



Full Length Article

Physio-Biochemical and Yield Responses of Two Contrasting *Camelina sativa* Breeding Lines under Drought Stress

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Abstract

As a major abiotic stress, drought seriously limits global crop productivity. Limited water resources, rising populations and an increased demand for edible oils, necessitates the evaluation and commercial-scale introduction of drought-resilient alternative oil seed crops like camelina (*Camelina sativa* L.). Therefore, this study was conducted in a rain-exclusion structure to evaluate the effects of drought stress on water relations, antioxidant activity, seed yield and fatty acid profile of a drought-tolerant (line 7126) and drought-sensitive camelina breeding (8046) lines. These were grown at 80, 60 and 40% water holding capacity (WHC) levels in sand-filled plastic pots, with a 100% WHC treatment serving as a control. The highest decrease in leaf water relations, photosynthetic pigments, yield, oil content, stearic acid, linolenic acid and erucic acid contents was observed at 40% WHC level for the drought-sensitive breeding line. However, significant ($P \leq 0.05$) increases in antioxidant activity, seed protein, palmitic acid, oleic acid and linoleic acid content were noted under drought stress treatments, with a maximum increase at 40% WHC in for the drought-tolerant breeding line. With good tissue water retention, better photosynthetic performance and enhanced antioxidant activity, the drought-tolerant breeding line showed greater drought resilience than the drought-susceptible breeding line, and ultimately better yield and oil quality. In conclusion, the physiological and biochemical basis of drought tolerance in camelina breeding lines should be utilized to develop novel camelina cultivars with improved drought tolerance in future. Moreover, the drought tolerant camelina breeding line (7126) should be further investigated under different field conditions and ecological zones to evaluate its adaptation potential. © 2019 Friends Science Publishers

Keywords: Antioxidant activity; Camelina oil; Fatty acids; Water deficit; Water relations; Seed yield

Introduction

One of the main concerns arising from global climate change is variable precipitation patterns leading to frequent and erratic drought episodes (Lobell *et al.*, 2011). Drought stress can cause substantial decreases in crop yields through its negative impacts on crop growth, physiology and reproduction (Barnabas *et al.*, 2008; Hussain *et al.*, 2016, 2018; Shareef *et al.*, 2018). Drought stress hinders the photosynthetic pathway, alters the crop's chlorophyll content and ultimately deteriorates the plant's photosynthetic machinery (Nayyar and Gupta, 2006). Under these conditions reactive oxygen species (ROS) are generated, leading to oxidative stress and damage to plant's

membrane lipids, photosynthetic pigments, nucleic acids and proteins (Yordanov *et al.*, 2000; Arora *et al.*, 2002).

Oilseed crops are predominantly cultivated for the edible oil they bear. These consist of fatty acids, a rich source of energy, not only satisfying half of our calorific diet requirements but also utilized for non-food purposes (Lu *et al.*, 2011). An oilseed crop's oil yield and quality are adversely affected by drought stress (Enjalbert *et al.*, 2013; Shahsavari *et al.*, 2014), particularly the level of saturated fatty acids (Shekari *et al.*, 2015). Oilseed crop production suffers from major constraints, particularly in developing countries. Though Pakistan is an agrarian country, it still faces an acute deficit of edible oils, and the mounting population is making the situation worse (Ali *et al.*, 2010).

Local cultivation of mustard (*Brassica rapa* L.), cotton (*Gossypium hirsutum* L.) and sunflower (*Helianthus annuus* L.) contribute to domestic edible oil production, it only meets half of the country's demand (Zaidi, 2014). Cotton is mainly cultivated for lint, but cottonseed contributes about 50–60% to domestic oil production as a byproduct (Mustafa *et al.*, 2015). In 2016–2017, a total of 2.426 million tons of edible oil were availability in Pakistan, of which only 0.446 million tons (19%) were contributed by local production. The remaining 1.98 million tons (81%) were imported at a cost of US\$ 1.45 billion (G.O.P., 2017), making Pakistan the world's fourth largest importer of edible oils (Zaidi, 2014). The limited domestic production of edible oils has led to a wide gap between demand and supply, a gap bridged by importing large quantities of edible oil at the expense of the country's precious foreign exchange. Moreover, more than 70% of Pakistan consists of arid and semi-arid regions, lacking sufficient rainfall to support dry land or irrigated crops (Shah *et al.*, 2011). This situation demands the cultivation of drought tolerant, non-traditional oilseed crops to minimize the mounting deficit in edible oils.

Camelina (*Camelina sativa* L.) has the potential to become an important alternative oilseed crop for sub-arid and irrigated water deficit areas (Waraich *et al.*, 2013). Recent interest in camelina was triggered by a search for novel sources of crucial fatty acids, predominantly plant derivatives of ω -3 fatty acids (Karvonen *et al.*, 2002). Camelina seed oil content lies in the range of 30–48%, while, seed protein ranges between 27–32% (Gugel and Falk, 2006; Vollmann *et al.*, 2007). With over 90% unsaturated fatty acids, camelina oil possesses an extraordinary fatty acid profile. These fatty acids bear a significant amount (30–42%) of linoleic acid and low levels of erucic acid (Zubr and Matthauss, 2002). Because sufficient antioxidants are present in its seeds, camelina oil shows good stability during storage and has been proven good for cooking purposes (Pilgeram *et al.*, 2007). Moreover, as camelina cultivation requires few inputs it has gained farmers' attention (Gesch and Cermack, 2011). It has lower nitrogen demands than canola (*Brassica napus* L.) and exhibits superior drought and disease resistance (Lenssen *et al.*, 2012; Wysocki *et al.*, 2013). It grows well on marginal soils and shows better performance under drought conditions (Ehrensing and Guy, 2008).

Although several studies have been conducted on different aspects of camelina, few have assessed its response to drought stress. To the best of our knowledge, comparative analysis of drought tolerant and sensitive camelina breeding lines is sparse. Hence, this study was conducted in a rain-exclusion structure to evaluate the effects of drought stress on water relations, antioxidant activity, seed yield and fatty acid profile of a drought-tolerant (line 7126) and drought-sensitive camelina breeding (8046) lines. The findings of this study will help to understand the physiological and biochemical basis of drought tolerance in camelina, as well as to evaluate its

adaptation potential under different ecological zones for adjustment in existing cropping patterns of Pakistan.

Materials and Methods

Experimental Details

This pot study was carried out during 2015–2016 in a manually operated rain-out shelter equipped with movable, transparent flexible plastic sheet at Department of Crop Physiology, University of Agriculture, Faisalabad (UAF), Pakistan (31.25°N latitude, 73.09°E longitude and 184 m altitude). Over the experimental period (10 November 2015 to 19 March 2016) the site was subject to semi-arid conditions, with temperatures varying between 11.7°C and 24.2°C. Seeds of two camelina genotypes: 7126 (drought tolerant) and 8046 (drought sensitive) selected on the basis of early study (Ahmed *et al.*, 2017) were collected from Office of Research, Innovation and Commercialization (ORIC), UAF, Pakistan. The experiment was conducted in sand-filled plastic pots (16 cm diameter × 14 cm length). The pots were wrapped with plastic bags and each pot was filled with 5 kg washed, purified and fine sand. Water holding capacity (WHC) of sand was calculated by gravimetric method (Bethlahmy, 1952) for normal plants (100% WHC) *i.e.*, 1200 mL water for each pot. Fifteen seeds of each genotype were planted manually in each plastic pot on 10th November 2015. In the beginning, all pots were kept at 100% WHC level to achieve good germination and emergence. Seven days after seedling emergence, ten healthy seedlings were maintained in each plastic pot by thinning (Waraich *et al.*, 2017). Hoagland's nutrient solution (Hoagland and Arnon, 1950) used to fulfill the nutrients required by the seedlings.

Twenty days after sowing (DAS), plants were exposed to four drought treatments namely (i) 100% WHC (Control) (ii) 80% WHC (960 mL water) (iii) 60% WHC (720 mL water) and (iv) 40% WHC (480 mL water) where above mentioned drought stress treatments were maintained by withholding water supply (Ahmed *et al.*, 2017). The experiment was conducted in a completely randomized design with factorial arrangement having three replications. All pots were weighed twice daily at 9:00 a.m. (morning) and 5:00 p.m. (evening) by electrical balance (MK-500C, Japan) to measure the quantity of water lost through evapotranspiration from each pot (Allen *et al.*, 1998) and then re-watered each pot until it reached to its pre-defined weight. Drought stress treatments continued until harvesting.

Sampling

Leaf water relations, pigment content (chlorophyll and

carotenoid contents) and antioxidant levels were recorded on DAS 60, while yield and yield-related traits, seed oil contents, seed protein contents, and fatty acid composition were recorded at harvest.

Parameters for the Determination of Leaf Water Relations

Five fully-expanded leaves from the top of 60 DAS plants of each treatment \times replicate (each pot) were collected between 0800H and 1000H to determine leaf water potential (Ψ_w) with a Scholander type pressure chamber (ARIMAD, ELE-International) (Nawaz *et al.*, 2016). These leaves were then packed in re-sealable plastic bags and placed in a Biomedical Freezer (Sanyo Freezer MDF-U730) at -20°C for seven days prior to determining their osmotic potential (Ψ_s). Leaves were frozen to allow, upon thawing, to extract cell sap by crushing leaves with a glass rod. The (Ψ_s) was measured using an osmometer (Wescor, 5520). Leaf turgor pressure (Ψ_p) was calculated following Waraich *et al.* (2017):

$$(\Psi_p) = (\Psi_w) - (\Psi_s) \quad (1)$$

The relative leaf water content (RWC) of five fully expanded leaves drawn from three selected plants from each pot was calculated as suggested by Karrou and Maranville (1995):

$$\text{RWC} = [(Fw - Dw) / (Tw - Dw)] \times 100 \quad (2)$$

Where, Fw, Tw and Dw are the leaf fresh weight, turgid leaf weight, and leaf dry weight, respectively. Weights were obtained using a digital electrical balance (Chyo, MK-500 C).

Estimation of Pigments

Chlorophyll (Chla, Chlb and Chltot) and carotenoid (Car) pigments were estimated employing the methods of Arnon (1949) and Davies (1976). Fresh leaf samples (0.5 g) collected from each treatment were sliced into 0.5 cm fragments and then extracted in 20 mL of 8:2 acetone: water. The absorbance of the supernatant was measured at 645, 663 and 480 nm using a Hitachi U2000 (Japan) spectrophotometer. Levels of the leaf pigments (mg g^{-1} F.W.) were calculated as:

$$\text{Chl } a = (12.7 \text{ OD}_{663} - 2.69 \text{ OD}_{645}) \times V/1000W \quad (3)$$

$$\text{Chl } b = (22.9 \text{ OD}_{645} - 4.68 \text{ OD}_{663}) \times V/1000W \quad (4)$$

$$\text{Carotenoids} = A^{\text{car}}/E_{\text{mx}}^{100} \quad (5)$$

Where V is the volume of sample extract and W is the weight of the sample.

Assays of Antioxidant Enzymes

Leaf antioxidant activity, including catalase (CAT),

peroxidase (POD) and superoxide dismutase (SOD) activities were measured from camelina leaf samples homogenized in 50 mM phosphate buffer with 7.0 pH and 1 mM dithiothreitol (Dixit *et al.*, 2001). The CAT and POD activity were measured by the method of Liu *et al.* (2009), while the measurement of SOD activity followed the method of Stagner and Popovic (2009).

Yield and Related Traits

At 130 DAS, five randomly selected plants from each treatment replicate were harvested. Plant height (cm) was measured using a measuring tape. The same plants were used to assess the number of branches per plant, number of pods per plant and 1000-seed weight (g). Overall biomass yield (g) per plant, seed yield (g) per plant and harvest index (%) was also recorded.

Seed Oil, Protein Content and Fatty Acid Composition

Seed oil and protein contents of 5.0 g of whole camelina seed were measured (on a dry matter basis) using near-infrared reflectance spectroscopy (NIRS) using a Model 6500 NIR spectrophotometer (McVay and Khan, 2011). The fatty acid profile of the camelina seeds was determined from 1.0 g seed samples using the methods of Oliva *et al.* (2006) and McVay and Khan (2011), employing a Shimadzu gas chromatograph (GC-2010 series).

Statistical Analyses

The recorded data were statistically analyzed by following Fisher's analysis of variance technique using Statistix-9.1 software. Comparison of significant means was performed by least significant difference (LSD) test at 5% probability level (Steel *et al.*, 1997).

Results

Leaf Water Relations

All leaf water parameters showed an individual significance of breeding line and drought stress level, as well as a significant interaction between the two factors ($P \leq 0.05$). Maximum values for Ψ_w (-0.82 MPa), Ψ_s (-0.63 MPa), Ψ_p (1.63 MPa) and leaf RWC (68%) were recorded for the drought tolerant line at 100% WHC, while the minimum values of Ψ_w (-2 MPa), Ψ_s (-2.25 MPa) and Ψ_p (0.25 MPa) along with leaf RWC (16.68%) were recorded for the drought-sensitive line grown at 40% WHC (Fig. 1). Under all drought stress treatments, the drought-tolerant breeding line maintained higher values of (Ψ_w , Ψ_s , Ψ_p and RWC) than the drought-sensitive breeding line (Fig. 1).

Table 1: Effect of different drought stress levels on yield and yield-related traits of two camelina genotypes

Drought stress levels	Camelina genotypes	Plant height (cm)	Number of branches/plant	Number of pods/plant	1000-seed weight (g)	Biological yield/plant (g)	Seed yield/plant (g)	Harvest index (%)
100% WHC	7126	87.17 ± 0.74a	12 ± 0.33a	143 ± 1.45a	1.54 ± 0.03a	2.90 ± 0.35a	1.32 ± 0.13a	45.88 ± 0.56a
	8046	84.22 ± 1.39a	11 ± 0.35a	137 ± 1.40a	1.48 ± 0.02ab	2.80 ± 0.30a	1.28 ± 0.10a	45.46 ± 0.67a
80% WHC	7126	80.25 ± 1.99b	9 ± 0.33b	131 ± 1.76b	1.41 ± 0.02b	2.47 ± 0.49b	1.05 ± 0.17b	42.72 ± 0.83b
	8046	75.06 ± 1.02c	8 ± 0.32c	122 ± 1.66c	1.32 ± 0.03c	2.17 ± 0.32c	0.87 ± 0.15c	40.12 ± 0.69c
60% WHC	7126	73.83 ± 0.77c	8 ± 0.32c	116 ± 2.18d	1.26 ± 0.02c	1.92 ± 0.43d	0.73 ± 0.11d	37.87 ± 0.60d
	8046	61.93 ± 0.95d	6 ± 0.38d	107 ± 1.77e	1.06 ± 0.02d	1.62 ± 0.33e	0.58 ± 0.12e	35.68 ± 0.65e
40% WHC	7126	50.87 ± 0.95e	7 ± 0.35e	68 ± 2.08f	1.05 ± 0.03d	1.40 ± 0.43f	0.43 ± 0.1f	31.01 ± 0.63f
	8046	41.13 ± 0.87f	4 ± 0.39f	53 ± 1.76g	0.83 ± 0.02e	1.08 ± 0.32g	0.28 ± 0.12g	26.43 ± 0.55g
LSD value at 5%		3.44	0.87	5.38	0.08	0.10	0.07	1.75

Mean ± SE values in each column with different letters indicate that treatments are statistically different at $P < 0.05$

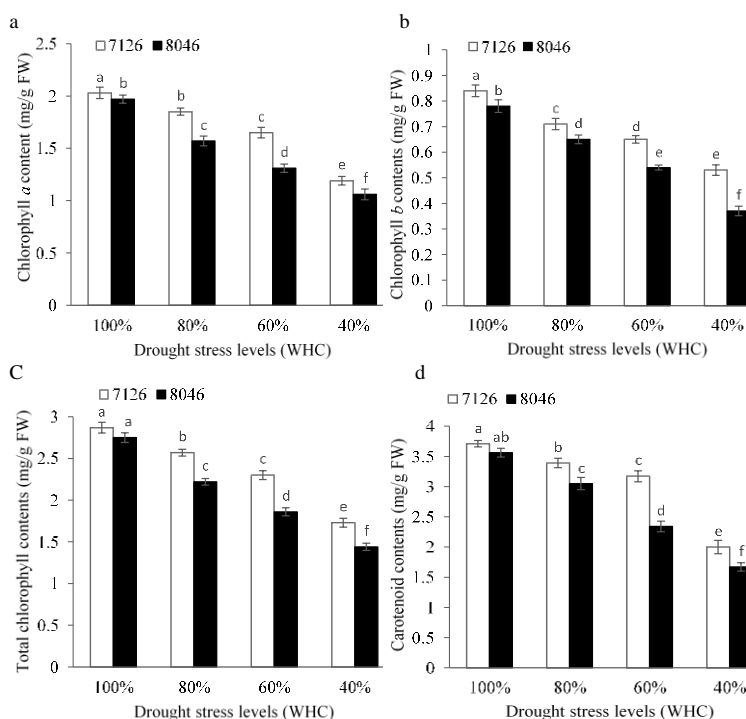


Fig. 2: Effect of drought stress levels (100, 80, 60 and 40% WHC) on photosynthetic pigments, (a) chlorophyll *a* (*Chl_a*) (b) chlorophyll *b* (*Chl_b*) (c) total chlorophyll (*chl_{tot}*) (d) carotenoids (*Car*) of two *Camelina* breeding lines (7126 and 8046) under rainout shelter conditions during the 2015-2016 growing season. Different letters indicate significant differences at $P \leq 0.05$ using the least significant difference test (LSD)

Leaf Chlorophyll and Carotenoid Content

Leaf chlorophyll (*Chl_a*, *Chl_b* and *Chl_{tot}*) and carotenoid (*Car*) showed an individual significance of breeding line and drought stress level, as well as a significant interaction between the two factors ($P \leq 0.05$). The drought-tolerant line grown at 100% WHC maintained the highest values for *Chl_a* (2.03 mg g⁻¹ FW), *Chl_b* (0.84 mg g⁻¹ FW), *Chl_{tot}* (2.87 mg g⁻¹ FW) and *Car* (3.71 mg g⁻¹ FW), while the drought sensitive line grown at 40% WHC showed the lowest values of *Chl_a* (1.06 mg g⁻¹ FW), *Chl_b* (0.37 mg g⁻¹ FW), *Chl_{tot}* (1.44 mg g⁻¹ FW) and *Car* (1.67 mg g⁻¹ FW) (Fig. 2). Although both breeding lines showed a decrease in leaf chlorophyll and carotenoid contents under drought

stress treatments, the magnitude of the decrease was less in the drought-tolerant breeding line than in the drought-sensitive breeding line.

Antioxidant Enzyme Activity

The activity of antioxidant enzymes showed an individual significance of breeding lines and drought stress levels, as well as a significant interaction ($P \leq 0.05$) between the two factors (Fig. 3). Antioxidant activity increased with increasing drought stress levels in both breeding lines. The highest CAT, POX and SOD activities (23, 18.66 and 11.87 U mg⁻¹ protein, respectively), were recorded for the drought-tolerant line grown at 40% WHC level, while the lowest

values of these enzymes (12.25, 7.9 and 3.96 U mg⁻¹ protein, respectively) were recorded for the drought-sensitive breeding line grown at 100% WHC (Fig. 3). Thus, at all drought stress levels, the drought-tolerant camelina line 7126 showed greater antioxidant enzyme activity than did the drought-sensitive breeding line.

Yield and Yield-related Traits

Yield and yield components showed an individual significance of breeding line and drought stress level, as well as a significant interaction ($P \leq 0.05$) between the two factors (Table 1). Exposure to drought stress treatments significantly reduced yield and yield-related traits in both camelina breeding lines. Maximum values of plant height (0.87 m), number of branches per plant (12), number of pods per plant (143), 100-seed weight (1.54 g), total biomass per plant (5.84 g), seed yield per plant (2.64 g) and harvest index (46%) were obtained with the drought-tolerant breeding line grown at 100% WHC, while the drought-sensitive breeding line showed minimum values of plant height (0.51 cm), number of branches per plant (7), number of pods per plant (68), 100-seed weight (0.83 g), total plant biomass per plant (2.17 g), seed yield per plant (0.57 g) and harvest index (26%) at the 40% WHC level (Table 1). For all yield and yield-related traits, at all drought stress treatment levels, the drought-tolerant camelina breeding line showed greater values than the drought-sensitive breeding line.

Seed Oil and Protein Content

Seed oil and protein contents showed an individual significance of breeding line and drought stress level, as well as a significant interaction ($P \leq 0.05$) between the two factors (Fig. 4). Seed oil contents decreased with increasing drought stress levels in both breeding lines, but the drought-tolerant breeding line performed better than the drought-sensitive breeding line normal and water deficit conditions. The drought-tolerant camelina breeding line showed the highest seed oil content (36.5%) at the 100% WHC level, while the drought-sensitive breeding line showed the lowest seed oil content (19.5%) at the 40% WHC level (Fig. 4a). Conversely, seed protein content has been found to increase with increasing drought stress. The maximum seed protein content (31%) was recorded for the drought-tolerant breeding line at 40% WHC level, while the minimum value (17.3%) was recorded for the drought sensitive breeding line grown at 100% WHC (Fig. 4b).

Fatty Acid Profile

Regarding the fatty acid profile of camelina oil, the concentration of palmitic acid, oleic acid and linoleic acid showed an individual significance of breeding line and drought stress level, as well as a significant interaction ($P \leq$

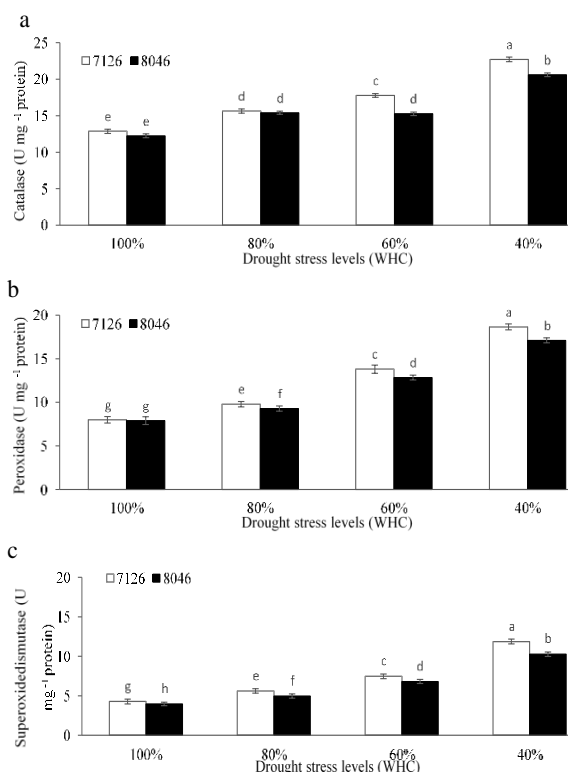


Fig. 3: Effect of drought stress levels (100, 80, 60 and 40% WHC) on antioxidant activity, (a) catalase (CAT), (b) peroxidase (POD) (c) superoxide dismutase (SOD) of two *Camelina* breeding lines (7126 and 8046) under rainout shelter conditions during the 2015-2016 growing season. Letters indicate significant differences at $P \leq 0.05$ using the least significant difference test (LSD)

0.05) between the two factors (Fig. 4). The concentrations of palmitic acid, oleic acid and linoleic acid increased under drought stress reaching their maximum values (6.3, 14.64 and 21.21%) for the drought-tolerant breeding line grown at 40% WHC, while the drought-sensitive breeding line showed the lowest values (3.7, 9.29 and 14%) at the same WHC level (Fig. 4c, e and f).

For both breeding lines, the concentrations of stearic acid, linolenic acid and erucic acid declined against as drought stress level increased. The drought-tolerant camelina breeding line exhibited the highest levels of stearic acid (2.87%), linolenic acid (36.12%) and erucic acid (2.90%) values when grown at a 100% WHC level (Fig. 4d, g and h).

Discussion

Leaf water potential (Ψ_w), leaf osmotic potential (Ψ_s), leaf turgor potential (Ψ_p) and leaf relative water contents (RWC) of both camelina breeding lines were significantly reduced by drought stress. However, the fact that the amplitude of this reduction differed between the drought-tolerant and drought-sensitive breeding lines

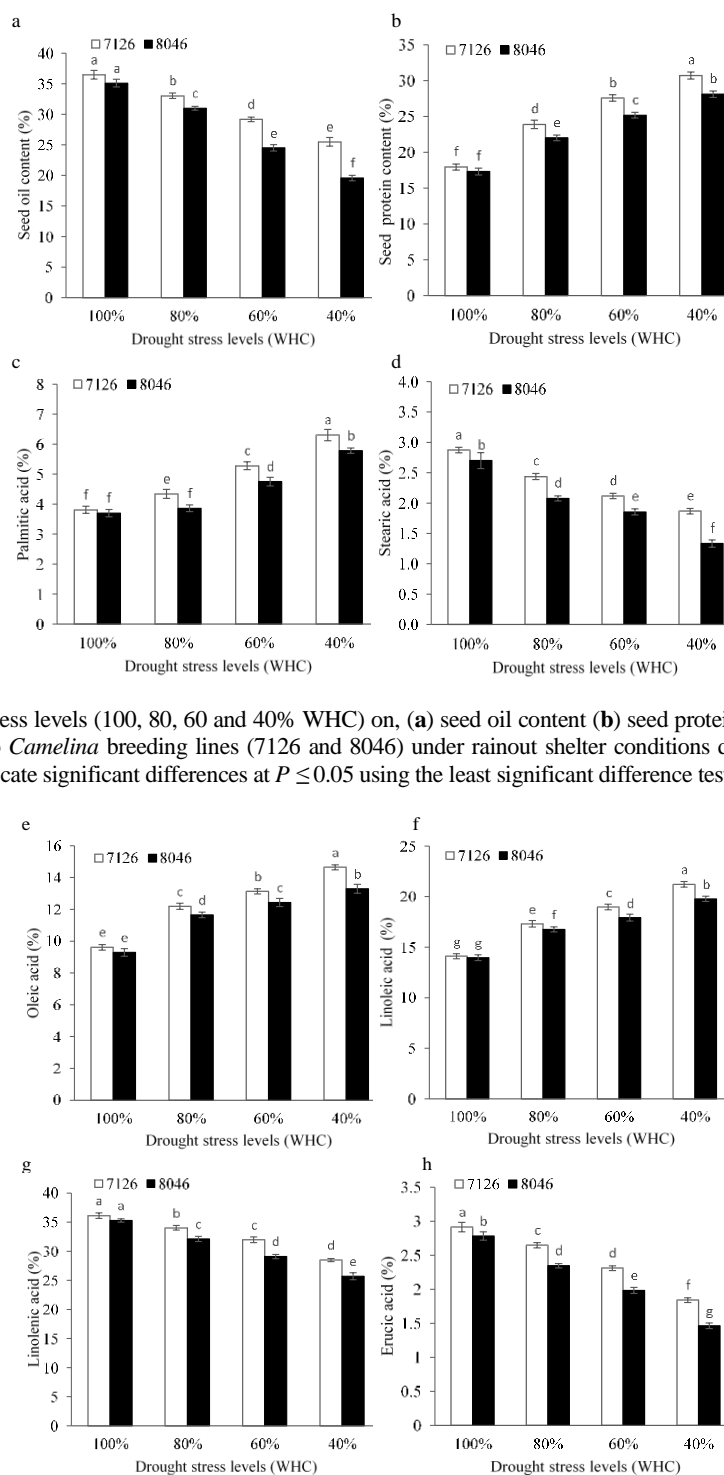


Fig. 4: Effect of drought stress levels (100, 80, 60 and 40% WHC) on, (a) seed oil content (b) seed protein content (c) palmitic acid (d) stearic acid contents of two *Camelina* breeding lines (7126 and 8046) under rainout shelter conditions during the 2015-2016 growing season. Different letters indicate significant differences at $P \leq 0.05$ using the least significant difference test (LSD)

Fig. 4: Effect of drought stress levels (100, 80, 60 and 40% WHC) on (e) oleic acid (f) linoleic acid (g) linolenic acid (h) erucic acid contents of two *Camelina* breeding lines (7126 and 8046) under rainout shelter conditions during 2015-2016 growing season. Different letters indicate significant differences at $P \leq 0.05$ using the least significant difference test (LSD)

might be attributed to the difference in their ability to sustain tissue turgor (Siddique *et al.*, 2000; Terzi and Kadioglu, 2006). A reduction in Ψ_w constitutes a

primary defense approach of plants to adapt the water deficit stress by maintaining water and osmolytes in a tolerable range (Kaldenhoff *et al.*, 2008; Ali *et al.*, 2009;

Hussain *et al.*, 2018). Likewise, drought-induced reduction in Ψ_s generates a gradient for water flux into the plant cell that helps to maintain Ψ_p (Serraj and Sinclair, 2002). Consistent with our results Hura *et al.* (2007) also reported more negative Ψ_w , Ψ_s and greater maintenance of turgor in sunflower and triticale varieties under drought stress, showing their ability for better osmotic adjustment. Furthermore, the decline in RWC of both camelina breeding lines would have been caused by reduced Ψ_w under drought stress, a conclusion consistent with the studies of Živčák *et al.* (2009) and Raza *et al.* (2012). Maintenance of higher RWC under drought stress is considered an indicator of drought tolerance (Altinkut *et al.*, 2001; Zhang *et al.*, 2018).

Drought stress caused a drastic reduction in photosynthetic pigments in both camelina breeding lines with respect to their respective 100% WHC controls. This reduction under drought stress could be attributed to photo-inhibition, stomatal closure and inhibition of gas exchange, thereby limiting the activity of photosynthetic pigments (Jaleel *et al.*, 2009). Moreover, the greater reduction in photosynthetic pigments in the drought-sensitive breeding line might have occurred owing to ultra-structural alteration of plastids along with changes in thylakoid proteins, resulting in the breakdown of the portion of PSII that absorbs photons. Accordingly, its efficiency would be reduced (Yang *et al.*, 2007), thereby decreasing the energy transfer between chlorophyll a and chlorophyll b (Centritto, 2005; Kannan and Kulandaivelu, 2011). On the other hand, the drought-tolerant breeding line showed a higher photosynthetic pigment content, which may be attributed to its more stable photosynthetic apparatus under water limited conditions (Souza *et al.*, 2013).

In this study, activities of CAT, POD and SOD enzymes in leaves of both camelina breeding lines showed a gradual increase with increasing water deficit stress. This rise in enzyme activity might be the result of active oxygen species produced in a response to water deficit stress (Athar *et al.*, 2008; Al-GHamdi, 2009; Lum *et al.*, 2014). Earlier Hosseini *et al.* (2015), Ahmadi *et al.* (2015) and Mishra and Panda (2017) found a substantial increase in the concentration of POD and SOD enzymes in canola and rice (*Oryza sativa* L.) cultivars under drought stress. Increased activities of CAT and POD under drought conditions were found to eliminate H_2O_2 from stressed cells and minimize cellular damage by enhancing the oxidative capacity of plants to tolerate stress (Nojavan and Khorshidi, 2006). Moreover, they found that the relationship between antioxidant and ROS production defined the susceptibility or tolerance of a breeding line under drought stress (Mittler, 2002). The higher CAT, POD and SOD activities of the drought-tolerant (vs. drought-sensitive) camelina breeding line suggests that it has a better ROS scavenging ability compared to the drought-sensitive breeding line.

In the present study drought stress significantly reduced yield and yield-related components in both drought-tolerant and drought-sensitive camelina breeding lines. The decrease in plant height, number of branches, number of pods per plant and 1000-seed weight may be attributed to reduction in tissue water content and photosynthetic pigments under drought stress (Lawler and Comic, 2002).

Reduced tissue water content caused shrinkage of cell and damage to biological membranes while decreased photosynthetic pigments disrupted the photosynthetic activity due to ROS production under drought (Farooq *et al.*, 2009; Hoekstra *et al.*, 2001; Hussain *et al.*, 2017). Reduced photosynthetic activity resulted in decreased production of food assimilates (Rad and Zandi, 2012). These assimilates are considered vital for the development of reproductive structures and their limited availability resulted in seed shrinkage, weight loss and ultimately reduction of seed yield (Sinaki, 2007; Nasri *et al.*, 2008; Sangtarash *et al.*, 2009). Concurring with our findings, Sadaqat *et al.* (2003) and Rad *et al.* (2014) also reported a similar decrease in seed yield due to the reduction in yield components in canola cultivars subjected to drought conditions. The higher yield of the drought-tolerant camelina breeding line 7126 would be the consequence of a better array of photosynthetic pigments and improved tissue water levels (Daneshmand *et al.*, 2008). Most probably, enhanced antioxidant activity under drought might have protected and stabilized the membranes and photosynthetic pigments by scavenging ROS (Turkan *et al.*, 2005; Saglam *et al.*, 2011), which helped to improve the plant water relations and photosynthetic activity hence resulted in better yield (Patel and Hemantaranjan, 2012).

Reduction in seed oil content and an increase in seed protein content was found in both camelina breeding lines under drought stress. Concurring with our results, Yang *et al.* (2014) illustrated that water deficiency could alter the seed composition of both breeding lines due to reduced photosynthesis or a shift in metabolic processes associated with seed development and formation. Furthermore, the limited availability of carbohydrates for triacylglycerol biosynthesis could reduce the accumulation of oil in seeds (Elferjani and Soolanayakanahally, 2018). On the other hand, an increase in seed protein content could be the result of reduced seed oil content because both are negatively correlated to each other (Elferjani and Soolanayakanahally, 2018). Consistent with our findings Richard *et al.* (2000) and Natali *et al.* (2003) found that greater protein production and accumulation might be the result of a decreased conversion of metabolites into oil under drought stress. The variation between drought-tolerant and drought-sensitive breeding lines regarding oil and seed protein content under drought stress might have resulted from the difference in their genetic makeup (Ghamkhar *et al.*, 2010).

Composition of fatty acids in camelina oil was drastically affected by drought stress in both drought-tolerant and drought-sensitive breeding lines. Increased palmitic,

oleic, linoleic acid and decreased stearic, linolenic and erucic acid contents occurring under drought stress could be ascribed to different enzymes responsible for the biosynthesis and conversion of fatty acids in different cellular compartments (Flagella *et al.*, 2002; Caterina *et al.*, 2007; Hernández *et al.*, 2009). Consistent with our findings Mekki *et al.* (1999) and Pavlista *et al.* (2016) reported increases in oleic acid, linoleic acid and decreases in linolenic and erucic acid contents in sunflower and camelina. Increased levels of oleic acid might be due to the action of the $\Delta 12$ desaturase enzyme, which it converts oleic acid into linoleic acid, being inhibited under to water deficiency conditions (Baldini *et al.*, 2000; Sobrino *et al.*, 2003). Water deficiency reduced the unsaturation level of fatty acids mainly due to inhibition within the biosynthetic pathway of fatty acids through a limited activity of desaturases (Dawood and Sadak, 2014). The differing response of breeding lines in terms of fatty acid profile suggested that the drought-tolerant breeding line would have an efficient fatty acid biosynthetic pathway and developed the seeds with a desirable fatty acid profile, whereas the drought-sensitive breeding line might have delayed the production of these components under drought stress conditions (Pavlista *et al.*, 2016).

Conclusion

Camelina breeding line 7126 exhibited higher drought tolerance than breeding line 8046 due to better physiological and biochemical mechanisms under drought stress. Moreover, camelina breeding line 7126 showed promising agronomic potential with better yield and oil quality traits under drought stress conditions. Hence, findings of this study will be highly resourceful to develop and introduce novel drought-resilient camelina genotypes particularly for those areas which are threatened by drought.

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