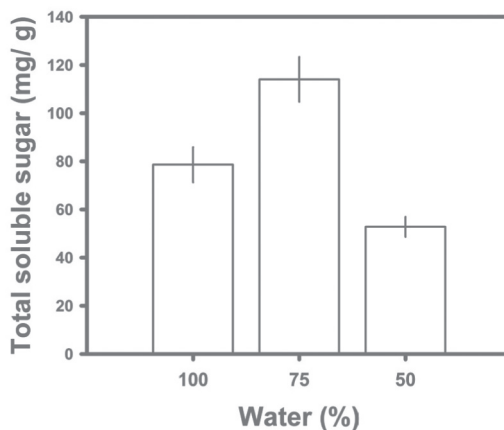


Figure 3. Total soluble sugar (± 2 SE) in *Lactuca sativa* individuals measured at 80 days under 100%, 75% and 50% of water availability treatments. (Different letters indicate significant differences; Tukey test, $\alpha < 0.05$).

Water use efficiency

Individuals distributed in the treatment with 75% irrigation showed significantly greater water use efficiency ($F_{33,2} = 67.47$, $P < 0.0001$), followed by those with 100% irrigation and finally by individuals who received only 50% irrigation (Figure 4). Analysis showed a significant effect in the Time x Treatment interaction factor ($F_{66,4} = 28.52$; $P < 0.0001$). While individuals distributed in the treatment of 100% and 75%

irrigation increased their water use efficiency over time, those under treatment 50% irrigation greatly decreased their efficiency over time (Figure 4).

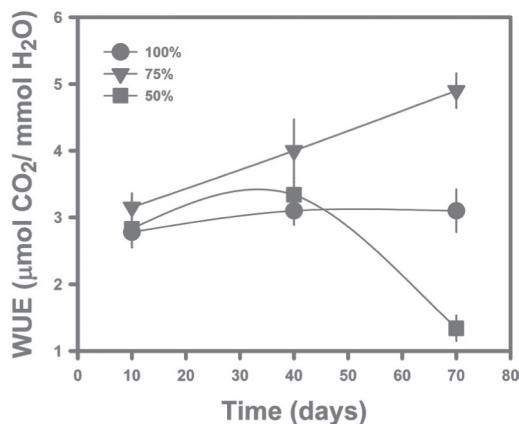


Figure 4. Variation in water use efficiency (± 2 SE) in *Lactuca sativa* individuals measured at 10, 40 and 70 days of exposition to water availability treatments of 100%, 75% and 50%.

Discussion

Lettuce is one of the most consumed crops worldwide and is very susceptible to water stress (Karam *et al.*, 2002; Boroujerdnia *et al.*, 2007), which makes its production highly dependent on environmental variations. Despite the limitations for cultivation, the demand is growing constantly, thus many studies have aimed to evaluate the effects of water availability on physiology and production (Gallardo *et al.*, 1996; He and Lee, 1998; Boroujerdnia *et al.*, 2007; Acar *et al.*, 2008).

This work has found that different individuals subjected to a decreased water availability condition decreased their gas exchange parameters, thus affecting the accumulation of fresh biomass. Similar results have been found in other studies. For instance, Gallardo *et al.* (1996) reported that the photosynthetic rate and the stomatal conductance decreased in 31 and 26%, respectively, in response to reductions in water availability. On the other hand, Karam *et al.* (2002) showed that different lettuce cultivars presented lower numbers of leaves and a 39%

drop off in the fresh biomass triggered by water deficit. While a decrease in water availability affects the physiology and productivity of lettuce plants, other effects such as loss of turgor, flavour, aroma and colour, and increased susceptibility to attack by pathogens, can become more economically harmful (Pessaraki, 2007).

Normally, more than a half of the carbon fixed by photosynthesis is lost in respiration, but under a severe water stress, this ratio may change (Flexas *et al.*, 2006), causing a reduced availability of biomass resources to be assigned. While individuals subjected to 50% water availability recorded the lowest fresh biomass, the latter process could explain this reduction; however, additional studies should be performed to better evaluate this hypothesis.

On the other hand, it has been reported that a severe water stress may reduce photosynthesis by independent pathways to stomatal conductance like the diminished potential photochemical efficiency, the rate of electrons transportation or the variation in oxygen concentration (Kaiser, 1987; Pessaraki, 2007). This effect might be aggravated with another related stress factor like high temperature or high luminous radiation (Björkman and Ponles, 1984; He *et al.*, 2001; He and Lee, 2004). In this study, the individuals exposed to 50% water presented higher foliar temperatures, which, in addition to the high luminous radiation, might further stress the water shortage effect, resulting in a lower photosynthetic rate (Barker *et al.*, 2002). It has been reported that increases in leaf and root temperature, together with a remarkable water deficit, induce stomatal closure in different crops. This increase in temperature is mainly due to the lack of water and heat regulation mechanisms through leaf transpiration (Du and Tachibana, 1994), leading to lower photosynthetic rates and fresh biomass (He and Lee, 2004; Pessaraki, 2007).

It has been shown that several negative effects from water stress in many crop productivity may be diminished through an osmotic fit (Rodríguez-Maribona *et al.*, 1992; Moustafa *et al.*, 1996). Although the specific mechanism has not been totally determined yet, the current

evidence indicates that may be due mainly to turgor, membrane stability and the maintenance of the cell expansion, even under water shortage (Crowe *et al.*, 1992; Ingran and Bartels, 1996). The osmotic fit is the decrease of osmotic potential due to solute accumulation within the cells. Soluble sugar is an example of solutes participating in the diminished negative effects of water shortage in different crops, which is accumulated in the cytoplasm (Sánchez *et al.*, 1998; Pelah *et al.*, 2008). Although osmotic fit is a mechanism commonly used by different vegetal species, the metabolic cost of storing photosynthates and their use for osmotic fit may be high, even exceeding the cost of converting the carbohydrate reserves into a new biomass (Pesarakli, 2007). Therefore, the sugar expressions might be efficient mechanisms for conditions of short term or low intensity water shortage, as some studies have found a positive correlation between the tolerance to moderate or seasonal water stress and the soluble sugar concentration (Lambers *et al.*, 1998; Stikic *et al.*, 2003; Pelah *et al.*, 2008). This is coherent with the results obtained in the present study, as the individuals presenting only a 25% decrease of water availability presented high levels of soluble sugars along with a high photosynthetic rate and accumulation of fresh biomass.

Several studies have been performed to maximize the strategies involved on increasing the efficiency of water use in lettuce crops (Jackson *et al.*, 1994; Tennakoon and Milroy 2003). Nevertheless, most of them have reached unfavourable or slightly positive results, because the water volumes used for lettuce production are very high, due to the superficial radicular system, as well as the scarce shading that lettuce crops are exposed to (Gallardo *et al.*, 1996; Barker *et al.*, 2002). Although management to regulate irrigation and maintain the plants at a physiological rest period is currently available, these techniques limit photosynthesis, foliar growth and, therefore, productivity (Matthews and Anderson, 1988).

In general, plants subject to water shortage assign their resources to roots until the water capture increases (Pesarakli, 2007). Thus, lettuce

may survive by lengthening the roots when the surface soil is dry, in addition to moving leaves to regulate the water use efficiency and maintain positive photosynthesis rates (Werk and Ehleringer, 1984). Although, variations in the radicular system or foliar movements as mechanisms to increase the water use efficiency (WUE) were not evaluated in the present study, the stability of the photosynthetic rate and stomatal conductance in the individuals with 75% water might be the main reason for the high WUE presented. The above mentioned suggests that small variations in the water contribution along with the expression of soluble sugars would allow lettuce crops to maintain a high WUE for photosynthesis, resulting in a high productivity with low water cost.

Lettuce crops are most sensitive to water shortage due to their slightly- deep radical system, an effect that becomes evident on the production of their vegetal tissue, which demands water levels from soil close to field capacity (Pesarakli, 2007). On the other hand, lettuce crops are grown widely in zones where temperatures and luminous radiation are high, which leads to the producer to a continuous water application that, in most cases, becomes greater than their needs (Gallardo *et al.*, 1996). However, the water available for irrigation is reduced in most countries as a result of the global climate changes and the changes on soil use. Therefore, the knowledge on how lettuce crops respond on their physiology and productivity in the presence of variations on water availability will allow maximizing water use efficiency in lettuce crops, maintaining good quality under a future scenario of climate changes in Central Chile.

Acknowledgements

The author thanks the career of Agronomy of Universidad Santo Tomás, Los Ángeles, for the facilities to carry out this study. This article corresponds to activities of “Centro de Biotecnología para el Desarrollo en Zonas Áridas (BIOTECZA) Innova-Chile (06FC01 IBC-71)”.

Resumen

M.A. Molina-Montenegro, A. Zurita-Silva y R. Oses. 2011. Efecto de la disponibilidad hídrica sobre el desempeño fisiológico y productivo de un cultivo de lechuga (*Lactuca sativa*). Cien. Inv. Agr. 38(1): 65-74. El agua es un elemento esencial para las plantas, afectando la mayoría de los procesos fisiológicos implicados en el crecimiento y productividad. La sequía es uno de los factores de estrés más común que puede limitar la productividad agrícola a nivel mundial. Muchos cultivos poseen altas demandas hídricas, no obstante en muchos países y producto del cambio climático global, el agua disponible para riego se torna limitante. De hecho, los actuales modelos de cambio climático global señalan a Chile como una de las zonas donde la disminución en las precipitaciones sería más evidente. En el presente trabajo, se evaluó la variación en el intercambio gaseoso y producción de biomasa fresca en cultivos de lechugas sometidos a diferentes niveles de disponibilidad hídrica. Adicionalmente, se evaluó la concentración de azúcares solubles totales y la eficiencia en el uso del agua (EUA) como mecanismos implicados en la tolerancia al déficit hídrico. En general, aquellos individuos sometidos a menor disponibilidad hídrica presentaron menores valores de intercambio gaseoso y biomasa fresca, en comparación a sus con-específicos crecidos con el 75 y 100% de la disponibilidad hídrica. Por otro lado, aquellos individuos con la disponibilidad hídrica intermedia presentaron mayores contenidos de azúcares solubles totales y una mayor EUA. Los resultados de la presente investigación sugieren, que aquellos cultivos sometidos a eventos prolongados o intensos de sequía podrían verse afectados en su fisiología y productividad. No obstante, leves disminuciones en la disponibilidad hídrica permitirían a los cultivos de lechugas mantener una elevada EUA, manteniendo una elevada tasa fotosintética y una alta productividad.

Palabras clave: Azúcares solubles, eficiencia en el uso del agua, estrés hídrico, lechuga, tasa fotosintética.

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