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EFFECT OF WATER DEFICIT STRESS ON GROWTH, PROLINE ACCUMULATION, LIPID CONTENT AND FATTY ACID COMPOSITION OF PURSLANE (*PORTULACAOLERACEA* L.)

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ABSTRACT

Purslane is a drought- and salt-tolerant plant, containing high amounts of ω-3 fatty acids and antioxidants. In this study, purslane seedlings were subjected to different soil water contents; 75%, 50% and 25% field capacity(FC), their growth, leaf relative water content (RWC), maximum photochemical efficiency (Fv/Fm), chlorophyll, proline, total lipid content (SPAD index) and the fatty acid composition were determined. Water deficit stress significantly reduced shoot and increased root dry matter. Leaf RWC was decreased 8% and 14% under moderate and severe water deficit stress respectively. The (Fv/Fm) ratio was not affected by water deficit. There was a steady rise in chlorophyll contentwith increase in the stress.Total lipid content increased in the leaves of purslane due to water deficit stress. Linolenic acid (C18:3) proportion increased progressively related to the stress. This increase was accompanied by linoleic, oleic and stearic acid reduction. The ratio of omega-3 to omega-6 fatty acids was significantly changed due tothe stress. Increasing severity of water stress

caused an increase in proline content. These results suggest that water deficit tolerance of purslane plants might be closely related to the increased content of linolenic acid and with the accumulation of proline under water deficit conditions.

Keywords: Purslane, water deficit stress, maximum photochemical efficiency,proline, α-linolenic acid.

INTRODUCTION

Drought, or more generally, limited water availability is the main factor limiting crop production (Ceccarelli and Grando 1996). Therefore, replacement of crops characterized by high water requirements by drought tolerant crops is an efficient strategy under water shortage conditions (Seghatoleslami et al. 2008). Purslane (*Portulacaoleracea* L.) is a heat-, salinity- and drought- tolerant plant, and grows readily in soils that may be arid and saline (Aronson 1989). The shoot is a rich source of omega-3 fatty acids (Palaniswamy et al. 2001), with an extremely good ratio of ω-6 to ω-3 fatty acids as well as antioxidants, minerals and proteins (Teixeira and Carvalho 2008; Teixeira et al. 2010). It is eaten fresh, cooked or dried and interest in cultivating it as a food crop has increased all over the world in recent years (Aronson 1989; Yazici et al. 2007; Teixeira and Carvalho 2008)however very little is known about its production as a food crop and the effects of cultural conditions on its nutritional value. There have been some studies carried out to determine the best cultural conditions to obtain higher levels of fatty acids in purslane leaves, under greenhouse conditions (Palaniswamy et al. 2001). The presence and concentration of α-linolenic acid in purslane may vary with the cultivar, geographic distribution, developmental stage, and environmental factors (Teixeira et al. 2010).

Water deficit induces significant alterations in plant physiology and biochemistry. Some plants have a set of physiological adaptations that allow them to tolerate water stress conditions (Save et al. 1995). The maximum quantum yield of photosystem II can be expressed as Fv/Fm. PSII fluorescence can be regarded as a biosensing device for stress detection in plants. Fv/Fm can be an indicator of a plant to tolerate stress and the amount damage that has occurred to the photosynthetic capabilities of the plant (Maxwell and Johnson 2000). The use of this ratio from intact and attached leaves proved to be a reliable, non-destructive method for monitoring photosynthetic events and for judging the physiological status of the plant (Riza et al. 2001). This phenomenon is a criterion for thylacoide membrane integrity

and electron transfer efficiency from photosystem II (PSII) to photosystem I (PSI) (Ma et al. 1995). This ratio is widely used to estimate the degree ofphotoinhibition (Osmond and Grace 1995) and has been shown to respond to drought in various plants (Cornic and Massacci 1996; Flagella et al. 1998; Tezara et al. 1999). Environmental stresses that affect PSII efficiency leads to a characteristic decrease in the Fv/Fm ratio (Krause and Weis 1991; Mamnouie et al. 2006).In many observed cases chlorophyll content declines under stress conditions. Potato leaves show a significant decline in chlorophyll content with increasing water stress (Nadler and Bruvia 1998).

One of the most common stress tolerance strategies in plants is the overproduction of different types of compatible organic solutes (Serraj and Sinclair 2002). Proline is one amongst the most important cytosolutes and its free accumulation is a widespread response of higher plants, algae, animals and bacteria to low water potential (Zhu 2002). Along with proteins, lipids are the most abundant component of membranes and they play a role in the resistance of plant cells to environmental stresses (Suss and Yordanov 1986). Plant leaf cell membranes and particularly chloroplastic membranes contain high levels of trienoic fatty acids. In C18-plant species, linolenic acid (18:3) is the major fatty acid (Torres-Franklin et al. 2009).

Unsaturated fatty acids like linolenic and α-linolenic acids belong to the ω-6 and ω-3 families of fatty acids respectively (Palaniswamy et al. 2001). They are essential fatty acids synthesized in plant tissues from oleic acid by the introduction of double bonds between the existing double bond and the terminal methyl group. These double bonds are inserted by specific fatty acid desaturase enzymes (Shanklin and Cahoon 1998). Omega-3 fatty acid desaturases catalyze the insertion of a third double bond into linoleic acid precursors to produce linolenic acid. Two full-length cDNA clones PoleFAD7 and PoleFAD8, encoding plastidial ω-3 fatty acid desaturases were isolated from purslane (Teixeira et al. 2010). Many reports indicate that environmental stresses such as cold, heat, drought and salt induce changes in FA composition, mainly in the content of linolenic acid (18:3) (Zhang et al. 2005). Drought stress was found to reduce the amount of 18:3, for example in *Pachyrhizusahipa* (Matos et al. 2002). Conversely, there are few reports suggesting that drought stress caused an increase in omega-3 fatty acids mainly in chloroplast lipids (Douglas and Paleg 1981; Repellin et al. 1997).

Purslane grows readily in soils that may be

arid and saline (Aronson 1989), but there was no data on drought tolerance potential and effect of water deficit on purslane. Therefore, the aim of this study was to (1) determine water deficit stress tolerance potential of purslane (2) determine whether water deficit change lipid content and fatty acid composition especially polyunsaturated fatty acids and (3) investigate proline accumulation under water deficit stress in purslane.

MATERIALS AND METHODS

The experimentwas conductedat the department of Horticultural Sciences, University of Tabriz, Iran under greenhouse conditions. Pots (8 L) filled with 8 kg of loamy sand soil and were irrigated up to field capacity (FC). Soil pH and electrical conductivity were 7.97 and 2.25 dS/m respectively. Applied fertilizer consisted of 100 kg/ha N as ammonium nitrate, 20 kg/ha P as superphosphate and 60 kg/ha K as potassium sulphate. Purslane seeds bought from a local market were sown in the pots that were arranged in a completely randomized design with four replications. Plants were thinned to 18 plants per pot when they were at the stage of 2 true leaves. The soil water content was monitored with ECH2O probes (Decagon Devices, USA) daily. Plants were subjected to three water regimes: (i) well watered treatment, where plants were constantly irrigated and maintained up to physiological maturity under soil moisture condition of 75% from total soil water capacity; (ii) reduced regime 1 (50% container capacity, FC; (iii) reduced regime 2 (25% FC). Plant samples for analysis were harvested at flowering.

Growth characteristics analysis

After harvesting, leaf number, shoot and root length were measured. Leaf area of plants was measured by means of leaf area meter (Li-cor Model Li-1300-USA). Then leaves, stem and root were weighed separately to obtain their fresh weight. Thereafter, dry weight of leaves, stem and roots were determined by drying them in an air forced oven at 70 ˚C for 48 hr. Specific leaf area (SLA) and leaf area ratio (LAR) were calculated.

Relative water content (RWC) determination

The relative water content stated by Slatyer in 1967 is a useful indicator of the state of water balance of a plant essentially because it expresses the absolute amount of water, which the plant requires to reach artificial full saturation. Relative water content of leaves was measured according to Jensen et al. (1996) at the end of experiment. Relative water content (RWC) was estimated by determining the turgid weight of 0.5 g fresh leaf samples by keeping them in water for 4 hr, followed by drying in hot air oven till

constant weight using the following formula.

RWC (%) = [(W-DW) / (TW-DW)] ×100

W represents sample fresh weight; TW represents sample turgid weight; DW represents sample dry weight.

Leaf chlorophyll content

The leaf chlorophyll content (SPAD index) was estimated non-destructively for four leaves per treatment, using the SPAD-502 portable chlorophyll meter (Minolta Camera Co., Osaka, Japan), following a protocol proposed by Levi et al. (2009). This index was used due to the strong relationship between the read values from this chlorophyll meter and leaf chlorophyll content, as demonstrated by Torres Netto et al. (2005).

Photochemical efficiency of photosystem II

The photochemical efficiency of photosystem II (PSII) was determined at the ambient temperature in leaves adapted to darkness for 30 minutes using the ratio between variable fluorescence and maximum fluorescence (Fv/Fm) was measured by using a Pulse Amplified Modulated Fluorometer (FMS 2 Hansatech, Inc. Co. UK) according to Basu et al. (2004). The quantum yield (Fv/Fm) measures the efficiency of excitation energy capture by open PSII reaction centers representing the maximum capacity of light dependent charge separation (Basu et al. 2004).

Proline content determination

Determination of free proline content was done according to Bates et al. (1973). Samples were homogenized in 10 mL 3% (w/v) sulfosalicylic acid, and proline was assayed by the acid ninhydrin method. The absorbance was measured spectrophotometrically at 520 nm.

Lipid analysis

A sample of 50 g of fresh tissue leaves was dehydrated in an incubator at 60 ˚C for 48 hr and ground to a powder. The resultant flour was placed in airtight glass jars and stored at 20 ˚C until analysis. Lipid samples were extracted according to the method described by Azadmard-Damirchi et al. (2005). Fatty acid methyl esters (FAMEs) were prepared from the lipid samples according to the method reported by Savage et al. (1997). The FAMEs were analyzed by gas chromatography according to the method described by Azadmard-Damirchi and Dutta (2006). The GC instrument was equipped with a flame ionization detector and a split/splitless injector. A 50 m 90.22 mm, 0.25 lm film thickness fused-silica capillary column BPX70 (SGE, Austin, TX, USA) was used for analysis. Injector and detector temperatures were 230 and 250 ˚C, respectively. Oven conditions were 158 ˚C increased to 220 ˚C at a rate of 2 ˚C /min

and maintained for 5 min. Helium was used as the carrier gas and nitrogen as the make-up gas at a flow rate of 30 ml/min. The FAMEs were identified by comparison of their retention times with standard FAMEs and the peak areas reported as a percentage of the total fatty acids.

2.7. Statistical analysis

Analysis of variance was carried out by SAS 8.2 software. The mean comparisons were performed by Duncan's test at 0.01 and 0.05 probability levels.

RESULTS AND DISCUSSION

Water deficit stress imposed significant effect on purslane growth characteristics (Table 1). Mean leaf fresh weight decreased 35 % and 78 % in 50 % FC and 20 % FC treatment. Water deficit stress decreased total number of leaves (Table 1), but there was no significant difference in total leaf number between 50% and 25% FC treatments. The average leaf area was decreased significantly by water deficit stress (Table 1). Researchers reported on decreasing leaf area due to reducing leaf expansion rate (Phillips and Riha 1993). The specific leaf area (SLA),was increased with increasing water deficit (Table 1). SLA must imply important anatomical changes in mesophyll and palisade layers (Hiesey 1971). Mean leaf area ratio [LAR,cm^2(g dry weight shoot)$^{-1}$] was increased significantly by water deficit stress (Table 1). Bulder et al. (1989) reported increasing LAR in water stress treatment in cucumber genotypes. The increase in LAR may be attributed to the increase in specific leaf area (SLA). Water deficit stress decreased height, fresh and dry weight of stem significantly (Table 1). Impaired mitosis, cell elongation and expansion result in reduced plant height, leaf area and crop growth under water deficit conditions (Nonami 1998). Mean root length of purslane plants was decreased by water deficit stress but there was no significant difference in root length between 50% and 25 % FC. Water deficit stress decreased shoot dry matter and increased root dry matter accumulation. An increase in root dry matter under drought stress is a common physiological response and functions to alleviate the stress by generating more roots to absorb available water (Barta et al. 2002). Root to shoot dry weight ratio was increased progressively with reduction in the soil water content (Table 1). The ratio between root length and total leaf area (RL/LA ratio), as a measure of the relative capture of below and above-ground resources, was increased 2 fold in 25% FC compared to that in 50% and 75% FC. Growth of the roots alone has limited importance unless the above-ground growth is considered. When water supply is limiting, allocation of assimilates tend to be

modified in favor of root growth and leads to increase root dry weight and consequently the root to shoot ratio increases (Hsiao and Acevedo 1974). Although growth of both roots and shoots decreases under drought conditions, the root: shoot ratio generally increases (Kramer and Kozlowski 1979). This is true because above-ground growth is affected more severely than below-ground growth (Wilson 1988). Joly et al. (1989) considered this as an adaptation that restricts transpiration surface area and increases water absorption from the soil.

Relative water content (RWC) was decreased significantly by water deficit stress. When soil water content reduced to 25% FC, the decrease of RWC was 14% compared to that in 75% FC. Reduction of RWC in 50% FC condition, was about 8% (Fig 1). Because the reduction of leaf RWC is a general response when plants are under osmotic stress conditions as it implies the water status in the plant (Rodriguez et al. 1997), reduced leaf RWC seems to suppress the growth of purslane plants under water deficit stress condition. Our results suggest that, although the purslane plants were exposed to severe water deficit stress, they were able to maintain the water levels in the leaves.

The Fv/Fm ratio, which is an indication of the maximum yield of photosystem II photochemistry, was not affected by water deficit (Table 2). This behavior reveals that the photochemical apparatus was not damaged by the severity of the water deficit imposed, showing that PSII in purslane is highly stable under water deficit. The unaffected Fv/Fm means that there is no loss in the yield of PSII photochemistry and confirms the resistance of the photosynthetic machinery to water deficit stress (Chaves et al. 2002; Cornic and Fresneau 2002). Similar results have been reported by other authors (Massacci et al. 2008; Shangguan et al. 2000; Izanloo et al. 2008; Niari et al. 2010; Brito et al. 2011). There was a steady rise in chlorophyll contentwith increase in water stress (Table 2). Izanloo et al. (2008) showed that in all cultivars of bread wheat the imposition of drought stress resulted in an increase in chlorophyll content until plants reached anthesis. Following anthesis the chlorophyll content of less tolerant cultivars to drought decreased, whilst the chlorophyll content of more tolerant cultivar to drought continued to increase. The slight increase in total chlorophyll under water stress suggests that the chlorophyll pigments in purslane leaves were somewhat resistant to dehydration. There are also some reports suggest that water deficit stress increased chlorophyll content in cotton (Brito et al. 2011), lettuce (kang 2008), onion (Beeflink 1985) and

mango (Luvaha et al. 2007).

Free proline content of leaves of purslane increased 1.8 and 3 fold in 50% FC and 25% FC conditions respectively compared to that in 75% FC (Fig 2). Blum and Ebercon, (1976) reported that free proline accumulation in water stressed leaves of grain sorghuom was associated positively with 'recovery resistance", possibly by serving as a source of respiratory energy to the recovering plant. Vendruscolo et al. (2007) found that proline is involved in tolerance mechanisms against oxidative stress and this was the main strategy of plants to avoid detrimental effects of water stress. Yazici et al. (2007), suggested salinity tolerance of purslane plants might be closely related with the accumulation of osmoprotectantproline under salinity conditions. Taken together the available data, it can be assumed that purslane has the efficient mechanisms to maintain water levels in its leaves like accumulation of proline under water deficit and salinity stress conditions.

Total lipid content was increased significantly by water deficit stress in purslane leaves. Total lipid increased by two and three fold in 50% FC and 25% FC treatments respectively compared to that in 75% FC (Fig 3). Water deficit stress induced increases in total lipids was also reported in *Zea mays* (Douglas and Paleg 1981), cucumber (Bulder at al. 1989) and grapevine (Toumi et al. 2008). Douglas and Paleg (1981) suggested that the accumulation of fats and oils in seeds may be related, at least partially, to the drying out period during maturation, and that in any commercial attempt to extract fats and oils from leaf or stem tissues, a pre-extraction desiccation period may be potentially useful. Christiansen and Thimann (1950) also reported an inverse relationship between fats and growth.

Chromatographic analysis revealed that the main fatty acids in purslane leaves are linolenic (C18:3), followed by linoleic (C18:2), palmitic (C16:0) and oleic (C18:1) and at much lower amounts palmitoleic (C16:1), myristic (C14:0) and stearic (C18:0) acids (Table 3). Water deficit stress had a marked effect on fatty acid composition of purslane leaves. Linolenic acid proportion was increased progressively due to water deficit stress. This increase was accompanied by linoleic, oleic and stearic acid reduction. Guerfel et al. (2008) reported that, there was an increase in the proportion of linolenic acid (18:3) in the two cultivar of olive studied under water deficit stress. This increase was paralleled by decreases of palmitoleic (16:1), hexadecatrienoic (16:3), stearic (18:0), and linoleic acid (18:2) in one cultivar and decreases of stearic (18:0) and oleic (18:1)

acid in another cultivar. An increase of linolenic acid accumulation in water stressed purslane leaves may be associated with the activation of octadecanoic pathway to produce jasmonic acid (JA), since linolenic acid is a known precursor for this stress signaling molecule. Stresses activate the octadecanoic pathway in which linolenic acid is converted to JA, resulting in a significant accumulation of this hormone (Teixeira et al. 2010). Experiments with transgenic tobacco cells and plants demonstrated that overexpression of omega-3 desaturases, which increases 18:3, increases tolerance to salt and drought stress (Zhang et al. 2005). It is reported that, in the drought-sensitive cultivar of cowpea plants, linolenic acid contents decreased in all lipid classes in response to water deficit stress, as did FAD3 and FAD8 gene expression levels. Conversely, the leaves of the tolerant cultivar displayed increasing ALA contents under mild drought conditions (Torres-Franklin et al. 2009). Increase of linolenic acid due to water deficit stress was also reported in drought tolerant cultivars of grapevine. Conversely, sensitive cultivars, showed reductions in total lipid contents and linolenic acid (Toumi et al. 2008). Zhang et al. (2005) suggested a high level of this fatty acid is the most relevant parameter contributing to elevated drought tolerance. Linolenic and linoleic acid content and their ratio were also expressed on a dry weight basis in table 3. This ratio was increased by water deficit stress and was maximum in 25% FC treatment. Based on Zhang et al. (2005) findings that higher drought tolerance is acquired following increasing the ratio of 18:3 to 18:2, they proposed that the decrease in 18:3 observed earlier under drought conditions (Matos et al. 2002) reflects damage, whereas the few cases where increased levels of 18:3 were found under water deficit stress (Repellin et al. 1997) probably reflect a component of a defense mechanism. Their result pointed to the potential of exploiting FAD overexpression as a tool to ameliorate drought tolerance (Zhang et al. 2005). The results obtained on coconut trees (Repellin et al. 1997), olive trees (Guerfel et al. 2008) and our results in the present study, on purslane, allow us to suggest a relationship between the capacity of a plant to maintain (or increase) its polyunsaturated fatty acids contents and its resistance to water deficit stress. However, higher unsaturation also corresponds to higher peroxidant and lipolytic attacks. Such higher amount of linolenic acid under severe water deficit stress needs a powerful antioxidative system (Torres-Franklin et al. 2009). Yazici et al. (2007) suggested that purslane increased capacity of antioxidative system

under salinity conditions to scavenge reactive oxygen species and thus suppressed level of lipid peroxidation. Lim and Quah (2006) showed that all tested cultivars of purslane were capable of inhibiting lipid peroxidation. Therefore, it is possible that water deficit tolerance of purslane is related to increase of antioxidant system of purslane under water deficit stress conditions.

Table 1: Effect of water deficit on growth characteristics of purslane

Growth characteristics	Soil water content		
	75% FC	50% FC	25% FC
Stem length (cm)	25.80a	18.80b	14.70c
Root length (cm)	14.00a	9.70b	8.70b
Total number of leaves	48.00a	32.00b	22.00b
Leaf fresh weight (g)	7.05a	4.59b	1.57c
Stem fresh weight (g)	7.30a	2.82b	1.14c
Root fresh weight (g)	1.47a	0.57b	0.31c
Shoot dry matter (%)	11.37a	9.28b	9.17b
Root dry matter (%)	16.04b	21.67a	23.08a
Root dry weight/shoot dry weight	0.14b	0.17b	0.29a
Leaf area (cm^2)	101.09a	70.72b	32.55c
LAR,cm^2(g dry weight shoot)$^{-1}$	62.30c	104.19b	131.25a
Specific leaf area (SLA)	154.97c	205.27b	240.82a
Root length/Leaf area	0.13b	0.13b	0.27a

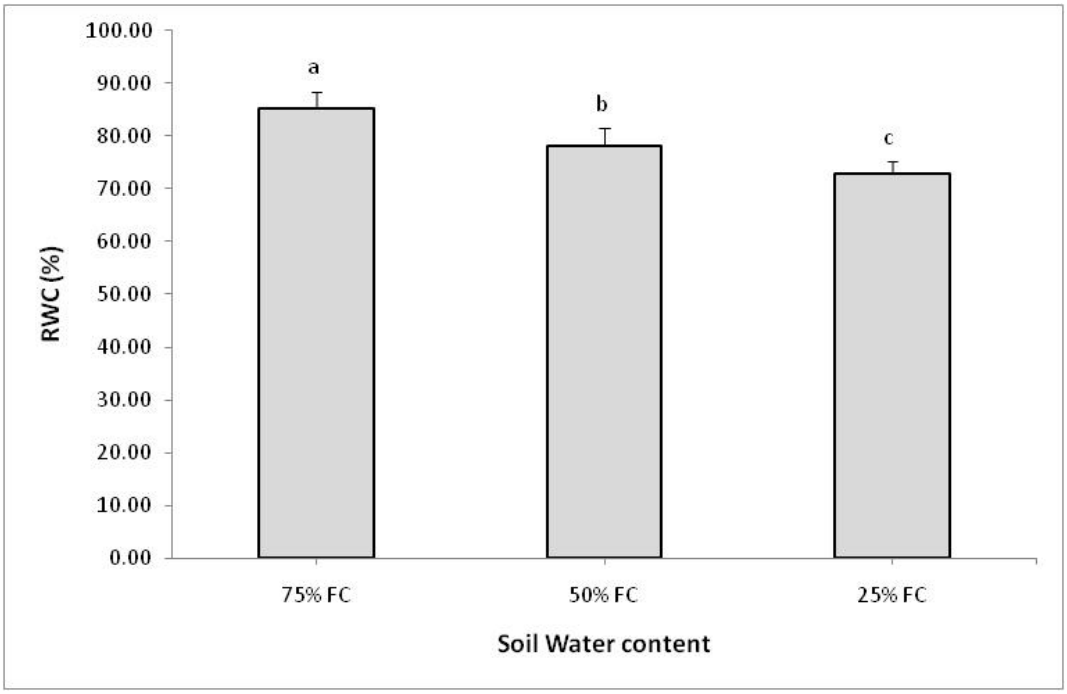

Fig. 1. Leaf Relative Water Content (RWC) of purslane plants exposed to different soil water content.

Table 2: Effect of water deficit on chlorophyll content and Fv/Fm ratio

Soil water content	Chlorophyll content	Fv/Fm
75% FC	31.02b	0.778a
50% FC	34.35a	0.770a
25% FC	35.05a	0.771a

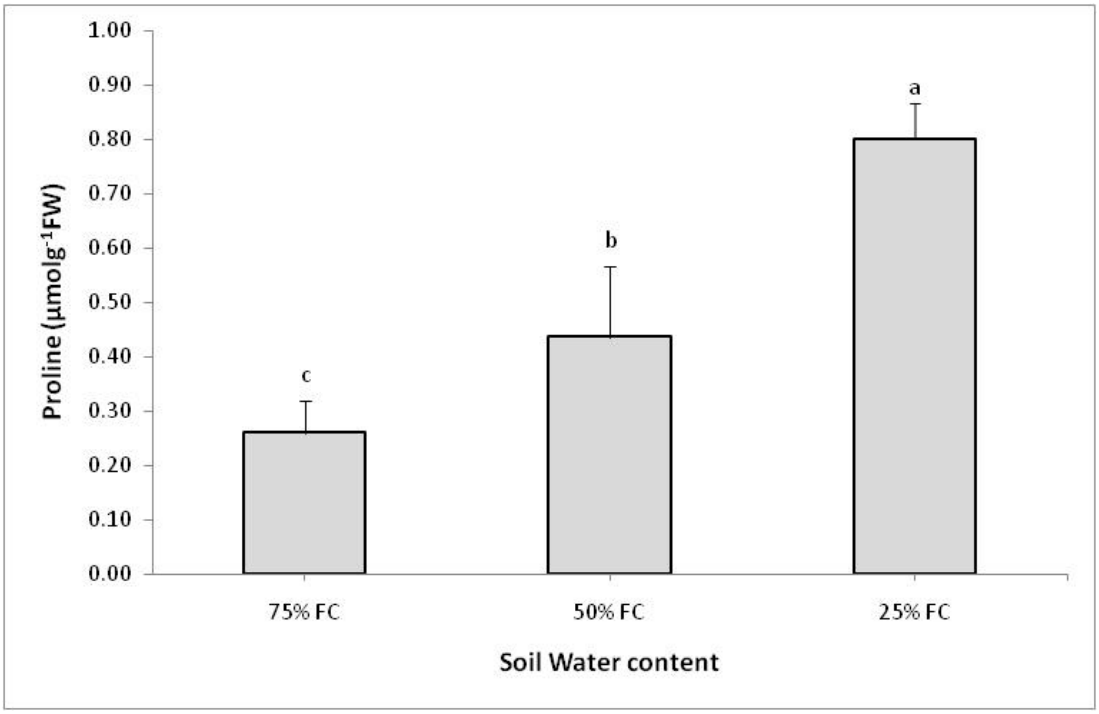

Fig. 2.Free proline content of purslane leaves in response to water deficit stress.

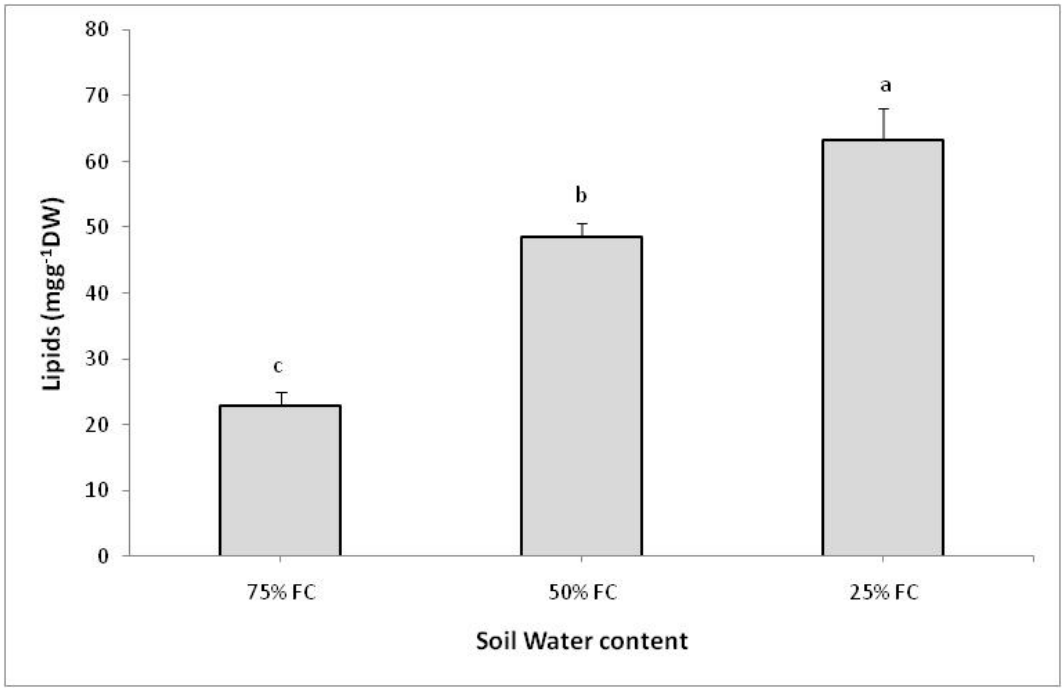

Fig. 3. Effect of water deficit stress on total lipid content of purslane leaves

Table 3: Effect of water deficit on the composition of total lipids of purslane. Linoleic (LA) and α-Linolenic (ALA) acids content in purslane leaves are expressed as mg g^{-1}DW

Soil water content	Fatty acids (mg g^{-1}DW)			Fatty acids (%)						
	ALA (ω-3)	LA (ω-6)	ω-3/ ω-6	C14:0	C16:0	C16:1	C18:0	C18:1	C18:2	C18:3
75% FC	8.26c	5.58b	1.47b	0.6	22.3	0.4	7.2a	11.7a	23.3a	34.4c
50% FC	19.87b	8.78a	2.25ab	0.8	22.5	0.5	6.3a	11.7a	17.8b	40.2b
25% FC	31.03a	10.5a	2.97a	0.7	21.8	0.5	5b	9.1b	15.9b	47a

CONCLUSION

It can be stated that purslane is tolerant to severe water deficit stress.

Adaptation to water deficit may be related to proline accumulation and osmotic adjustment to some extent. Also, our present results concurred with others to suggest that adaptation to water deficit implies processes such as enhanced levels of 18:3 and probably reflect a component of a defense mechanism of purslane. According to this study, purslane appears particularly well suited for cropping in semi arid and arid areas.

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